

Cognitive Performance Across the Life Course of Bolivian Forager-Farmers With Limited Schooling

Michael Gurven and Eric Fuerstenberg
University of California, Santa Barbara

Benjamin Trumble
University of California, Santa Barbara and
Arizona State University

Jonathan Stieglitz
Institute for Advanced Study in Toulouse, Toulouse, France

Bret Beheim
University of New Mexico

Helen Davis
University of Utah

Hillard Kaplan
University of New Mexico

Cognitive performance is characterized by at least two distinct life course trajectories. Many cognitive abilities (e.g., “effortful processing” abilities, including fluid reasoning and processing speed) improve throughout early adolescence and start declining in early adulthood, whereas other abilities (e.g., “crystallized” abilities like vocabulary breadth) improve throughout adult life, remaining robust even at late ages. Although schooling may impact performance and cognitive “reserve,” it has been argued that these age patterns of cognitive performance are human universals. Here we examine age patterns of cognitive performance among Tsimane forager-horticulturalists of Bolivia and test whether schooling is related to differences in cognitive performance over the life course to assess models of active versus passive cognitive reserve. We used a battery of eight tasks to assess a range of latent cognitive traits reflecting attention, processing speed, verbal declarative memory, and semantic fluency ($n = 919$ individuals, 49.9% female). Tsimane cognitive abilities show similar age-related differences as observed in industrialized populations: higher throughout adolescence and only slightly lower in later adulthood for semantic fluency but substantially lower performance beginning in early adulthood for all other abilities. Schooling is associated with greater cognitive abilities at all ages controlling for sex but has no attenuating effect on cognitive performance in late adulthood, consistent with models of passive cognitive reserve. We interpret the minimal attenuation of semantic fluency late in life in light of evolutionary theories of postreproductive life span, which emphasize indirect fitness contributions of older adults through the transfer of information, labor, and food to descendant kin.

Keywords: cognitive performance, fluid versus crystallized intelligence, cognitive reserve, aging, education, Tsimane

Supplemental materials: <http://dx.doi.org/10.1037/dev0000175.supp>

A growing consensus among psychologists suggests that human cognitive performance is not a generalized ability but is instead composed of multiple interrelated abilities marked by distinct life course trajectories (Craik & Bialystok, 2006; Salthouse, 2004, 2010). “Fluid” intelligence represents the ability to problem-solve and reason in novel situations, “crystallized” intelligence represents the ability to effectively apply acquired knowledge and

learned skills (Carroll, 1993; Cattell, 1971), and some related abilities such as processing speed and working memory arguably may not fit the classical “fluid” versus “crystallized” distinction (Schaie, 1989; Zimprich & Mascherek, 2010). Fluid and other associated cognitive abilities (hereafter referred to as “effortful processing” abilities sensu Tucker-Drob & Salthouse, 2011) often decline from the mid-20s or 30s onward, whereas crystallized

This article was published Online First September 1, 2016.

Michael Gurven and Eric Fuerstenberg, Department of Anthropology, University of California, Santa Barbara; Benjamin Trumble, Department of Anthropology, University of California, Santa Barbara, and Center for Evolutionary Medicine, Arizona State University; Jonathan Stieglitz, Institute for Advanced Study in Toulouse, Toulouse, France; Bret Beheim, Department of Anthropology, University of New Mexico; Helen Davis, Department of Anthropology, University of Utah; Hillard Kaplan, Department of Anthropology, University of New Mexico.

We thank the Tsimane for participating and THLHP personnel for collecting and coding data. Research was supported by grants to Michael Gurven and Hillard Kaplan from the National Institutes of Health (NIH)/National Institute on Aging (NIA) (R01AG024119, R56AG024119) and the National Science Foundation (NSF) (BCS-0422690). Jonathan Stieglitz and Michael Gurven acknowledge support from the Agence Nationale de la Recherche (ANR)? Labex IAST.

Correspondence concerning this article should be addressed to Michael Gurven, Department of Anthropology, University of California, 2060 HSSB, Santa Barbara, CA 93106. E-mail: gurven@anth.ucsb.edu

abilities often improve up through the sixth decade of life (Bugg, Zook, DeLosh, Davalos, & Davis, 2006; Horn & Cattell, 1967). Performance on effortful processing tasks not only declines earlier in life but also more rapidly than performance on tasks drawing more from crystallized abilities (Harada, Natelson Love, & Triebel, 2013). These distinct age patterns have been demonstrated for both sexes in large-scale studies (Bugg et al., 2006; McArdle, Ferrer-Caja, Hamagami, & Woodcock, 2002; Schaie, 2005; Singh-Manoux et al., 2012; Tucker-Drob, 2011; Wang & Kaufman, 1993), including recent Weschler Adult Intelligence Scale IV and Weschler Memory Scale IV normative samples (Salthouse, 2010). Despite more nuanced taxonomies for classifying cognitive abilities and subtle differences in rates of change, these broad age patterns generally appear to be consistent across and within populations. Given their consistent replication, these age patterns have been identified as universals of human cognitive aging (Hedden et al., 2002; Park & Gutches, 2006; Park et al., 2002; Salthouse, 2009).

Despite these claims of universality, the extent to which these patterns exist among preindustrialized populations with limited exposure to formal schooling remains understudied. An adequate attempt to describe and explain “universal” age patterns of human cognitive performance should include studies of preindustrialized populations and highlight the costs and benefits of different cognitive abilities with age under socioecological conditions more representative of human evolutionary history (e.g., energy limited, subsistence production, higher fertility, pathogen exposure). Humans lived as hunter-gatherers for the vast majority of their evolutionary history, and thus natural selection on cognitive aging and development, as well as its associated neural substrates, occurred in the context of a foraging lifestyle. Yet virtually nothing is known about how cognition develops and declines among traditional subsistence-level populations with limited schooling. For example, a pattern where all cognitive abilities senesce concurrently with physical declines would contradict existing evolutionary theories of aging that emphasize that postreproductive life span evolved to transfer difficult-to-acquire resources and information to descendant kin (Gurven, 2012; Kaplan & Robson, 2002; Lee, 2003); based on this logic, one should instead expect some cognitive abilities (especially crystallized) to persist into late adulthood.

Although literacy and schooling are nearly universal in industrialized populations, this was not the case throughout the vast majority of human history. Most studies find strong impacts of higher education on cognitive performance (Alley, Suthers, & Crimmins, 2007), although such studies generally only examine differences between secondary and postsecondary education, as primary schooling is compulsory in most industrialized populations. Current consensus of the effects of schooling on cognitive performance is based on a narrow range of populations where compulsory schooling is commonplace in a competitive skills-based wage economy (Ardila, Ostrosky-Solis, Rosselli, & Gómez, 2000; Ardila & Rosselli, 2007; Baker et al., 2015) and where certain socioecological factors (e.g., reduced nutrient availability, high pathogen burden, high fertility, and demand for childcare) pose fewer constraints to accruing human capital in controlled settings. Some researchers have argued that observed age patterns of cognitive performance may be specific to the Western, educated, industrialized, rich, and democratic (WEIRD) societies

(Henrich, Heine, & Norenzayan, 2010) and may not generalize to a broader range of populations. If alternative socioecologies favor different kinds of skills at different ages, then age profiles of cognitive performance might vary from those documented in WEIRD societies. Furthermore, the extent to which cognitive performance is affected by differential exposure to schooling at the lower tail of the schooling distribution is unclear. Identifying human-typical patterns of cognitive development and decline in the absence of schooling, as was typical for most of human history, is therefore difficult given the complicated and potentially reinforcing effects of modern environments.

Cognitive Performance and Schooling

Although pathways by which schooling affects cognitive task performance are still not clearly defined, it is clear that literacy, numeracy, and abstract logic are often necessary for occupational success in industrialized populations, unlike in traditional subsistence societies (Furnham & Cheng, 2013). Schooling plays a critical role in directly cultivating many of the cognitive skills that underpin performance on intelligence tests and eventual economic success in adulthood (Ceci, 1991). Across all ages, those with higher educational attainment develop various cognitive skills more rapidly than those with minimal schooling (Alley et al., 2007). Positive associations between schooling and cognitive performance (Alley et al., 2007; Deary, Strand, Smith, & Fernandes, 2007; Lam et al., 2013; Schoon, 2010), as well as between both adult income and job performance, are well established (Cheng & Furnham, 2012; Feinstein & Bynner, 2004; Schmidt & Hunter, 2004). Cohort studies tracking school attendance and reverse causality due to dropout have also consistently reported strong positive associations between schooling and multiple domains of cognitive performance (Brinch & Galloway, 2012; Carlsson, Dahl, Öckert, & Rooth, 2015).

