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# Navigational Experience and the Preservation of Spatial Abilities into Old Age Among a Tropical Forager-Farmer Population

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## Abstract

Navigational performance responds to navigational challenges, and both decline with age in Western populations as older people become less mobile. But mobility does not decline everywhere; Tsimané forager-farmers in Bolivia remain highly mobile throughout adulthood, traveling frequently by foot and dugout canoe for subsistence and social visitation. We, therefore, measured both natural mobility and navigational performance in 305 Tsimané adults, to assess differences with age and to test whether greater mobility was related to better navigational performance across the lifespan. Daily mobility was measured by GPS tracking, regional mobility through interview, navigational performance through pointing accuracy and perspective taking in environmental space, and mental rotation by a computerized task. Although mental rotation and spatial perspective taking declined with age, mobility and pointing accuracy remained high from mid-life through old age. Greater regional mobility was

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associated with greater accuracy at pointing and perspective taking, suggesting that spatial experience at environmental scales may help maintain navigational performance in later adulthood.

*Keywords:* Spatial cognition; Aging; Mobility; Gender differences; Navigation; Foragers

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## 1. Introduction

Normal aging is associated with declines in spatial ability that parallel other cognitive processes. Yet, it is possible that the magnitude of this decline may be reduced in societies where older individuals are highly mobile throughout life and must cope with navigational challenges into old age. This pattern of mobility is typical of the Tsimané and other subsistence populations who travel regularly on small footpaths to gardens and in pursuit of game and other resources, and to visit family and friends in nearby communities. Understanding the pattern of spatial cognitive aging in a population like the Tsimané, therefore, is likely to shed light on cognitive aging in a context closer to that in which our navigational abilities evolved, as well as holding potential lessons for aging in industrial societies, where mobility is often constrained. We use data on the Tsimané to assess whether the rate of decline in spatial ability differs from that described for other populations, whether individual differences in range size during mid-life and beyond predict spatial performance, and whether these patterns differ for women and men.

The age-related decline in spatial ability, observed in post-industrialized societies, is found across a wide range of spatial tasks (Techentin, Voyer, & Voyer, 2014), including navigation (Barrash, 1994; Coutrot et al., 2018; Kirasic, 2000; Liu, Levy, Barton, & Iaria, 2011; Moffat, Zonderman, & Resnick, 2001, 2007; Wilkniss, Jones, Korol, Gold, & Manning, 1997). The decline is also associated with a shift in wayfinding strategy with age, with older people relying more on a "route strategy" (finding one's way to a destination by following a known route and turning left or right at local landmarks) and less on a "survey strategy," which involves attending to cardinal directions and other geospatial cues that provide a birds-eye view knowledge of the environment. Route knowledge is facilitated by remembering one's position relative to local landmarks (i.e., an egocentric frame of reference), while survey knowledge requires that one learns the position of environmental features relative to each other irrespective of one's own position, hence uses an allocentric (or absolute) frame of reference. Older individuals have more difficulty acquiring an allocentric frame of reference and switching between these navigational strategies (Colombo et al., 2017; Harris & Wolbers, 2014; Wiener, de Condappa, Harris, & Wolbers, 2013). These changes typically begin in mid-life (Yu et al., 2021). While an egocentric strategy will enable a person to travel along familiar routes, only an allocentric frame of reference provides a cognitive map that facilitates wayfinding in novel areas. These strategy shifts are consistent with observations of younger Tsimané hunters being more likely to go off trail when searching for game, whereas older hunters rely more on established trails (Trumble, Gillespie, Stieglitz, Kaplan, & Gurven, 2014). Although age-related deficits in navigation reflect volume changes in a range of brain structures (Moffat, Kennedy, Rodrigue, & Raz, 2007), this difference in strategy is consistent with a physiological basis for changes in navigation with normal aging, since these two styles of navigation are subserved by different brain areas: an allocentric (place) strategy by the hippocampus and associated structures, and an egocentric (response) strategy by the caudate (Lithfous, Dufour, & Després, 2013; Marchette, Bakker, & Shelton, 2011).

Although these age patterns are robust, we know that spatial ability and hippocampal volume can be modified by training, as well as through individual differences in environmental experience. Training has been shown to improve performance on a variety of spatial tasks (Baenninger & Newcombe, 1989, 1989; Uttal et al., 2013), including navigation. Lövdén et al. (2012) showed that navigational training in a virtual environment while using a treadmill improved performance and protected against declines in hippocampal volume, among both younger and older men, with changes maintained over a 4-month period.

The experience of coping with navigational challenges in daily life is also likely to lead to improved performance (although the causation could go both ways, as better performers may be more comfortable engaging in navigationally challenging travel). Adults who reported engaging in more spatially challenging activities in daily life were better at spatial visualization, although this was equally true for younger and older adults (Salthouse & Mitchell, 1990). Living in a navigationally challenging environment also appears to foster better survey (allocentric) navigational ability. In a cross-national sample, people who grew up in cities, especially grid-like cities, performed more poorly on a virtual navigational task than did those who grew up in rural or suburban environments (Coutrot et al., 2020). Similarly, in a comparison of people in Salt Lake City (which has a grid-like street system) and Padua (an old city with irregular streets), the Salt Lake City residents pointed less accurately to places in their city and were less likely to take short-cuts in a virtual navigation task (Barhorst-Cates, Meneghetti, Zhao, Pazzaglia, & Creem-Regehr, 2021).

Large ranges are also more navigationally challenging, and several correlational studies show larger natural ranges to be associated with better performance on mental rotation (Ecuyer-Dab & Robert, 2004; Vashro, Padilla, & Cashdan, 2016), and with navigation in a virtual environment (Padilla, Creem-Regehr, Stefanucci, & Cashdan, 2017). Causation is harder to demonstrate, but a longitudinal study of London taxi drivers showed that the 4 years of training required to learn London's complex street system increased posterior (and decreased anterior) hippocampal volume (Woollett & Maguire, 2011). This pattern of change was associated with years of driving experience in taxi drivers but not bus drivers matched for driving experience (Maguire, Woollett, & Spiers, 2006), which suggests that more complex navigational experience appears to be specific for allocentric, not egocentric, spatial strategies. Since it is the former that declines most with age, greater wayfinding experience may be especially important for preserving these spatial abilities in older adults.

Wayfinding experience in daily life is highly variable across and within cultures, for reasons of ecology, economy, and modes of travel. In most subsistence economies, particularly those that depend in part on hunting and gathering wild foods, people are quite mobile until late in life. This is the case for the Tsimané, a Bolivian people who live in the Amazon River Basin and depend heavily on horticulture, hunting, fishing, and foraging for their livelihood (Kraft et al., 2018). Although market integration is increasing in the area, and travel by vehicle along roads or motorized boats along rivers to the market town has grown in frequency and importance, most of the travel in this heavily forested region remains on foot, along small and winding footpaths. Wayfinding challenges are increased further in this context due to a viewshed limited by dense tropical forest vegetation, and limited access to roads, public transportation, maps, and electronic navigational aids. This cultural context, while unusual from the perspective of the typical cognition study sample, resembles the way humans lived for most of our history as a species.

Our first aim is to see whether Tsimané adults experience the same decline in mobility and spatial ability with age that we see in other populations. Given the spatially active lifestyle of the Tsimané, we anticipate a shallower slope of decline in both mobility and navigational ability. We also want to know whether the rate of change with age is the same for women and men. The literature on gender differences in spatial ability finds that males outperform females at many spatial tasks (Cashdan & Gaulin, 2016; Halpern, 2013; Voyer, Voyer, & Bryden, 1995), including navigation (Nazareth, Huang, Voyer, & Newcombe, 2019). The gender disparity in navigational ability extends throughout adulthood, with most studies finding a similar rate of decline for women and men (Coutrot et al., 2018; Ferreira et al., 2014; McCarrey, An, Kitner-Triolo, Ferrucci, & Resnick, 2016). However, prior studies with Tsimané adults (Trumble, Gaulin, Dunbar, Kaplan, & Gurven, 2016) and children (Davis & Cashdan, 2019) show little or no gender difference in spatial abilities. We build on those findings here, using a larger sample of older individuals, direct measures of mobility patterns, and additional spatial data.