In addition to direct effects of schooling on cognitive outcomes, participation in the structured, routinized, controlled learning environment of formalized education also fosters “noncognitive” traits associated with concentration, improved attention span, and self-regulation that predict success in academic, professional, and social environments (Blair & Raver, 2014; Komarraju, Ramsey, & Rinella, 2013). Formalized schooling places demands on executive function—the ability to avoid distractions, focus attention, hold relevant information in working memory, and regulate impulsive behaviors. A well-developed working memory and the ability to control attention enable individuals to focus and process information more efficiently, which further supports the retention of knowledge (Bull & Scerif, 2001; Ruchkin, Grafman, Cameron, & Berndt, 2003). The ability to avoid distractions and stay on-task for extended periods of time (i.e., “grit”; Duckworth, Peterson, Matthews, & Kelly, 2007) affects a range of cognitive, scholastic, occupational, and social outcomes. Schooling also rewards high performance on exams, thereby instilling test-taking motivations, including effort and persistence—traits that may not exist for individuals with minimal or no exposure to timed testing (Eklöf, 2010).

Cognitive Decline: Active Versus Passive Reserve

Many cognitive abilities decline with age, although such declines are usually less steep for more educated individuals (Alley

et al., 2007). This consistent attenuation in age-related decline has raised new questions regarding how differential schooling earlier in life might affect later-life cognition. “Cognitive reserve” reflects the ability for individuals to be buffered from some aspects of cognitive aging (Barulli & Stern, 2013; Le Carret et al., 2003; May, 2011). The extent to which schooling plays a role in mitigating age-related cognitive decline has been vigorously debated (Anstey & Christensen, 2000; Lebovici, Ritchie, Ledéser, & Touchon, 1996; Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012; Tucker-Drob, Johnson, & Jones, 2009; Van Dijk, Van Gerven, Van Boxtel, Van der Elst, & Jolles, 2008; Zahodne et al., 2011), and the mechanisms remain poorly understood.

The “active reserve” model focuses on brain plasticity for recruiting alternative cognitive capacities and reorganizing cognitive networks to counter age-dependent cognitive degradation. Proponents argue that schooling encourages more efficient cognitive processing and neural networks, which facilitates cognitive reorganization and buffers against effects of normal cognitive aging (Stern, 2002). This model suggests that more educated individuals will (a) outperform their less educated counterparts throughout adult life and (b) show a slowing of the typical age-related patterns of cognitive decline. In support of this model, greater schooling has been associated with lower rates of cognitive decline in healthy adults (e.g., Butler, Ashford, & Snowdon, 1996; Farmer, Kittner, Rae, Bartko, & Regier, 1995; Lyketos, Chen, & Anthony, 1999) and with slower transition from mild cognitive impairment to dementia (Poletti, Emre, & Bonuccelli, 2011).

The “passive reserve” model focuses on building physical reserve capacity (e.g., neuronal network density, synapse count) and clinical impairment beyond a threshold level of brain pathology (Satz, 1993). This model also predicts that greater schooling leads to higher cognitive performance but, unlike the active reserve model, predicts no difference in rate of cognitive decline as a function of schooling (Stern, 2002). Instead, greater schooling should be associated with enhanced retention of physical cognitive reserves, delayed attainment of brain pathology, and delayed onset of cognitive decline. However, longitudinal studies consistently show no significant attenuating effect of schooling on rate of cognitive decline at older ages (Alley et al., 2007; Karlamangla et al., 2009; Tucker-Drob et al., 2009; Van Dijk et al., 2008; Zahodne et al., 2011).

Most studies of schooling’s effects on the age pattern of cognitive performance compare adults with relatively high educational attainment or children varying in secondary schooling but who have all received compulsory primary schooling (reviewed in Ceci, 1991). Variability in cognitive performance throughout adulthood at low levels of schooling may be instructive for helping to distinguish the relative impacts of cumulative exposures that incrementally improve cognitive performance over time versus attitudes, expectation formation, and other schooling-related factors whose impacts on cognitive performance may be learned with even low levels of schooling.

The Present Study

To shed light on cognitive performance and “reserve” in a unique non-WEIRD socioecology characterized by low levels of schooling, we report age patterns of cognitive performance among Tsimane forager-horticulturalists of Bolivia. Despite the low over-

all level of schooling, we test whether variation in schooling is associated with (a) cognitive performance and (b) age-related differences in cognitive performance using a cross-sectional study design. Both active and passive reserve models predict that more educated individuals will outperform their less educated counterparts at all ages, but only the active reserve model predicts that greater levels of schooling are associated with a shallower rate of cognitive decline; the passive reserve model predicts no relationship between schooling and rates of decline.

To our knowledge, this is the largest study ($n = 919$ individuals, 49.9% female) of cognitive performance in a traditional small-scale population. Not all Tsimane villages have had access to schools, and those that do vary in the duration of their establishment and efficacy of the teachers. Thus, schooling is not heavily confounded with age cohort in the current sample, as might be expected if schools were uniformly established across the Tsimane territory at the same time. We are therefore able to leverage regional variation to disentangle availability and quality of schooling and age in our analytic approach despite the cross-sectional design, which makes the Tsimane an ideal population in which to study the effects of schooling on cognitive development and aging.

Method

Study Population

The Tsimane are a semisedentary population of ~15,000 forager-horticulturalists living in the Bolivian Amazon. They inhabit 90+ villages ranging in size from 50–500 individuals. They cultivate plantains, rice, corn, and sweet manioc in small swiddens, and they regularly fish and hunt. Traditional foods comprise > 90% of the calories in the diet, with the remainder purchased from market stores or obtained from trade with merchants (Martin et al., 2012). Tsimane live in extended family clusters, where the majority of food and labor sharing occurs. Mortality has been traditionally high, with approximately 20% of children dying before age 5 (Gurven, Kaplan, & Supa, 2007). The Tsimane rarely use modern contraceptives, and total fertility rate is high (9.1 births per woman; McAllister, Gurven, Kaplan, & Stieglitz, 2012). The population growth rate is also high at 3.6% per year. Mean (*SD*) age of first birth for men and women is 22.8 (4.2) and 18.6 (2.9) years, respectively (McAllister et al., 2012).

Many villages now have elementary schools (up to fifth grade) taught by bilingual (Spanish-Tsimane) teachers. For over three decades, bilingual Tsimane teachers (all young men) were trained by Protestant missionaries, who produced all instructional materials (Godoy et al., 2007). Up until 2000, no village had a middle or high school, although several large villages near town had educational programs 1 week per month where teenagers and adults who completed elementary school could obtain up to a high school diploma. Unlike in most of Bolivia where indigenous children were taught in Spanish, Tsimane children were taught in their own language, and curricula prioritized Tsimane literacy. However, since the early 2000s, more teachers are Bolivian nationals, and curricula have shifted to emphasize more Spanish fluency and to conform more with standards set by the Bolivian Ministry of Education. Secondary schools now exist in several larger villages near the closest market town of San Borja, and young adults are starting to become high school graduates (5% of adults aged

18–25). However, in general, school attendance rates are either low or inconsistent for many students, and overall adult literacy rate is low (18%). We suspect that much variability in educational attainment, especially up to the fifth-grade level, is based on the number and types of schools in a participant's natal village and labor demands in the family that might otherwise affect attendance (Bock 2002a). Fluency in the Tsimane language is universal as Tsimane remains the native language (unrelated to Spanish); roughly 65% of adults in our sample are at least moderately fluent in Spanish. Although Spanish is taught in schools, Tsimane also gain Spanish fluency from greater interaction with Bolivian nationals.

Cognitive Battery and Recruitment

A sample of 919 Tsimane (49.9% female) aged 8–88 (mean \pm $SD = 33.85$ y \pm 18.58) completed a battery of eight tasks (described in greater detail below) to assess a wide range of latent cognitive traits, based in part on those used by the Mexican Health and Aging Study (Mejía-Arango, Wong, & Michaels-Obregón, 2015) and the Cross-Cultural Cognitive Examination dementia screening (Glosser et al., 1993). These tasks largely assess verbal declarative memory (short-term learning and recall), attention (visual scan, digit forward), psychomotor speed (visual scan), and semantic fluency (category fluency). Subjects were participants of annual biomedical surveillance by the Tsimane Health and Life History Project (THLHP) between January 2008 and July 2009 (see Trumble et al., 2015). Given the THLHP's focus on aging, all village members age 40+ are eligible for complete biomedical surveillance, including behavioral and cognitive assessment, whereas younger individuals receive medical attention but further data collection exists only on a subsample (~30%). From a THLHP census population of 2,768 individuals age 8+ across the 34 villages sampled in this study, 2,003 (72%) were seen by the THLHP; excluded are those who (in descending order of relative frequency) were visiting other villages, engaged in multiday foraging excursions or other subsistence work (e.g., hunting) entailing travel away from the village, and those who did not wish to participate. Of the 439 adults age 40+ who received medical exams by THLHP physicians, 345 (79%) participated in the cognition study. Of the 1,020 Tsimane age 8–24 years across the 34 villages, 338 (33%) were sampled to in the cognition study. The main reason for excluding this age category from the cognition study was logistical: The bilingual Tsimane researchers conducting the cognition study were also conducting other interviews, and their time was thus limited. Over a third of participants (31.0% males, 38.4% females) had no schooling (see the online supplemental materials Figure S1). Although years of schooling ranged from 0–12 (mean \pm $SD = 2.38 \pm 2.80$; median = 2), nearly 60% of the sample had ≤ 2 years (see the online supplemental materials Figure S2). It is worth noting, however, that a year of schooling among Tsimane may contain significant gaps in attendance and is unlikely to be equivalent to a year of schooling in industrialized societies.

Cognitive tests were conducted in the Tsimane language by a trained Tsimane research assistant with multiple years of experience conducting interviews as part of the THLHP. Tests were conducted at participants' homes or elsewhere in the village in a private location. Interviews were conducted entirely in the Tsi-

mane language, with the exception of the Spanish numbers in the digit forward test.

Consent was provided at three levels: Tsimane government (Gran Consejo Tsimane), village leadership, and study participants. All procedures were approved by the institutional review board at the University of California, Santa Barbara.

Immediate and delayed recall. Verbal memory was assessed by immediate and delayed recall tasks (Unsworth, Redick, Heitz, Broadway, & Engle, 2009). Participants were read a list of eight Tsimane nouns three times and then asked each time to repeat the list immediately in any order. After 10 min, participants were also asked to recall in any order as many of the eight words from the original list as possible.

Digit forward. Attentional capacity was assessed by digit span tasks. Digit forward tasks require participants to store and sequentially update a list of single-digit numbers and then retrieve the list from working memory at the end of a trial (Maylor, Vousden, & Brown, 1999). Participants repeat a series of digits increasing in length until failure on two consecutive trials. This test was first administered in the Tsimane language. Some Tsimane numbers have multiple syllables (e.g., *yavatidye* [seven], *arajtac* [nine]), and so a second version using Spanish numbers was conducted. Even though Spanish fluency varied in the sample, Spanish numbers up to 10 are understood by all Tsimane. In a third spatial span task, the interviewer touched a predetermined sequence of numbered boxes on a poster, which participants were asked to replicate. This task draws upon spatial processing and mental mapping in addition to working memory.

Visual scan. A visual scan task required participants to locate in 2 min as many instances as possible of a target symbol in an array of jumbled symbols. Visual scanning requires discrimination between target stimuli and distractors, as well as executive processing skills such as psychomotor speed, sustained attention, and interference avoidance (Glosser et al., 1993).

Semantic fluency. Semantic fluency tasks assess semantic memory in two locally salient domains: animals and fish (Ardila, Ostrosky-Solís, & Bernal, 2006). Participants had 2 min to generate as long a list of items in each category as possible. Performance on semantic fluency tasks is considered a good measure of crystallized intelligence (Carroll, 1993; Ekstrom, French, & Harman, 1976) based on the ability to retrieve information from long-term memory and to filter distractions and limit responses to relevant objects.

Data Analysis

Data analysis was conducted in R version 3.1.2 and SAS 9.2. Individual performance in each cognitive test was first converted to z scores, allowing direct comparisons across tests with different scoring protocols. The z scores for separate tasks were also averaged to create composite measures for "effortful processing" ability (immediate and delayed recall, digit forward, and visual scan) and semantic fluency (animals and fish).

Multivariate linear regression models were used to assess relationships between cognitive performance, age, and years of schooling, controlling for sex and Spanish fluency. Interaction terms between age and schooling were added to estimate the effect of schooling on age-related decline in cognitive performance. Because of possible nonlinear age patterns of cognitive perfor-

mance, age² terms are included in all models. Generalized additive models (GAMs; R package *mgcv*) were used to examine age trends in composite effortful processing and semantic fluency domains, while controlling for sex, Spanish fluency, and schooling, that is, $Y|X_1, X_2, X_3 = B_0 + S_1(X_1) + X_2 + X_3$, where $S(X_1)$ is a nonparametric smooth function (spline) for age, and X_2 and X_3 are sex and schooling, respectively.

To better isolate age patterns of cognitive performance at early and later life stages, we used segmented linear regression (R package *segmented*) to estimate (a) age of peak performance, (b) the slope of age-related differences (i.e., “decline”) for those older than this peak, and (c) the age-related slope of “increase” before this peak. Segmented linear models permit identification of transition points that may otherwise be obscured when using quadratic functions or nonparametric estimates from GAMs (Fortenbaugh et al., 2015). Additional regressions of preadult and early adult cognitive performance are restricted to ages <25 years, whereas those focused on middle-age and older adult cognitive performance are limited to ages 40+.

Inter- and intravillage variation. Because villages varied in access to and quality of teachers and schools, each of the 34 communities in this study was treated as a random effect in a mixed-effects model. We also make adjustments due to nonindependence from biological kinship among individuals in our sample, using detailed genealogy and census records on all 919 participants (Gurven et al., 2007). Among $919 \times 918/2 = 421,821$ possible unique dyads, 677 are parent–offspring dyads, and 1,510 are sibling dyads; 97.4% reflect nonkin relationships (Wright’s coefficient of relatedness $r = 0$), 1.6% reflect $0 < r \leq .125$, 0.6% reflect $0.125 < r \leq .25$, and 0.4% reflect $r \geq .25$. To adjust for shared kinship, we add two random intercept terms for members of the same 139 matriline and 143 patriline in all mixed-effects regression models.

Results

Descriptive Statistics

Summary statistics on cognitive performance and covariates by age and sex are shown in Table 1. On average, males are more educated than females (Mann–Whitney U , $z = 2.28$, $p = .023$; Figure S1) and speak Spanish more fluently, and so sex and

Spanish fluency are included as controls in all models. However, highest grade achieved and Spanish fluency were similar between young males and females <25 years (grade: 3.1 years; Spanish competence: 2.3 out of 4, Table 1; see the online supplemental materials Figures S2, S3); adult men had slightly higher educational attainment and Spanish fluency than women (schooling: 3.1 vs. 2.1 for ages 25–39, 1.9 vs. 1.2 for ages 40+; Spanish: 2.7 vs. 2.0 for ages 25–39, 2.5 vs. 2.1 for ages 40+; Table 1). For both sexes, highest educational attainment is lower with age (Table 1; Figure S2), but Spanish fluency varies minimally with age (Table 1; Figure S3). Even controlling for schooling and Spanish fluency, males outperform females in all tasks. There was no significant age difference between sexes, $t(914.21) = -0.52$, $p = .60$ (see Table 1).