Our prediction is that larger Tsimané ranges throughout life will be associated with preservation of navigational abilities, and possibly other spatial abilities also, in both women and men. In order to see whether these variables are also associated across individuals, we follow our descriptive analyses by testing whether Tsimané adults who have acquired greater spatial experience through larger ranges and greater mobility do better at our navigation tasks, and, if so, whether this relationship is moderated by age. Because formal schooling is variable across the population, and has been shown to improve performance at mental rotation and other abstract tasks in this population, we also include a measure of education in these models.

Our measures of wayfinding experience include both daily navigational challenges (GPS measures of distance traveled) and regional travel (visits to other villages in the previous year and cumulatively over the lifespan). Our cognitive measures include both mental rotation (the ability to imagine what an object would look like when rotated) and tasks indicative of functional wayfinding ability (pointing accurately to other locations in the region and spatial perspective taking within the same region). Although the navigational tasks are most directly related to mobility, we measured mental rotation also because some studies have found that better navigators (Moffat, Hampson, & Hatzipantelis, 1998, 2001; Silverman et al., 2000) and more mobile individuals (Ecuyer-Dab & Robert, 2004; Vashro et al., 2016) also excel at mental rotation. We include experience with formal schooling as a covariate because it brings increased familiarity with testing procedures and has been shown to enhance measures of abstract reasoning among the Tsimané (Davis et al., preprint; Gurven et al., 2017).

### 1.1. *Tsimané ecology and education*

The Tsimané are a semi-sedentary population of approximately 16,000 forager-farmers living in the Bolivian Amazon. They inhabit 90+ villages ranging in size from 50 to 500 individuals. Historically, the Tsimané were only minimally integrated into broader Bolivian society. The relatively recent (i.e., past ~40–50 years) introduction of roads, outboard motors

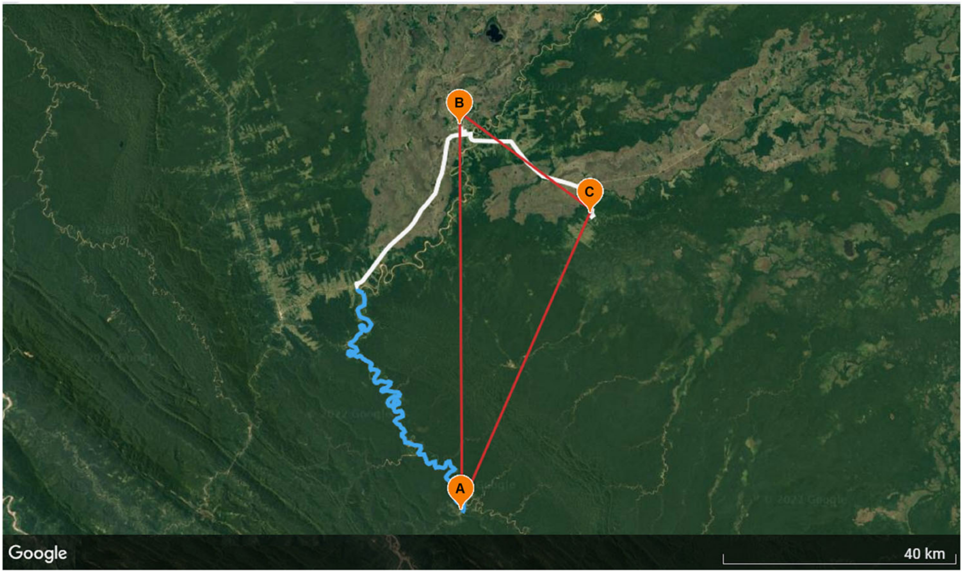

Fig. 1. Map and spatial ability tasks. GPS map shows travel paths between points of interest using the serpentine Maniqui River (in blue) and road travel (in white). While the straight lines (in red) represents travel paths as the crow flies from (A) to (B), with a total distance of 25.87 km, the river and road travel route from (A) to (B) has a total distance of 124 km. To measure pointing error, participants were asked to point from their location (A) to a target location (B). The perspective-taking task required participants to point as though they were at a distant location (B) to separate targets (e.g., A and C).

for canoes, and subsequent encroachment by neighboring Bolivian ranchers and loggers has increased market access and wage labor opportunities for many Tsimané villages (Gurven, Jaeggi, von Rueden, Hooper, & Kaplan, 2015), particularly over the last two decades in the nearest market town, San Borja (population ∼43,000). Though a small amount of food is purchased from market stores or obtained from trade with merchants, traditional foods comprise >90% of the calories in the diet (Kraft et al., 2018), consisting of crops grown in small swiddens accessed by foot (e.g., plantains, rice, corn, and sweet manioc) and wild foods obtained through foraging and hunting in the forest, and fishing in rivers, lagoons, and streams.

Although Tsimané villages differ in their access to the market town of San Borja, all the villages included in this study are in similarly complex forest environments. All participants live in rural communities, which consist of multiple forest clearings of clustered thatch-roofed dwellings, connected by a series of trails, and surrounded by a mix of high canopy primary forest and dense low-canopy secondary forest. This makes it more challenging for navigators to use allocentric navigational strategies to acquire a survey knowledge of the landscape, since they cannot rely on visible distal landmarks for cues to cardinal directions. Topographical features near each community, such as the serpentine Maniqui river and smaller tributaries, provide unreliable cues to cardinal directions (Fig. 1). Navigational skill through the forest and along the river, therefore, is required for daily travel and food acquisition.

Mate-seeking behaviors, the sexual division of labor, and household size can also affect individual mobility and spatial exploration during different phases of adulthood.

Retrospective interview data on locations visited during childhood, adolescence, and adulthood indicate that Tsimané men have significantly higher rates of travel during adolescence but do not differ from women in terms of travel to other communities in childhood or after marriage, although women with more dependents had been to fewer locations (Miner, Gurven, Kaplan, & Gaulin, 2014). However, even if husbands and wives are likely to exhibit similar patterns in annual mobility (i.e., visiting other communities together for more than one night), women's daily mobility is still likely to be affected during their childbearing years. Because the Tsimané rarely use modern contraceptives, the total fertility rate is high, 9.1 births per woman (Mcallister, Gurven, Kaplan, & Stieglitz, 2012), with a mean (SD) age of first birth for men and women being 22.8 (4.2) and 18.6 (2.9) years, respectively, leaving women to care for multiple young dependent offspring during their 20s and 30s.

Languages differ in their spatial frames of reference, and this can also affect navigation. For example, some nonindustrial populations lack terms for right and left, and so might say that the salt is east of the plate on the table, using a an absolute (geocentric) frame of reference in preference to our customary relative (egocentric) one. These differences appear to shape not only speech but also spatial cognition (Levinson, 2003), although to varying degrees (Bohnemeyer, 2011). Speakers of languages that rely on absolute spatial reference frames appear to be excellent navigators with highly accurate cognitive maps (Levinson, 1997). Our study did not explore Tsimané spatial use of language and so we do not address it further here except to note that the Tsimané language, like English, includes terms for relative frames of reference—quinve/tacve (left/right)—as well as absolute reference frames (e.g., cashve/ntsche for downstream/upstream).

## 2. Methods

All interviews and tasks were developed in the Spatial Cognition and Navigation Lab (SCAN) at the University of Utah, and a standard Spanish language version has been utilized across several fieldsites in three Spanish speaking countries. For this study, tasks and interviews were conducted in the Tsimané language, which required translating from the Spanish language versions available through the SCAN lab. Each interview and task was translated from Spanish into Tsimané by a Tsimané research assistant and then separately back-translated from Tsimané into Spanish by another Tsimané research assistant to confirm the accuracy and clarity. The data were collected by HED and three Tsimané research assistants over the course of 4 months. All Tsimané research assistants were educated and trained in field methods, qualitative and quantitative data collection, and translating through the Tsimané Health and Life History Project (THLHP)—an ongoing anthropology and biomedical research project that has been in continuous operation since 2003 (Gurven et al., 2017). All procedures and methods were approved by the University of Utah's Human Subjects Review Board.