Table 2 shows the sex-specific Pearson correlations in performance among all cognitive tasks and two composites, semantic fluency and effortful processing, for all other domains. Most correlations between effortful processing hover between 0.2 and 0.5, and 0.6 among the two semantic fluency tasks. Long-term recall, spatial forward, and visual scan are most strongly correlated with the effortful processing composite. In the complete sample, effortful processing and semantic fluency composites are uncorrelated with each other; correlations among effortful processing and semantic fluency composites are significant only for those <20 years ($r = .16$, $p = .007$, controlling for sex) and for schooled adults (1–2 years: $r = .35$; 3+ years: $r = .21$, $ps < .0001$, controlling for age and sex). The average correlation among all cognitive tasks varies little by age group (<20 years: $r = .226$, $n = 279$; 20–39 years: $r = .210$, $n = 291$; 40–59 years: $r = .175$, $n = 252$; 60+ years: $r = .191$, $n = 77$, controlling for sex) or by level of schooling (0 years: $r = .191$, $n = 306$; 1–2 years: $r = .245$, $n = 227$; 3+ years: $r = .235$, $n = 364$). Thus, we find little evidence that the cognitive abilities assessed in this study change consistently in their degree of independence from zero to low levels of schooling or across the life span (see Tucker-Drob, 2009, and citations therein).

Age Patterns of Cognitive Performance

Tables 3 and 4 test the relationship between age, schooling, and Spanish fluency on cognitive performance for the full sample, younger individuals (<25 years old), and middle-aged and older adults (aged 40+). In the full sample, age is significantly positively associated with performance on all cognitive measures,

Table 1
Descriptive Sample Statistics by Age and Sex

Variable	Age <25				Age 25–39				Age 40+			
	Male		Female		Male		Female		Male		Female	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Age (y)	14.1	4.3	14.9	4.6	33.3	4.0	31.8	4.3	54.1	11.2	53.1	11.3
Highest grade (0–12)	3.1	2.5	3.1	2.4	3.1	3.6	2.1	2.8	1.9	3.0	1.2	2.1
Spanish fluency (0–4)	2.3	1.2	2.3	1.0	2.7	1.0	2.0	1.2	2.5	1.2	2.1	1.2
Average short-term learning (0–8)	5.1	1.2	4.9	1.2	5.4	1.2	5.1	1.2	4.7	1.1	4.5	0.8
Long-term recall (0–8)	6.2	1.2	6.4	1.3	6.5	1.1	6.1	1.2	5.6	1.3	5.5	1.4
Tsimane digit forward (0–18)	10.4	1.9	9.9	1.8	11.1	2.0	9.9	1.9	10.2	2.1	9.3	1.8
Spanish digit forward (0–18)	10.7	2.1	10.5	2.3	11.6	2.0	10.1	2.1	10.8	1.9	9.6	2.0
Spatial forward (0–7)	4.2	1.1	4.1	1.0	4.4	1.1	4.0	1.2	4.0	.9	3.5	0.9
Visual scan (# correct – # wrong)	34.4	14.7	33.6	14.9	39.3	14.5	28.8	15.2	20.6	16.7	14.3	14.0
Total # animals in 2 min	22.2	6.0	19.9	5.6	27.1	5.9	22.7	5.3	25.9	6.2	23.5	5.2
Total # fish in 2 min	19.1	5.3	17.0	5.1	24.2	5.0	20.4	4.9	23.7	5.3	21.5	5.1

Table 2
Pearson Correlations Between Cognitive Tasks, All Ages Combined

Task	Short-term recall	Long-term recall	Tsimane digit forward	Span digit forward	Spatial forward	Visual scan	Animal fluency	Fish fluency	Effortful processing	Semantic fluency
Short-term recall	—	.425***	.160**	.201***	.213***	.192***	.079†	.064	.387***	.054
Long-term recall	.429***	—	.232**	.240***	.244***	.387***	.141*	.131*	.572***	.157**
Tsimane digit forward	.206***	.213***	—	.570***	.387***	.301***	.080†	.042	.601***	.075†
Span digit forward	.257***	.248***	.505***	—	.383***	.364***	.079†	.032	.639***	.058
Spatial forward	.199***	.299***	.192***	.274***	—	.510***	-.016	-.058	.698***	-.046
Visual scan	.252***	.438***	.233***	.229***	.354***	—	-.098+	-.151**	.728***	-.144*
Animal fluency	.141*	.092+	.173**	.183***	.01	.026	—	.612***	.017	.859***
Fish fluency	.036	.007	.113+	.120**	-.005	-.059	.636***	—	-.043	.865***
Fluid	.495***	.655***	.544***	.576***	.611***	.693***	.121*	.017	—	-.03
Semantic fluency	.100+	.074	.158**	.165**	.005	-.002	.876***	.871***	.074	—

Note. Correlations above the diagonal reflect females ($n = 461$). Correlations below the diagonal reflect males ($n = 458$).
† $p < .10$. + $p < .05$. * $p < .01$. ** $p < .001$. *** $p < .0001$.

whereas the age² term is significantly negatively associated with cognitive performance, demonstrating lower age-related performance at older ages in all abilities (all $ps < .001$).

Because of these nonlinear effects, we use GAMs to provide greater resolution on age patterns of cognitive performance. Controlling for sex, schooling, and Spanish fluency, many abilities show peaks during early adulthood (20s and 30s), followed by a considerable plateau throughout mid-adulthood before witnessing declines throughout later life (Figure 1). Although the age profiles of many tasks are similar, delayed recall and visual scan tasks show slightly earlier peaks than other abilities, and visual scan shows fewer age-related differences at later ages (see Figure 1). On the other hand, semantic fluency performance improves consistently throughout early life and mid-adulthood before showing slightly lower performance at later ages (see Figure 1).

We employ segmented multivariate linear regressions to estimate the ages of peak performance and differences in performance at ages earlier and later than the peak (see Table 5). Most effortful processing tasks peak earlier (average: 16.2 years) than semantic fluency tasks (average: 30.6 years, $p < .001$; Figure 2, Table 5). These peak ages are somewhat earlier than those displayed in GAMs (see Figure 1). Effortful processing abilities improve significantly from early age until mid-adolescence ($\beta = 1.409$, $p < .001$) and then show lower

performance thereafter ($\beta = -0.314$, $p < .001$). Semantic fluency abilities improve significantly from early age until mid-adulthood ($\beta = 1.042$, $p < .001$) and are only slightly lower among older adults ($\beta = -0.081$, $p < .001$).

Effects of Schooling on Acquisition and Age of Peak Performance

We use segmented linear regressions to consider whether schooling plays a significant role in the cognitive performance of adolescents and thereby on the peak age of cognitive performance. Performance in effortful processing abilities peaks 10.6 years earlier and 1.21 *SD* higher for individuals with 2+ versus <2 years of schooling (see Figure 3). Across most ages, those with low or no schooling perform significantly below the population average. Performance on semantic fluency tasks exhibits a different pattern than the other tasks: Those with 2+ years of schooling display rapid improvement throughout adolescence followed by minimal change or even slight increase with age (see Figure 3). Those with <2 years of schooling exhibit a similar pattern at early ages but then show slightly lower performance from age 20 onward. Comparing Tsimane with no schooling to those with some (1–2 years) or more (3+ years) shows similar dose-response patterns across different cognitive tasks (see the online supplemental materials Figure S4).

Table 3
Multivariate Regressions Predicting Performance on Each Fluid Subtask for All Individuals

Variable	Short-term recall	Long-term recall	Tsimane digit forward	Spanish digit forward	Spatial digit forward	Visual scan	Effortful processing	Animals	Fish	Categorical fluency
Age	.022***	.023***	.023***	.019**	.012*	.016**	.018***	.070***	.068***	.072***
Age ²	-.0004***	-.0004***	-.0003***	-.0003***	-.0002**	-.0004***	-.0003***	-.0007***	-.0007***	-.0007***
Sex	.195***	.055	.350***	.379***	.321***	.305***	.292***	.457***	.441***	.453***
Years of schooling	.031**	.038**	.079***	.066***	.102***	.086***	.060***	.029*	.022†	.030*
Spanish fluency	-.427***	.213***	-.004	.027	.042	.073†	.072**	.050	.054	.084†
Variance between communities	.419	.176	.106	.187	.277	.403	.239	.290	.272	.289
Variance within communities	.807	.912	.935	.914	.848	.773	.448	.855	.846	.833

Note. Community, matriline, and patriline are random effects in the model. Parameter estimates are regression coefficients in raw units of the predictor variables. Cognitive task performance is in z score units.
† $p \leq .10$. * $p \leq .05$. ** $p \leq .01$. *** $p \leq .001$.