### 2.1. Sample characteristics and demographic measures

The study was conducted among Tsimané between the ages of 20 and 84 years old ($N = 305$; 52% female) from seven communities. Age was determined through two channels:

cross-validating interviews and an extensive population register collected and continuously updated since 2002 by the THLHP, one of the longest health and anthropology projects within a subsistence-based society to date (Gurven et al., 2017). Age estimation by the THLHP relies on in-depth demographic interviews, relative age lists determined from reproductive histories, and baptism records (see Gurven et al., 2017 for more details). For analysis, we consider age as a continuous variable, and also categorize participants into one of three age bins (20–39, 40–59, and 60+) to assess potential nonlinearity in outcomes. Our smaller sample size, particularly the GPS data, precluded a finer age breakdown.

We included a measure of schooling (reading ability) as a covariate in models looking at the association between regional travel and spatial skills because schooling has been shown to improve performance on some spatial and other cognitive tasks, and it can interact with the other independent variables (Davis & Cashdan, 2019; Davis et al., preprint). For the current study, we report two measures of schooling, the highest achieved grade level and reading ability, but use reading ability as the sole measure in our models. Because of variation in access and quality of schooling, years of schooling is a relative, and often inaccurate, measure (Hanushek & Woessmann, 2012). Reading ability has been shown to be a reliable proxy for the development of school-based skills (Davis et al., 2021), and it can help to avoid pitfalls associated with fluctuations in schooling access and quality across wide age ranges (Gurven et al., 2017). The education data were collected by the THLHP (Gurven et al., 2017) and cross-validated through self-reported interview questions conducted by HED. Our scale of reading ability ranged from 0 to 2, where ability was recorded as 0 = none, 1 = some, and 2 = good. Reading ability in this population has been shown to be a reliable measure of schooling exposure—and is associated with the development of other school-based skills—in this population (Davis et al., preprint).

## 2.2. *Mobility measures*

### 2.2.1. *Daily mobility*

Daily mobility was measured by GPS tracking. Each participant wore a QStarz BT-Q1000XT GPS data logger, which was placed in a small, water-resistant case, secured to a lanyard and worn around the neck. The aim was to track daily mobility for at least 3 consecutive days for each person. However, each GPS unit required approximately 2–4 h of charging for 3 days of battery power. Given the remote locations where data were collected, power was only provided through portable solar panels and a 12-volt battery. Due to cloud cover and frequent tropical storms, there was variable availability of solar and stored battery power, limiting the overall sample of GPS data. On some days, weather conditions also interfered with the ability of the units to maintain sufficient contact with satellites, resulting in some missing data. After data cleaning, an additional 31 tracks from 72 individuals were removed from the current data set because participants traveled as passengers to the market town by taxi or motorcycle while wearing their GPS units.

Geospatial analyses on the GPS tracks were performed by the University of Utah DIGIT laboratory, which provides geospatial expertise to the University and outside groups. DIGIT first cleaned the tracks of spurious track points and then calculated for each person-day the average daily distance traveled. Though the missing GPS data are considered Missing at Random, we did not rely on data imputation in the analyses.

### 2.2.2. *Regional mobility*

While daily mobility assessed through GPS tracking is a good way to assess people's typical daily travel, most daily travel takes place in the home village, which is familiar and poses few navigational challenges. In order to better capture individual differences in navigational ability, therefore, we also interviewed participants about larger scale travel. Two regional measures were calculated: "annual mobility" and "lifetime mobility." To measure regional travel during the past year ("annual mobility"), participants were asked to recall all full day and overnight trips taken during the previous 12 months (location, purpose, and who they went with). The measure used in these analyses is the number of unique places visited (i.e., repeated visits to the same location were not included). To measure longer term regional mobility ("lifetime mobility"), we created a list of 30 locations, which included other Tsimané villages and Bolivian towns, and for each location asked whether participants had been there never (0), once (1), a few times (2), or many times (3), and then averaged the scores across the 30 places. The lifetime mobility measure, therefore, reflects both number of places and frequency of travel to them.

## 2.3. *Spatial ability measures*

### 2.3.1. *Pointing accuracy*

Our first measure of navigation was the accuracy with which participants were able to point to 10 known places in the region. The locations ranged from 5 to ~150 km away as the crow flies ($M = 22.79$ km, $SD = 16.62$ km), were not visible, and generally not accessible by a direct road or path (Fig. 1). Some were locations at other points along a river, but the river changes directions between locations. Success at this task, therefore, probably requires an allocentric cognitive map of the region. Participants were asked to point to each location, 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 pointing accuracy might reflect familiarity with each location, participants were first asked if they had ever been to the target location or if they were familiar with it (e.g., pass it while traveling downriver or through the forest en route to another location). If the participant was not at all familiar with the target, they were not asked to point to it. However, the majority of participants were familiar with the target locations ($M = 8.07$, $SD = 2.40$ locations). Sixteen people who reported being familiar with less than five places, and therefore pointed to less than five locations, were removed from the sample.

### 2.3.2. *Perspective taking*

Our second measure of navigation was a regional perspective-taking task (Fig. 1). It was done immediately after the direct pointing task and used a subset of three of the same

Fig. 2. Mental rotation task (MRTX). Two images from the MRTX 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.

locations. Participants were asked to point to a target location as before, but to imagine that they were standing not at their present location (A), but instead at one of the target locations from the pointing task (B). They were then asked to use the compass to point as though they were at location (B) to other locations in the region (e.g., C). To help practice for this task, at least two examples were provided using nearby visible objects and features. For example, (1) the participant was asked to imagine they were at that nearby object and to navigate back to the location where the task was taking place (i.e., where the administrator and the subject were standing with the compass), and then (2) the participant was asked to imagine they were at an object visible and nearby and then navigate to a second visible, nearby object. This helped ensure that the participant understood the task and its objects. As with the pointing task (above), error was measured as the difference between the correct and the pointed bearing.

### 2.3.3. *Mental rotation*

In order to test mental rotation in a way that would be accessible to Tsimané adults of all ages, we used a test of our own design that we have used successfully with other nonindustrial societies (Cashdan, Kramer, Davis, Padilla, & Greaves, 2016; Davis & Cashdan, 2019; Vashro et al., 2016) (Fig. 2), and which we call the MRTX. The task is designed to be suitable for cross-cultural work by incorporating elements of inclusive design: It provides nonverbal training, uses familiar stimuli, and removes abstraction in the response measure. Two sets of images are used in separate blocks, one of a human figure with an outstretched arm (one block each of front and back bodies), the other of a bent twig (two blocks). 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 within each block) 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" nonverbally, training trials show the target image at the top rotating to match the orientation of the correct image. In total, four blocks with 10 trials per block were conducted with each participant: one with the human figure facing forward, one with the human figure facing backward, and two with bent twigs. Trials were randomized within blocks, but participants did the blocks in the same order. Because our focus was on individual differences, we assessed each individual's average performance on (1) human figure trials and (2) twig trials.

We have used the MRTX successfully in several populations, including individuals of all ages. In a paper currently in revision, we have validated the task by showing that errors and response time increase with greater degrees of rotation, which suggests that individuals are mentally rotating the image, rather than solving the task using other strategies. We have also found that U.S. children show an angle by response time relationship using the MRTX, and their performance on the MRTX is correlated with performance on a letter rotation task. We are working to make the task and these analyses publicly available.

## *2.4. Statistical methods*

Data analysis was conducted in R version 3.6.3 using the ggplot2 (Wickham, 2010) and lmer4 (Bates, Sarkar, Bates, & Matrix, 2007) packages.

### *2.4.1. Descriptives*

We begin by reporting means (M) and standard deviations (SD) by sex and age group for all variables of interest: daily, annual, and lifetime mobility, small- and large-scale spatial tasks, and two measures of schooling (highest grade completed and reading ability). We then use Mann–Whitney U tests to assess variation between sample mean ranks of men and women who participated in the study. We then assess patterns of mobility by age and sex before adding other important covariates. To correct for experiment wise error due to multiple comparisons, we used the Bonferroni alpha adjustment procedure.

### *2.4.2. Mobility and spatial ability by age and sex*

In the analyses of age and sex on mobility and small-scale spatial abilities, we rely on general linear models. We initially assessed age$^2$ terms in the models. However, we found no meaningful effect of age$^2$; therefore, we did not include age$^2$ in the results reported below. To better isolate age patterns of cognitive performance at early and later life stages, we also evaluate mobility and spatial ability using age cohorts (20–39 years, 40–59 years, and 60+).