Table 4
 Multivariate Regressions Predicting Cognitive Performance for Individuals Aged <25 (n = 351) and Aged 40+ (n = 376)

Variable	Short-term recall	Long-term recall	Tsimane digit forward	Spanish digit forward	Spatial digit forward	Visual search	Effortful processing	Animals	Fish	Category fluency
Age <25										
Age	.028**	.015	.022*	.005	.017†	.027***	.013**	.068***	.066***	.065***
Male	.149	-.053	.267***	.113	.163†	.168*	.170***	.446***	.435***	.453***
Highest grade	.035	.050*	.096***	.128***	.134***	.065***	.084***	.030	-.008	.019
Spanish fluency	-.470	.279***	.137*	.077	.022	.091†	.126***	.086	.148*	.179**
Variance between communities	.431	3.44e-12	1.07e-08	.182	.257	.408	.178	.434	.321	.436
Variance within communities	.840	.910	.888	.934	.848	.679	.446	.775	.783	.753
Age 40+										
Age	-.022***	-.032***	-.013**	-.015**	-.010*	-.033***	-.021***	-.013**	-.005	-.009*
Male	.194*	.093	.396***	.551***	.454***	.349***	.377***	.379***	.382***	.354***
Years of schooling	.003	.0001	.040†	.010	.045*	.052**	.026**	.015	.021	.026
Spanish fluency	-.255***	.203**	-.104	-.019	.107	.073	.083*	.051	.005	.053
Variance between communities	.354	.1627	.210	.290	.292	.366	.286	.288	.246	.258
Variance within communities	.7138	.9375	.938	.843	.784	.732	.426	.864	.870	.841

Note. Community residence, matriline, and patriline are random effects.
 † $p \leq .10$. * $p \leq .05$. ** $p \leq .01$. *** $p \leq .001$.

Years of schooling and Spanish fluency are consistently positively associated with cognitive performance in effortful processing tasks, but only Spanish fluency is associated with performance in semantic fluency tasks (see Table 4). For individuals <25 years old, there is a significant *negative* interaction between age and

schooling on effortful processing composite performance and numerous subtasks (see Table 6); educated individuals perform higher than uneducated individuals at earliest ages, but then their performance proceeds at a slightly slower rate toward a higher peak than observed in less educated age-matched peers. There is

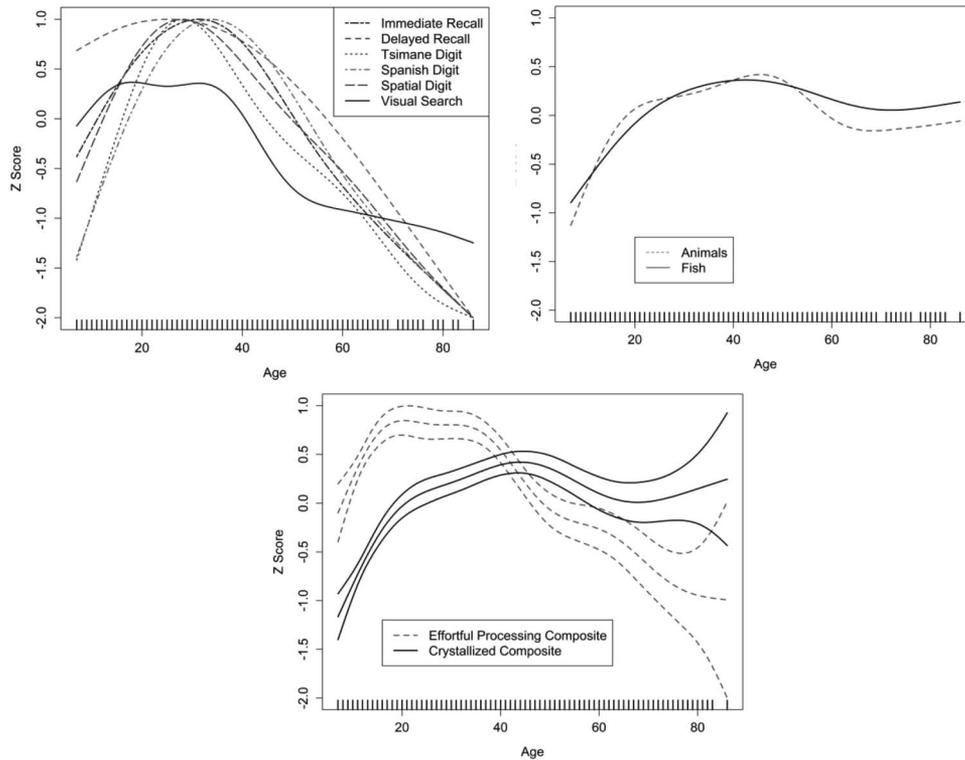


Figure 1. Smoothed curve of the effect of age on cognitive performance, controlling for sex, education, and Spanish fluency, based on generalized additive models (see text). Upper and lower lines of each curve represent 95% confidence intervals. Rug marks on the X-axis indicate the range of unique ages in the sample (range: 8–88 years). In all models, age represented a significant smoothing term ($ps < .001$). Sex, education, and Spanish fluency added as controls to the models.

Table 5
Segmented Linear Regression Predicting Peak Age of Cognitive Performance Across Subtasks
(*n* = 919 Individuals)

Variable	Age of peak (y)	Slope of increase to peak	Slope of decline from peak	Decline per decade
Cognitive task				
Immediate word recall	34.6	.237***	-.558***	-.300
Delayed word recall	15.6	1.961***	-.425***	-.229
Tsimane digit forward	16.1	1.731**	-.250**	-.135
Spanish digit forward	17.0	1.272*	-.231*	-.124
Spatial forward	14.7	2.107**	-.289**	-.155
Visual scan	16.3	2.149***	-.700***	-.377
Composite effortful processing	16.2	1.409***	-.314***	-.169
Category fluency				
Semantic fluency (animals)	30.8	2.404***	-.016***	-.009
Semantic fluency (fish)	30.7	.974***	-.046***	-.025
Composite	30.6	1.042***	-.081***	-.044

Note. Slopes are reported as standardized betas. Expected decline in performance is in standard deviation units per decade for each subtask and composite measure.
* $p < .05$. ** $p < .01$. *** $p < .001$.

no significant age-by-schooling interaction on semantic fluency performance (see the online supplemental materials Table S6a).

Effect of Schooling on Rate of Cognitive Decline

To test predictions of the passive and active models of cognitive reserve, we include an age-by-schooling term in the subsample of

adults aged 40+ ($n = 376$; Tables 4–6). A significant main effect of schooling on performance but no significant age-by-schooling term would be consistent with no buffering effect of schooling on cognitive decline, as predicted by the passive reserve model. A positive and significant age-by-schooling term would instead support the active reserve model, suggesting that there is an attenu-