For the large-scale spatial abilities, pointing error, and perspective-taking error, mixed effects models are used. Because each participant pointed to multiple locations, and because good navigators are more likely to point with greater accuracy to more locations when compared to poor navigators, we also consider potential interindividual correlations. Therefore, to deal with the nonindependence of each individual pointing to multiple (up to 10 targets) locations, individuals were entered as random effects. However, average pointing error and perspective-taking error are used for the descriptive statistics in Table 1 and in the scatterplots to help facilitate interpretation and comparisons with other variables.

## *2.5. Individual differences: Effects of mobility on spatial abilities*

Both multivariate general linear regression models and mixed effects models were used to assess our main research question, the relationships between spatial abilities and mobility.

Table 1
Descriptive statistics on key variables

| | Men | | | Women | | | |
|---|---|---|---|---|---|---|---|
| Variable (units) | *n* | Mean | SD | *n* | Mean | SD | U Test |
| Age (years) | 146 | 45.45 | 16.86 | 159 | 41.5 | 15.69 | $p = .03^{*}$ |
| Schooling (highest grade) | 129 | 3.32 | 3.37 | 151 | 1.80 | 2.33 | $p < .001^{***}$ |
| Schooling skills (reading ability: 0–2) | 128 | 0.99 | 0.89 | 151 | 0.49 | 0.76 | $p < .001^{***}$ |
| Daily mobility (km) | 29 | 9.88 | 6.13 | 40 | 7.55 | 5.62 | $p = .003^{**}$ |
| Annual mobility (unique visits) | 100 | 8.07 | 2.87 | 111 | 5.77 | 2.51 | $p < .001^{***}$ |
| Lifetime mobility (frequency: 0–2) | 95 | 1.62 | 0.54 | 105 | 1.18 | 0.49 | $p < .001^{***}$ |
| Pointing error (degrees) | 84 | 24.15 | 10.15 | 96 | 27.11 | 13.68 | $p = .27$ |
| Perspective-taking error (degrees) | 89 | 28.37 | 17.52 | 95 | 33.39 | 19.02 | $p = .05^{o}$ |
| MRT: Bodies (Proportion correct) | 99 | 0.75 | 0.17 | 111 | 0.72 | 0.14 | $p = .19$ |
| MRT: Twigs (Proportion correct) | 101 | 0.78 | 0.18 | 106 | 0.75 | 0.17 | $p = .15$ |

Note: Mann–Whitney U tests with Bonferroni corrections do not consider other explanatory variables.
Statistical significance markers: $^{o}$ $p \leq .1$. *$p \leq .05$. **$p \leq .01$. ***$p \leq .001$.

Specifically, we assess the main effects of our mobility measures (i.e., lifetime and annual mobility) on our large-scale navigational tasks (i.e., pointing and perspective taking) and our small-scale spatial task (i.e., mental rotation). Additionally, we consider the effects of formal schooling, which has been associated with greater performance on abstract tasks (Hruschka, Munira, Jesmin, Hackman, & Tiokhin, 2018), including among the Tsimane (Davis & Cashdan, 2019; Gurven et al., 2017). Model comparison and Akaike information criterion (AIC) provided estimates of the relative quality for statistical models with and without reading ability, and to compare two measures of regional mobility. Best-fit models are reported in the results.

## 3. Results

We begin by describing the sample characteristics and the means and standard deviations of variables of interest by sex and age. We then look at changes over the life course, first in mobility, then in spatial ability by age and sex, and then by age group and sex. Finally, we consider whether individual differences in navigation and mental rotation can be predicted by mobility and educational experience.

### 3.1. Descriptives

Table 1 summarizes all variables for the sample using Bonferroni corrections. When divided into 20-year cohorts, the sample size for participants in the youngest cohort (ages 20–39, $n = 128$) is slightly larger than those in the middle cohort (ages 40–59, $n = 119$) and double that of participants from the oldest cohort (ages 60+, $n = 58$). We provide averages for all measures of mobility and performance on spatial tasks in Table 1 for ease of interpretation.

Reading ability and years of schooling are far lower among the Tsimané than they are in most study samples, and this is particularly the case for older individuals, especially older women. Thus, sex and reading ability (i.e., schooling) are included as controls in all models that look at the associations between individual differences and spatial ability. Among individuals 60 years or older, years of schooling was minimal for men ($M = 1.32$, $SD = 1.54$) and virtually nonexistent for women ($M = 0.14$, $SD = 0.36$; $g = 0.97$). Schooling was more frequent among individuals 40–59 years, and more so for men ($M = 3.10$, $SD = 3.63$) than women ($M = 1.21$, $SD = 2.23$; $g = 0.96$). Participants in the youngest cohort (20–39 years) have attended more school than older cohorts ($p < .001$) and show less relative sex difference (men: $M = 4.87$, $SD = 3.23$; women: $M = 3.67$, $SD = 2.20$; $g = 0.74$). Reading ability shows a similar pattern: The youngest (20–39 years) demonstrate greater reading ability, with a smaller relative sex difference (men: $M = 1.23$, $SD = 0.88$; women: $M = 0.79$, $SD = 0.86$; $g = 0.51$), compared to levels of reading ability in the middle (40–59; men: $M = 0.98$, $SD = 0.88$; women: $M = 0.32$, $SD = 0.65$; $g = 0.76$) and oldest cohorts (60+; men: $M = 0.65$, $SD = 0.84$; women: $M = 0.00$, $SD = 0.00$; $g = 1.01$).

### 3.2. *Mobility by age and sex*

Fig. 3 shows the variation in daily, annual, and lifetime mobility for men and women. Though men demonstrate slightly higher averages in both measures of regional mobility, there is not an association between sex and daily mobility ($\beta = 2.36$, $p = .10$, 95% CI: –0.45, 5.17) when controlling for age ($\beta = –0.02$, $p = .66$, 95% CI: –0.11, 0.07), although there is a trend toward greater daily mobility among men compared to women during prime reproductive years (Fig. 4). In contrast, we find that men report greater annual mobility compared to women ($\beta = 2.44$, $p < .001$, 95% CI: 1.75, 3.15), and annual mobility decreases for both men and women with age ($\beta = –0.04$, $p < .001$, 95% CI: –0.07, –0.02). Similarly, men report higher lifetime mobility ($\beta = 0.47$, $p < .001$, 95% CI: 0.33, 0.61) compared to women. We also find a similar decrease with age ($\beta = –0.01$, $p < .001$, 95% CI: –0.013, –0.005) in men's and women's reported lifetime mobility.

Given the age pattern in daily mobility for men and women (Fig. 4), our reported regional measures of travel, and previous findings regarding mobility among the Tsimané (Miner et al., 2014), we divided the sample into age groups to determine if phases of adulthood (e.g., prime reproductive years, late reproductive years, and post-reproductive years) provide more detail about cohort-specific travel behavior. We do find a sex difference in average daily mobility, but only during women's prime reproductive years (20–39 years; Table 2 and Fig. 4). After age 40, daily mobility does not significantly differ for men and women (Table 2, Figs. 4 and 5A). As the boxplots in Fig. 5 show, the sex difference is larger for our regional mobility measures, with men reporting higher rates of annual and lifetime mobility compared to women (Fig. 5B and C), though the magnitude of the sex difference is lower for older cohorts (Table 2). The larger sex difference in regional mobility, particularly in the younger cohorts, could reflect mating or economic motives that take men farther from the home village; however, the apparent absence of a significant sex difference in daily mobility could also reflect

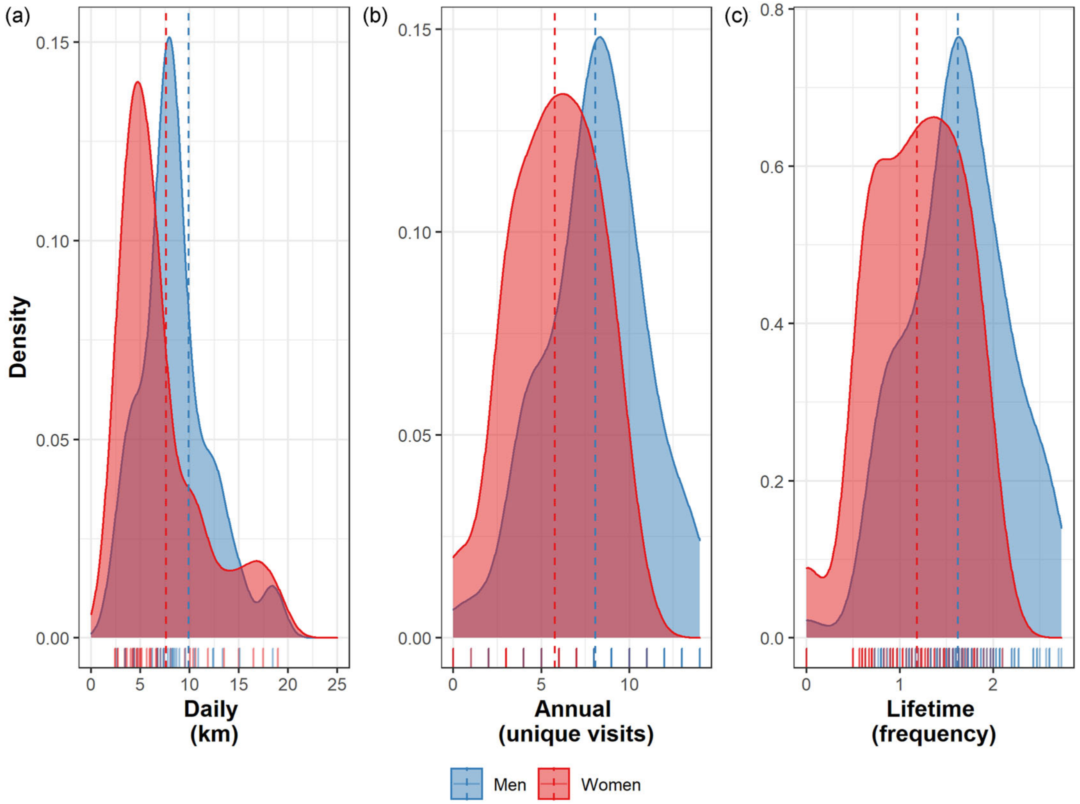

Fig. 3. Mobility patterns. Density plots display distribution of men and women's (A) daily (B) annual, and (C) lifetime mobility. Dotted lines indicate the mean for men and women. Daily refers to average km traveled per day (by GPS), annual is full day or overnight visits to other villages in the past year, lifetime is an ordinal measure of lifetime travel over the region (see Methods). Rug marks on the X-axis indicate the range of average daily travel (A) or unique responses (B, C) in the sample. Outliers (not shown here; $N = 4$) are included in the population means.

our smaller sample size for daily mobility ($N = 72$). Trends in reported annual and lifetime mobility by age might be the result of recent economic and technological advances.

### *3.3. Spatial ability by age and sex*

As with mobility, we analyzed the patterning in spatial ability by age and sex. For participants' performance on the pointing task and the perspective-taking task, we rely on linear mixed models with individuals entered as a random effect. We find no sex difference in average pointing accuracy across the lifespan, although there is a trend toward greater error for reproductive-aged females, mirroring their lower mobility during this life stage (Figs. 4 and 6A). Nor did we find a strong decline with age in pointing accuracy (Table 3 and Fig. 6A). In contrast, men demonstrate lower error compared to women on perspective taking, and error

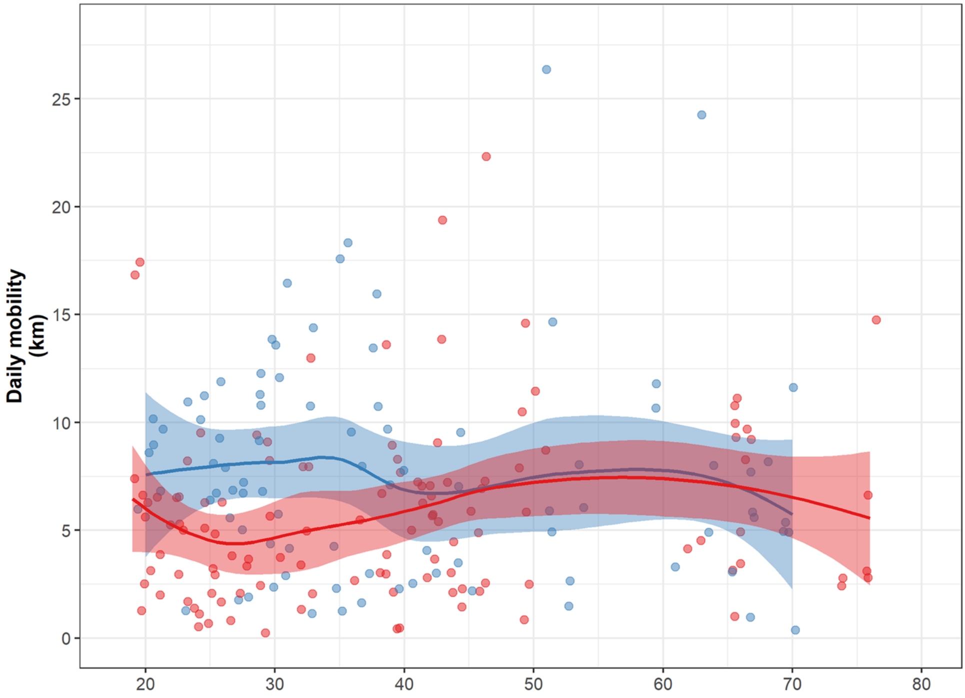

Fig. 4. Average daily mobility for women and men. During the prime reproductive years, women appear to have lower daily mobility compared to men in the same age cohort (i.e., 20–39 years). Lines are smooth splines. Shaded areas represent 95% CIs.

is higher for both older men and women (Table 3 and Fig. 6B); however, the rate of decline in performance (i.e., greater error) does not increase with age (Table 3, Figs. 6 and 7).

Average performance on the MRTX was analyzed using general linear models. Men outperformed women on this task, more so with the twig images ($\beta = 0.07$, $p = .004$, 95% CI: 0.02, 0.11) than with the body images ($\beta = 0.05$, $p = .02$, 95% CI: 0.01, 0.09) when controlling for age (Fig. 6). MRTX scores in both women and men declined on both tasks with age (body images: $\beta = –0.002$, $p < .001$, 95% CI: –0.004, –0.001; twig images: $\beta = –0.004$, $p < .001$, 95% CI: –0.005, –0.002), but the shape of the age decline differed between the tasks. With the body images, the performance of women in the middle age group (40–59) was 13.9% lower than those of younger women, but the rate of decline then decreased, with scores of older women (60+) declining only an additional 5.8%. The decline for men increased with each additional age cohort. Men between the ages of 40–59 scored on average just 3.8% lower than younger men, but that of men in the older cohort declined by 7% (Fig. 7).

To conclude this section, we find that both mobility and pointing accuracy remain high from mid-life through old age in both women and men, although performance on mental rotation and perspective taking decline with age, as they do in other populations. We also see an interesting pattern during the younger reproductive years, where men are traveling farther than women and also perform better on pointing accuracy. In order to investigate the

Table 2
Generalized linear models of daily, annual, and lifetime mobility by sex and age group

| | Dependent variables: | | | | | |
|---|---|---|---|---|---|---|
| | Daily mobility | | Annual mobility | | Lifetime mobility | |
| Age: 20–39 years | $\beta$ | (SE) | $\beta$ | (SE) | B | (SE) |
| Sex (ref group: women) | 7.00$^{\circ}$ | (3.57) | 2.82$^{**}$ | (3.57) | 0.55$^{**}$ | (0.10) |
| Constant | 7.90$^{**}$ | (2.43) | 6.35$^{**}$ | (0.35) | 1.33$^{**}$ | (0.06) |
| Age: 40–59 years | | | | | | |
| Sex (ref group: women) | 5.06 | (3.10) | 2.23$^{**}$ | (0.62) | 0.43$^{**}$ | (0.12) |
| Constant | 6.93$^{**}$ | (1.80) | 5.15$^{**}$ | (0.12) | 1.04$^{**}$ | (0.07) |
| Age: 60+ years | | | | | | |
| Sex (ref group: women) | –0.49 | (2.61) | 1.74$^{\circ}$ | (0.80) | 0.36$^{\circ}$ | (0.16) |
| Constant | 7.51$^{*}$ | (1.84) | 5.44$^{**}$ | (0.61) | 1.08$^{**}$ | (0.12) |

Statistical significance markers: $^{\circ}$ $p \leq .1$. $^{*}p \leq .05$. $^{**}p \leq .01$. $^{***}p \leq .001$.