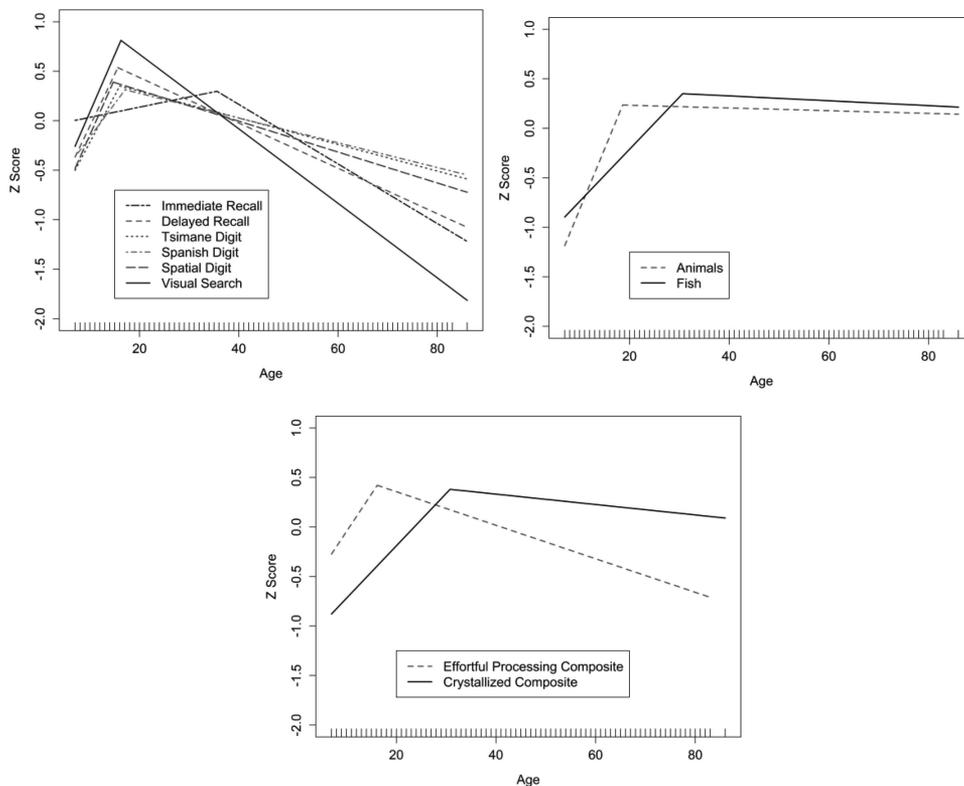


Figure 2. Estimated age of peak cognitive performance for all tasks. (a) Composite “effortful processing” components, (b) category fluency subtasks, and (c) composite scores. Rug marks on the X-axis represent the range of unique ages in the sample.

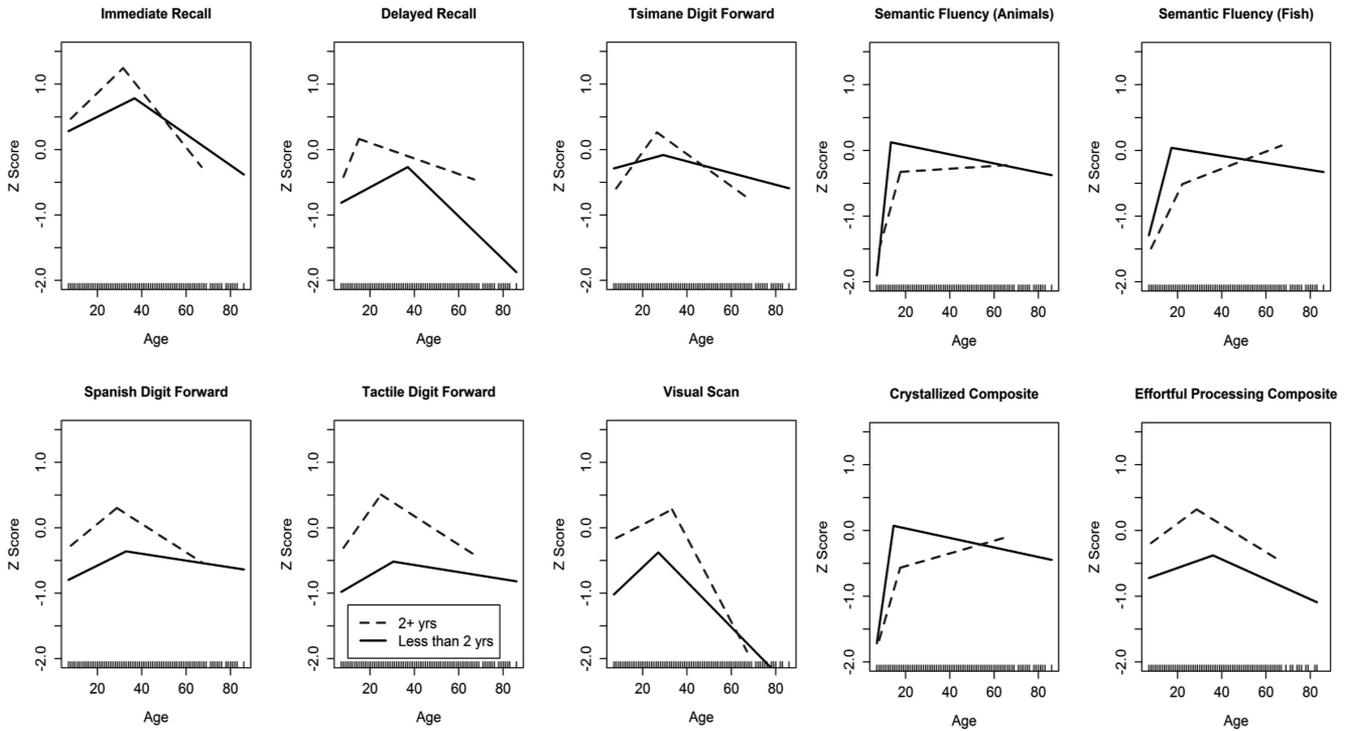


Figure 3. Segmented linear regression predicting cognitive performance across two levels of educational attainment (<2 years vs. 2+ years).

ating effect of schooling on cognitive decline at later ages. A third possibility, with a positive main effect of schooling and a negative age-by-schooling term, would instead suggest that the protective effects of schooling are smaller at late ages.

We find a positive effect of schooling on several tasks, including short-term recall and visual scan, no effect on other tasks or on the composite measures, and no significant age-by-schooling term for any measure (see Table 6), consistent with the passive reserve

model. To explore nonlinear effects of schooling on rates of effortful processing cognitive decline, we divided the sample into low (<2 years) and moderate to high (2+ years) schooling and similarly performed multivariate linear regression (see Table 7). In order to determine whether differences in schooling produce distinct patterns of decline, we conducted a *t* test for significant differences in slope with age. Results show that the slopes with age are similar across both groups, $t(342) = 1.093, p = .275$, confirm-

Table 6
Schooling and Rates of Cognitive Performance: Acquisition (<25 Years) and Decline (>40 Years)

Variable	Short-term recall	Long-term recall	Tsimane digit forward	Spanish digit forward	Spatial digit forward	Visual search	Effortful processing	Animals	Fish	Category fluency
Age <25										
Age	.046***	.036*	.022	.015	.047***	.055***	.034***	.074***	.054**	.062***
Male	.144	-.053	.267**	.112	.158†	.158*	.165***	.445***	.437***	.454***
Years of schooling	.165*	.197**	.095	.200*	.348***	.275***	.232***	.071	-.088	.004
Spanish fluency	-.465***	.279***	.137*	.079	.027	.103†	.129***	.088	.146*	.178**
Age-by-grade level interaction	-.007†	-.008*	.0001	-.004	-.011**	-.011***	-.008***	-.002	.004	.001
Variance between communities	.434	.004	2.87e-13	.184	.243	.371	.165	.440	.314	.434
Variance within communities	.835	.904	.888	.933	.838	.671	.438	.774	.782	.753
Age 40+										
Age	-.019**	-.032***	-.011*	-.012*	-.011*	-.030***	-.019***	-.009†	-.006	-.008†
Male	.184*	.093	.390***	.541***	.457***	.339***	.373***	.368***	.385***	.350***
Years of schooling	.144†	-.004	.116	.149	.005	.173†	.088	.168	-.025	.077
Spanish fluency	-.246***	.203**	-.099	-.011	.104	.081	.087*	.060	.002	.056
Age-by-grade level interaction	-.003†	.0001	-.002	-.003	.001	-.002	-.001	-.003	.001	-.001
Variance between communities	.348	.162	.204	.288	.293	.368	.285	.290	.243	
Variance within communities	.712	.938	.938	.841	.784	.730	.425	.861	.870	

† $p \leq .10$. * $p \leq .05$. ** $p \leq .01$. *** $p \leq .001$.

Table 7
Mixed-Effects Regressions Predicting Performance Among Adults Age 40 + on z Scores of Fluid Composite by Education Level With Community Residence, Matriline, and Patriline as Random Effects

Variable	Education			
	<2 y (n = 229)		2+ y (n = 117)	
	B	SE	B	SE
Intercept	.222	.190	.786**	.280
Age	-.020***	.003	-.018***	.005
Male	.299***	.065	.340***	.080
Spanish fluency	.140**	.030	-.029	.042
Variance between communities	.233	.054	.348	.075
Variance within communities	.424	.025	.384	.029

Note. Sample comprised all individuals aged 40+, broken into two levels of educational attainment.