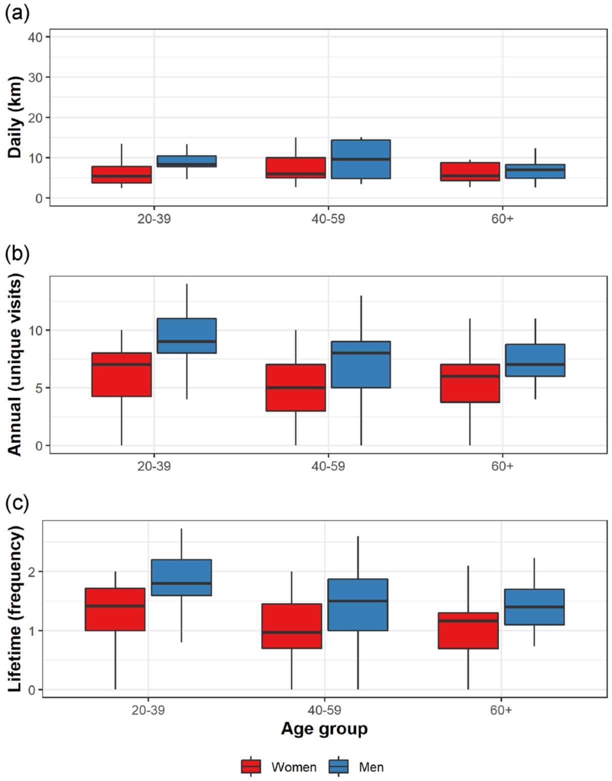

Fig. 5. Box plot indicating mean and first and third quartiles for (A) daily, (B) annual, and (C) lifetime mobility for women and men. Whiskers denote lower and upper adjacent values. Three extreme values in the 20–39 year age group were removed from the figure above but were still included in the calculations for cohort means, and first and third quartiles.

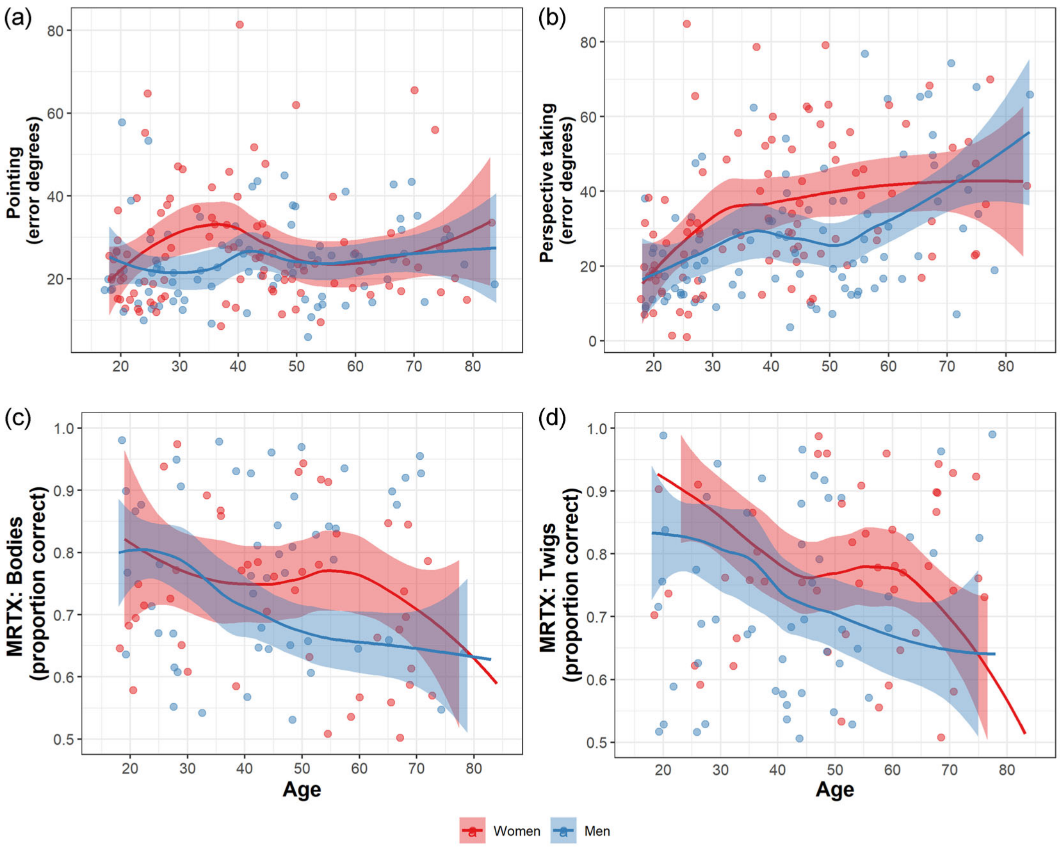

Fig. 6. Scatterplots of (A) pointing error ($N = 180$), (B) perspective taking ($N = 184$), (C) MRTX: Bodies ($N = 210$), and (D) MRTX: Twigs ($N = 207$) by age and sex. All scatterplots are fitted with a smoothing spline. Shaded areas represent 95% CIs.

relationship between mobility and navigation directly, we next assess whether a relationship between mobility and spatial ability can explain differences among individuals.

### *3.4. Individual differences: Effects of mobility and schooling on large- and small-scale spatial abilities*

The Pearson partial correlations between mobility, schooling, and large- and small-scale spatial tasks are shown in Table 4. Controlling for age and sex, all four spatial tasks correlate with both annual and lifetime mobility measures. Neither of the large-scale spatial tasks, pointing error, or perspective taking correlate with measures of schooling, whereas the small-scale spatial tasks (MRTX) do. MRTX and perspective taking are also correlated with each other.

Table 3
Results from linear mixed effects models on pointing accuracy ($N = 10$ target locations) and perspective- taking accuracy ($N = 3$ target locations) with individuals entered as random effects

| | Pointing error Model 1 | | Perspective-taking error Model 2 | |
|---|---|---|---|---|
| Variable *(range)* | *B* (CI) | *p* | *B* (CI) | *p* |
| Age *(years)* | 0.07 (–0.01, 0.14) | 0.08 $^{o}$ | 0.44 (0.30, (0.57) | <.001$^{***}$ |
| Sex *(ref group: women)* | –1.19 (–3.01, 0.63) | 0.20 | –6.56 (–11.07, –1.84) | .01$^{**}$ |
| Constant | 20.26 (16.94, 23.59) | <0.001$^{***}$ | 15.35 (8.81, 21.91) | <.001$^{***}$ |

Statistical significance markers: $^{o}$ $p \leq .1$. *$p \leq .05$. **$p \leq .01$. ***$p \leq .001$.