* $p < .05$. ** $p < .01$. *** $p < .001$.

ing that there is no significant difference in rates of decline for those with minimal or moderate schooling. A positive effect of Spanish fluency on effortful processing composite performance is only observed among individuals with less than 2 years of schooling (see Table 7).

Community Differences, Schooling, and Cognitive Performance

In all models, substantial variance in performance was captured by the random effect for community ID. Communities vary in the length of time schools have existed, in the quality of schools (e.g., building construction, classroom materials), and in the quality of teachers. To explore variable relationships between educational attainment in different villages, we grouped village schooling level into three categories—low (with no or relatively recent schools appearing in the past decade), moderate (schools have existed for about two decades), and high (schools have existed for longer than two decades)—and interacted this variable with education. We also consider quadratic schooling terms to explore potential nonlinear relationships between schooling and cognitive performance. Controlling for age, age², and Spanish fluency, we find that the effects of grade on effortful processing composite performance are greatest among those with lower levels of schooling and diminish among those at higher educational levels (significant negative quadratic term), especially among women (Table 8, Models 2 and 3; Figure 4). The effects of schooling, however, vary considerably depending on village residence. Coming from a village with low school quality is associated with 0.4–0.5 lower z scores in performance, on average, and the increase in performance with grade level is smaller in these villages (significant interaction terms between grade and village school level). Similar effects are found when examining each cognitive task separately, but interactions of village schooling history and grade are significant only for visual scan and verbal recalls (see the online supplemental materials Table S1). Schooling does not bear any nonlinear relationships with semantic fluency (Tables 8, S1). Yet more remote villages with the least history of schooling show roughly 0.4 z score units of *greater* semantic fluency.

Discussion

Consistent with many studies documenting distinct age patterns of cognitive abilities (Craik & Bialystok, 2006; Hedden & Gabrieli, 2004; McArdle et al., 2002; Schaie, 2005; Wilson, Beckett, Bennett, Albert, & Evans, 1999), we find that effortful cognitive performance spanning working memory, attention, and psychomotor speed domains peaked in early adulthood, and thereafter performance was lower than in tasks oriented around semantic fluency (Figures 1, 2). The present study is the first to replicate this general cognitive aging profile in a traditional subsistence population with low levels of schooling. We find ages of peak performance in early mid-adulthood and greater age-related differences in performance on effortful processing tasks tapping working memory, short- and long-term verbal declarative memory, visual search, and spatial memory (see Table 5). For short- and long-term verbal memory, declines manifest at an average recall of 4.1% and 3.7% fewer words per decade after age of peak performance, respectively. These age-related differences, although modest, are consistent with other studies in industrialized populations indicating earlier onset of decline in abilities related to cognitive processing and memory in healthy adult samples (Baltes & Lindenberger, 1997; Germine, Duchaine, & Nakayama, 2011; Halberda, Ly, Wilmer, Naiman, & Germine, 2012; Hartshorne & Germine, 2015; Murre, Janssen, Rouw, & Meeter, 2013). For example, a recent study of cognitive performance in the United Kingdom showed 10-year cross-sectional declines at ages 45–49 ranging from –2.9% to –3.6% in men and –6.5% to –11.4% in women (Singh-Manoux et al., 2012, Table 2); cross-sectional rates of decline among age-matched Tsimane in analogous tasks are –4.6% in men (ranging from –0.1% to –9.1%) and –4.5% in women (ranging from –1.9% to –8.8%).

Overall, we find no significant attenuating effect of relatively low levels of schooling on age-related differences in cognitive performance in later adulthood, consistent with the passive reserve model. In our subsample of adults aged 40+, those with greater schooling exhibited similar age-related differences in performance as their less-schooled counterparts. This finding supports recent longitudinal studies that failed to document the presence of active reserve among Western adults with higher levels of education than observed here (Alley et al., 2007; Karlamangla et al., 2009; Tucker-Drob et al., 2009; Van Dijk et al., 2008; Zahodne et al., 2011) and is also consistent with studies suggesting that, at least for some cognitive abilities, lower performance at late age may represent reductions in an individual's ability to sustain investment in metabolically expensive faculties in the face of persistent challenges (Minoshima et al., 1997; Trollor et al., 2005). Instead, we find significant positive main effects of schooling on cognitive performance over much of the life course, consistent with passive models positing improved cerebral and neural reserves among those with greater schooling (Stern, 2002). Further, these effects are greater in villages with a longer history of schooling, where teachers are more experienced and schools are generally of higher quality. For semantic fluency, schooling and Spanish fluency were weakly associated with greater performance. However, only for semantic fluency was performance *higher* in remote villages that only recently obtained schools. We suspect this is because there is more active hunting and fishing in these more remote

Table 8

Schooling Effects as a Function of Village History and Quality of Schooling (Captured by the Variable “Village School Level”)
($n = 844$)

Variable	Effortful processing tasks composite			Category fluency composite		
	Model 1 estimate	Model 2 estimate	Model 3 estimate	Model 1 estimate	Model 2 estimate	Model 3 estimate
Intercept	-.372***	-.563***	-.599***	-1.839***	-1.830***	-1.843***
Age	.017***	.020***	.020***	.071***	.071***	.071***
Age ²	-.000***	-.000***	-.000***	-.001***	-.001***	-.001***
Sex	.269***	.271***	.355***	.444***	.444***	.476***
Grade	.060***	.125***	.156***	.025 [†]	.011	.026
Grade ²		-.006***	-.008***		.001	-.000
Spanish	.084***	.154***	.151***	.034	.058	.058
Spanish ²		-.020	-.019 [†]		-.005	-.005
Sex × Grade			-.064*			-.031
Sex × Grade ²			.006*			.003
Village education level						
Low vs. high	-.495***	-.432***	-.438***	.416**	.407**	.404**
Moderate vs. high	-.072	-.043	-.052	.195	.191	.187
Grade × Village School Level						
Low vs. high	-.035	-.049*	-.049*	-.025	-.022	-.022
Moderate vs. high	-.050**	-.052**	-.049**	.052 [†]	.053 [†]	.055 [†]

Note. Models include random-effect terms for community, matriline, and patriline.

[†] $p \leq .10$. * $p \leq .05$. ** $p \leq .01$. *** $p \leq .001$.

villages (Gurven, Kaplan, & Gutierrez, 2006) and so greater firsthand and secondhand experience with a larger diversity of animals and fish.

We also show that schooling is associated with greater performance at earliest ages in cognitive skills such as working memory, spatial memory, and short- and long-term verbal recall, particularly throughout adolescence and early adulthood (Figures 3, S4). Because these cognitive skills are not directly taught in school, these results may be due, in part, to the reinforcing effects of

noncognitive skills that are associated with increased exposure to schooling, such as improved attentional control, increases in self-regulatory abilities, and benefits to executive functioning (Blair & Raver, 2014; Komaraju et al., 2013). In particular, literate individuals performed significantly better on the visual scan task as they tended to track the page from left to right in a systematic pattern, whereas nonliterate participants did not follow any organized routine. It is possible that Tsimane adolescents and young adults who have accumulated more experience in the classroom may be better equipped to succeed on tests of cognitive ability in part because of greater motivation to perform, sustained attention to focus on each cognitive task in the face of distractions, and expectations generated from formal teacher–pupil interactions (Eklöf, 2010). Yet despite the limited range of schooling among Tsimane, we see dose-dependent improvements in performance across levels of schooling (Figures 3, 4, S4), suggesting that there are additional positive effects of schooling on effortful processing performance beyond the cultivation of noncognitive supporting skills. These effects were independent of age, Spanish fluency, and village history of schooling.

Why Do Age Profiles of Cognitive Performance Vary by Domain?