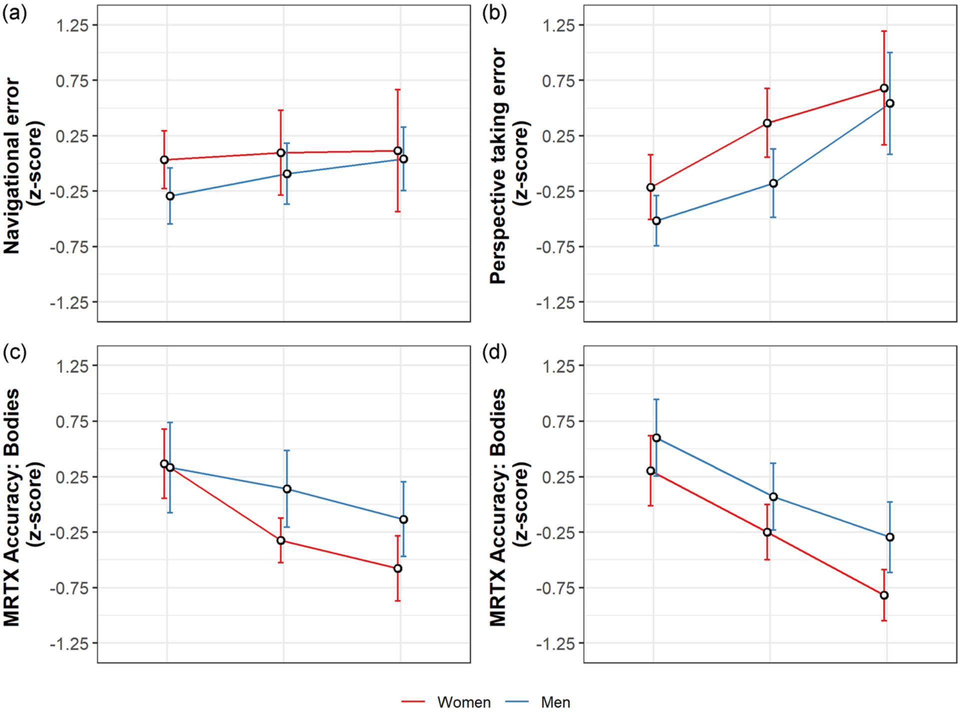

Fig. 7. Mean performance for each age cohort on individual average performance on both navigational (large-scale) tasks and mental rotation (small-scale), with scores normalized to facilitate comparison across tasks. Larger values in navigation indicate poorer performance (greater pointing error). For mental rotation, lower values indicate poorer performance. Error bars represent 95% confidence intervals.

We next examine the association between individual differences in mobility on large- and small-scale spatial performance, with schooling (i.e., reading ability) also entered in the models. Each model initially included our demographic measures, measures of regional mobility, and reading ability. We compared models with and without reading ability, and we compared our two measures of regional mobility on large- and small-scale spatial abilities. We report the best-fit models for each spatial task using AIC in Table 5. Higher scores on the

Table 4
Pearson's pairwise partial correlations between mobility, schooling, and spatial abilities, controlling for age and sex ($N = 305$)

| | Annual mobility | Lifetime mobility | Schooling: highest grade | Schooling: reading ability | Pointing error | Persp. taking error | MRTX: Bodies | MRTX: Twigs |
|---|---|---|---|---|---|---|---|---|
| Annual mobility | 1 | | | | | | | |
| Lifetime mobility | $0.93^{***}$ | 1 | | | | | | |
| Schooling: highest grade | 0.10 | 0.11 | 1 | | | | | |
| Schooling: reading ability | $0.21^{***}$ | $0.18^{*}$ | $0.72^{***}$ | 1 | | | | |
| Pointing error | $-0.12^{**}$ | $-0.15^{*}$ | –0.02 | –0.08 | 1 | | | |
| Persp. taking error | $-0.25^{**}$ | $-0.24^{**}$ | 0.01 | –0.09 | 0.18 | 1 | | |
| MRTX: Bodies | $0.16^{*}$ | $0.18^{*}$ | $0.25^{***}$ | $0.33^{***}$ | –0.05 | $-0.21^{***}$ | 1 | |
| MRTX: Twigs | $0.40^{***}$ | $0.40^{***}$ | $0.24^{***}$ | $0.21^{*}$ | –0.08 | $-0.21^{**}$ | $0.54^{***}$ | 1 |

Statistical significance markers: $^{o}$ $p \leq .1$. *$p \leq .05$. **$p \leq .01$. ***$p \leq .001$.

Table 5
Best-fit linear mixed effects and general linear models for large- and small-scale spatial abilities. Both mixed effects models include random intercepts for individuals

| | Dependent variable: | | | |
|---|---|---|---|---|
| | **Pointing error (mixed effects)**<br>$\beta$<br>(95% CI) | **Persp. error (mixed effects)**<br>$\beta$<br>(95% CI) | **MRTX: Bodies (GLM)**<br>$\beta$<br>(95% CI) | **MRTX: Twigs (GLM)**<br>$\beta$<br>(95% CI) |
| **Age** | 0.04<br>(-0.04, 0.11) | $0.36^{***}$<br>(0.22, 0.50) | -0.001<br>(-0.003, 0.001) | $-0.003^{**}$<br>(-0.005, -0.001) |
| **Sex (ref group: women)** | -0.18<br>(-2.15, 1.78) | -2.83<br>(-8.01, 2.33) | 0.01<br>(-0.03, 0.05) | 0.004<br>(-0.06, 0.07) |
| **Annual mobility** | | $-1.81^{***}$<br>(-2.82, -0.80) | $0.008^{o}$<br>(-0.001, 0.02) | $0.02^{**}$<br>(0.007, 0.03) |
| **Lifetime mobility** | $-3.32^{*}$<br>(-5.94, -0.69) | | | |
| **School skills**: **Reading ability** | | | $0.04^{*}$<br>(0.01, 0.08) | $0.05^{*}$<br>(0.01, 0.08) |
| **Constant** | $26.36^{***}$<br>(20.55, 32.16) | $29.86^{***}$<br>(19.70, 40.02) | $0.70^{***}$<br>(0.57, 0.82) | $0.74^{***}$<br>(0.58, 0.89) |
| **Observations** | 165 | 181 | 118 | 117 |
| **AIC** | 12699.2 | 37115.89 | -128.57 | -118 |

Statistical significance markers: $^{o}$ $p \leq .1$. *$p \leq .05$. **$p \leq .01$. ***$p \leq .001$.

large-scale navigation variables (degrees of error) are indicative of worse performance, while higher scores on the MRTX denote better performance.

For pointing accuracy and perspective taking, we again rely on linear mixed models with individual entered as a random effect. As shown above, daily travel distances (Fig. 4) and pointing accuracy (Fig. 5A) show a similar pattern across age, with men in their prime reproductive years (i.e., 20–39 age group) traveling a little farther and pointing a little more accurately than women, but with no significant sex difference or decline from that point through old age. However, individual differences in daily travel did not predict pointing accuracy when controlling for sex and age, and so daily mobility is not included in the models discussed below. We do find that annual and lifetime mobility better predict lower error on the pointing accuracy task (Table 5). Likewise, annual mobility predicted lower pointing error on the perspective-taking task (Table 5). Individual differences in average performance on the MRTX task were evaluated with general linear models. When controlling for age and sex, our model indicates that greater annual mobility and a higher reading ability predict greater performance on MRTX Twigs, and reading ability alone predicts greater performance on MRTX Bodies (Table 5).

When education and mobility were entered into the models, we find that the effect of age on mental rotation and perspective taking is no longer significant. However, this does not necessarily mean that the age patterns shown in Figs. 6 and 7 are spurious: older adults have had less education, and education improves performance on the MRTX, so with education in the model, there may not be enough variance left to find a relationship with age in our sample.

## 4. Discussion and conclusions

Navigation is among the most practical and necessary of the cognitive skills we use in daily life, and one that shows considerable individual variation in strategy and competence. There is, therefore, much to be gained from understanding how malleable that ability is, and how it responds to environmental context and spatial experience in daily life.

The most ubiquitous spatial experience of daily life is walking, and in most nonurban contexts that means navigating outdoors in "environmental spaces" where destinations cannot be seen from a single vantage point; one must integrate multiple views while traveling. This typifies the lives of Tsimané men and women, who, like people in most nonindustrial small-scale societies, travel daily along small footpaths in the context of producing or finding food, social visits, and the other necessities of daily life. In this study, therefore, we focused on individual differences in daily, annual, and lifetime travel as the primary independent variables, and navigational ability over environmental spaces as our primary outcome measure. We oversampled older adults in order to evaluate the cross-sectional rate of decline among women and men in spatial cognitive performance, and to see whether continued daily mobility might mitigate that decline. While the functional relationship between mobility and navigation is obvious, the spatial experiences that foster small-scale object-based spatial ability are less clear. We, therefore, also explored changes with age in mental rotation ability, and whether it was affected by individual differences in mobility and access to formal schooling.

### *4.1. Mobility, ecology, and navigation*

Daily mobility (km/day) and pointing accuracy showed a similar pattern across the life course, with male mobility and pointing accuracy exceeding that of females only during the early adult years. The sex difference in daily mobility during this period probably reflects pressures on both males and females: Men's ranges are larger than women's beginning in early adulthood, consistent with other findings of larger male than female ranges during the mate-seeking years, while parenting constraints contribute to a slight decline in daily mobility among women as they care for young children (Miner et al., 2014). However, in contrast to Western populations, both women and men remain highly mobile from their 40s through their 70s, with the average daily travel remaining unchanged throughout this period, and similar for women and men. This pattern of mobility is notable, given the age-related decline in daily steps taken by adults in the United States and three other industrialized populations (Bassett, Wyatt, Thompson, Peters, & Hill, 2010).

The age profile of pointing accuracy mirrors this pattern, with women and men remaining equally accurate and without significant decline from the 40s through the 70s, and greater male accuracy from about age 25 through 40. Tsimané accuracy at this task (average error of 24° for men and 27° for women) is impressive, given that the target locations participants were asked to point to were far away (35 km away, on average), could not be identified by visible distal environmental features, and were not accessible through a direct route. Although the age-sex patterns in pointing accuracy appear to reflect those in daily mobility, individual differences in daily mobility did not predict pointing accuracy, when controlling for age and sex.

In contrast, similar models using our regional mobility measures (annual and lifetime mobility) did find that more mobile individuals had lower pointing error, both with direct pointing (lifetime mobility) and perspective taking (annual mobility). Our perspective-taking task built on our direct pointing task by asking people to imagine they were at a different location before pointing to a third location and measuring the directional error in their pointing. Performance at this difficult task was impressive among young adults but (unlike with direct pointing) performance did decline significantly with age. Our regional mobility measures have the limitation of relying on self-report of prior travel, whereas daily mobility was measured directly by GPS. However, the regional measures may be a more relevant indicator of navigationally challenging travel than daily distance, since they assess travel over a longer period of time covering a larger area and on routes the individual has traveled less frequently. The regional measures also had larger sample sizes, due to challenges in collecting daily tracks via GPS in this field setting.

Our provisional conclusion, then, is that spatially challenging (regional) travel supports better navigational ability in this population. However, we recognize that the causation could go both ways, as more confident navigators may be more comfortable engaging in such travel. Although our sample is small, we also see an apparent rebound in women's pointing accuracy after their prime reproductive years (Fig. 6A), which mirrors the rebound in their mobility during this time (Fig. 4). This suggests that one can experience increases as well as decreases throughout the lifespan. If so, even sedentary individuals may be able to enhance their navigational abilities by increasing mobility at any stage of life.

Gender differences in this study were typically small or nonexistent, but where found they were in the expected direction, with males traveling farther, especially during the reproductive years and over the wider region at all ages. Although male scores on the spatial tests were slightly higher, these differences were small and, for the most part, not statistically significant. Schooling was also less frequent for older women, which may play a role in their slightly lower scores. These minimal gender differences are consistent with other data on the Tsimané, both in studies of children (Davis & Cashdan, 2019) and in an earlier study of pointing accuracy, which also found no gender differences (Trumble et al., 2016). The limited availability of distal landmarks and other geocentric cues in the tropical forest may also be a factor in the minimal sex difference we found in pointing accuracy, since males are more likely than females to rely on such geocentric cues when they are available, while both women and men are proficient at using proximal cues in navigation.

Although we have emphasized the influence of mobility on navigational performance, the physical environment in which people navigate also shapes wayfinding strategy and ability. People who live in navigationally challenging environments (rural areas and cities with irregular street plans) are more accurate at pointing and short-cut navigation than are people who live in grid cities with easily visible distal landmarks that can be used as cues to cardinal direction (Barhorst-Cates et al., 2021; Coutrot et al., 2022). The Tsimané live in a similarly challenging environment, with forest canopy and cloud cover obscuring distal landmarks, and they travel primarily along winding rivers and footpaths, the shape of which can also change fairly rapidly. Growing up in this type of habitat may contribute to the development of greater navigational skill, as seen also in BaYaka foragers in the Republic of Congo (Jang, Boesch, Mundry, Kandza, & Janmaat, 2019).

### *4.2. Formal schooling and mental rotation*

The strongest predictor of scores on mental rotation (the MRTX) was formal schooling, as assessed by reading ability, not large-scale environmental experience. The type of spatial experience, in other words, clearly matters. Formal schooling teaches many things that might foster skill on a task like the MRTX, including patience and experience with highly abstract and novel small-scale tasks involving 2-D pictorial representations. Tsimané with at least 3 years of formal schooling have also been shown to do better at other tests of abstract reasoning in both children (Davis et al., preprint) and adults, and their performance declines more slowly with age (Gurven et al., 2017). However, schooling does not necessarily improve navigational skills: Among Tsimané children, who have spent more time in school than adults, formal schooling was associated with better performance on the MRTX but worse performance at pointing in environmental spaces, probably because while they were in school, they were not out exploring and gaining large-scale environmental experience (Davis & Cashdan, 2020).

Although some studies have found correlations between large-scale (environmental) and small-scale (figural) spatial abilities like mental rotation, these different spatial abilities are partially dissociable (Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006), and the nature of the relationship between mental rotation, perspective taking, and navigation remains in debate (Allen, Kirasic, Dobson, Long, & Beck, 1996; Hegarty et al., 2006; Kozhevnikov, Motes, Rasch, & Blajenkova, 2006; Ruginski, Creem-Regehr, Stefanucci, & Cashdan, 2019). In our study, MRTX scores were correlated with perspective taking, and both MRTX and perspective taking showed a decline from young adulthood through old age in both women and men.

It is possible that some of the decline with age in the MRTX and perspective taking reflects difficulty with novelty as well as spatial ability, since both were unfamiliar and unusual tasks, unlike pointing to a known location, where performance did not decline with age. The decline with age in those tasks could be exacerbated further by the far more limited schooling of our older participants. The small male advantage in the MRTX and in perspective taking may also be due, in part, to the fact that older women had even less formal schooling ($M = 0.14$ years) than older men ($M = 1.32$ years). However, the rate of decline in cognitive processing and memory among Tsimané is similar to that described in other societies

(Gurven et al., 2017), and so the decline in our abstract spatial tasks is likely to also reflect more fundamental biological processes. Salthouse (2009) finds a performance difference in spatial visualization from age 18 to 60 of about 1 SD, which is in the same ballpark as we find for Tsimané performance on the MRTX and our perspective-taking task (Fig. 7). Mental rotation performance in a large global sample is reported to decline by about 40% from the 20s to the 60s, also with a large effect of education (Peters, Manning, & Reimers, 2007). Like these studies, our data are cross-sectional and so any inferences about age patterns are subject to cohort effects, such as the increase in formal schooling mentioned above.

Our navigational abilities evolved in a context where people traveled primarily by foot in natural environments, and without access to maps, other navigational aids, video media, or formal schooling. Given the influence each of these has on spatial cognition, there is much to be gained by studying spatial ability and navigation in small-scale populations, such as the Tsimané, where these influences are largely absent. The ecological relevance of working with the Tsimané, however, comes with limitations, chiefly our inability to control navigational cues in a consistent novel (real or virtual) environment. While navigating with a joystick on a desktop display may be feasible for younger Tsimané, particularly those who have had some formal education, it would be very challenging for the older Tsimané adults. Our much simpler MRTX, which required only touching one of two images, required considerable training for some participants. However, recent improvements in virtual reality headsets might make flexible testing more widely applicable in the future.

Although the navigational experience of horticultural-foraging groups such as the Tsimané is unusual today, wayfinding experience in daily life is also relevant in more evolutionarily novel contexts, such as the cities that most of us live in today. The importance of mobility to successful aging is widely acknowledged (Webber, Porter, & Menec, 2010), and there is concern that many older adults, particularly older women, have limited mobility over "life spaces" (Barnes et al., 2007). In addition to its other health benefits, the Tsimané experience suggests that the navigational demands of walking outdoors over environmental spaces may hold specific benefits for maintaining navigational abilities into old age.

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