Evolutionary perspective on cognitive aging. The genetic architecture underlying cognitive performance has been shaped by a number of evolutionary forces, where roughly 28%–51% of the variance in intelligence is due to the cumulative effect of thousands of minor-acting common genetic variants (Arslan & Penke, 2015). Gene-by-environment dynamics have likely played an important role in shaping the expression of cognitive traits (Penke & Jokela, 2016) and its developmental trajectory (Briley & Tucker-Drob, 2015). Although the evolutionary and behavioral genetics

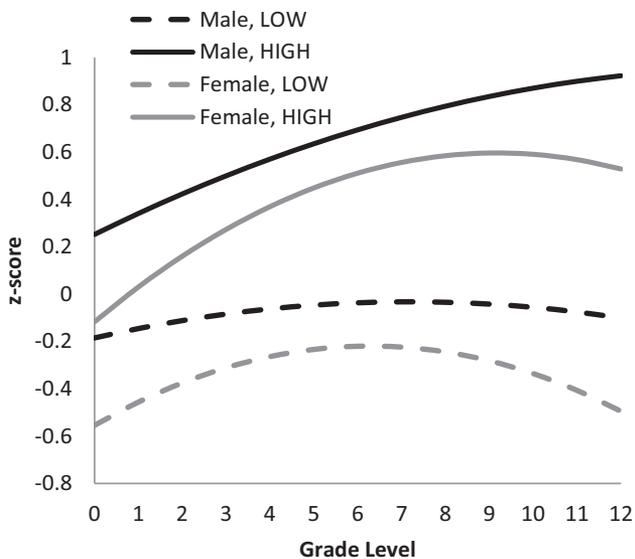


Figure 4. “Effortful processing” cognitive performance, schooling, and village history of schooling (only “low,” “high” shown here). Based on Model 3 in Table 8.

literature has helped address questions about interindividual variability, heritability, stability, and development, little attention has been placed on the functional logic of distinct age trajectories of cognitive traits.

If aging were a general process, somatic and cognitive function should decline at similar rates, in sync with declines in “reproductive value,” as suggested by Hamilton (1966). Common-cause models of aging often highlight the association between declines in cognitive and physical abilities (Christensen, Mackinnon, Korten, & Jorm, 2001; Clouston et al., 2013; Krall, Carlson, Fried, & Xue, 2014). For instance, Rosano et al. (2004) report a robust association between declines in executive control and declines in physical functioning in samples of healthy aging adults. Other work supporting common-cause models focusing on general reasoning and memory tasks indicates that declines in physical abilities such as gait speed and strength are often good predictors of cognitive deficiencies in elderly adults (Atkinson et al., 2007). Our findings are instead consistent with recent work that disaggregates performance on cognitive tasks (e.g., Hartshorne & Germine, 2015). They support the idea that there is no single age at which individuals perform at peak levels on all, or even most, cognitive tasks. Additionally, for many domains of cognitive performance, the functioning of older adults remains particularly strong throughout later life (Cavanaugh & Blanchard-Fields, 2006; Harada et al., 2013; Hartshorne & Germine, 2015), despite general declines in physical capabilities such as strength, muscle mass, and gait speed (Auyeung, Lee, Leung, Kwok, & Woo, 2014; Cooper et al., 2011) and despite increased risk of frailty-induced depression (Stieglitz, Schniter, Von Rueden, Kaplan, & Gurven, 2015). The delayed senescence of some cognitive domains relative to others, as well as the distinction between declines in physical and cognitive performance in later adult life, requires explanation. Although speculative, we offer one general account that might help provide an ultimate-level explanation for differences in age-related decline among cognitive domains.

The evolved human life history is characterized by large and encephalized brains, extended life span, downward intergenerational resource transfers, and midlife surplus production (Kaplan, Hill, Lancaster, & Hurtado, 2000). It has been proposed that these features were coevolved responses to a feeding niche consisting of nutrient-dense resources such as hunted game, extracted roots, and other resources that are difficult to acquire. Peak efficiency in food production among hunter-gatherers and forager-horticulturalists occurs in the fourth and fifth decades of life, well after peak physical capabilities are attained (Gurven & Kaplan, 2006; Gurven et al., 2006; Walker & Hill, 2003). The relatively slow acquisition of foraging and other skills is linked to the development of cognitive abilities, experience, and on-the-job training (Schniter, Gurven, Kaplan, Wilcox, & Hooper, 2015). Acquiring and storing extensive complex ecological knowledge (i.e., crystallized intelligence; Bock 2002b; Reyes-García et al., 2009) is a prerequisite for successful food production. Similarly, substantial subsistence endeavors, such as hunting and stalking prey, as well as careful planning of planting, harvesting, and burning schedules, all require developed executive function and other fluid abilities and the integration of knowledge from past experience. The accumulation and maintenance of a wide range of social relationships (i.e., social capital) also require diverse skills that together impact another domain of delayed production affecting

ego and descendent fitness (Dunbar & Shultz, 2007; Whiten & Byrne, 1997).

Understanding the origins of particular age profiles of cognitive development and senescence requires attention to the skills and fitness-related consequences thereof in the kinds of environments more similar to those of our ancestors. That many cognitive age profiles among Tsimane are similar to those in industrialized populations despite their remoteness and very distinct socioecology suggests that changes in the cognitive landscape throughout life relate in important ways to age-related changes in resource production. In all human populations, older, postreproductive individuals maintain roles as providers and investors in the embodied capital of their descendent kin. This often involves direct or indirect instruction, advising, conflict mediation, storytelling, and information sharing, especially when their own resource productivity is increasingly diminished (Gurven, Stieglitz, Hooper, Gomes, & Kaplan, 2012; Kline, 2014; Schniter et al., 2015; Stieglitz, Gurven, Kaplan, & Hooper, 2013).

If natural selection shaped cognition to promote the transition from knowledge acquisition (i.e., investment in a wide range of fluid and crystallized capabilities) in early life to production and investment in descendent kin (i.e., crystallized capabilities) throughout adulthood, then some effortful cognitive domains might be subject to degradation at a more rapid rate, whereas others preserved well into late age, depending on their relative contributions to fitness. If informational transfer provided dependable and measurable benefits to descendent kin above and beyond the costs associated with decreased productivity, selection should have retained those cognitive skills that are implicated directly in knowledge retention, memory retrieval, and information transmission, despite declining physical abilities and more fluid cognitive abilities. Those retained would include category fluency and other domains of crystallized abilities. Recent genetic evidence seems to support evolutionary scenarios where older adults are equipped to impact descendent kin. Schwarz et al. (2016) provide evidence of the relatively rapid proliferation of protective alleles unique to the human lineage that help maintain cognitive function at late ages, such as the immunoregulatory receptor CD33, ApoE, and PON1.

Several studies are consistent with our “trade-off” perspective to understanding cognitive aging. Reser (2009) reports that metabolic activity in the hippocampus and neocortex becomes increasingly more costly with age. Normal aging has been consistently associated with atrophy in general cerebral capacity, driven largely by reductions in both gray and white matter (Lemaitre et al., 2012; Pakkenberg et al., 2003). These effects are largely present in the prefrontal regions (Allen, Bruss, Brown, & Damasio, 2005; Tisserand & Jolles, 2003), which are implicated heavily in speed of mental processing, working memory, and overall executive control. The large metabolic cost of simultaneously preserving multiple fluid domains likely places a significant constraint on metabolic investment in older adults. As productivity declines in middle adulthood, it may be less beneficial to sustain high investment across all brain regions; young adults may be more inclined to pay such high-cost activation of expensive brain networks because they stand to benefit greatly over a long time period from the learning that accompanies it. Upon reaching adulthood, humans living in environments characteristic of

ancestral populations would have already sampled diverse aspects of the local ecology and internalized much of the social and ecological information that they need to become efficient producers and social contributors. Once an individual reaches mid- to late adulthood, the maintenance costs associated with many effortful processing capabilities may surpass their expected marginal returns to increased productivity and/or fitness. The consistent trade-off between investment in more fluid abilities during early adulthood and the reliance on crystallized information storage in later life may represent a functionally efficient compromise. The resulting age trajectories of cognitive skills affect production in predictable ways. For example, in modern industrialized societies, peak ages in productivity for jobs that reward experience, managerial ability, and other crystallized skills are relatively late in adulthood, despite declines in fluid abilities (Skirbekk, 2004, 2008).

Limitations and Future Directions

The cross-sectional design prevents assessment of individual life course trajectories. Cross-sectional data can also be problematic when there are cohort effects, although longitudinal data often suffer from bias due to retest practice effects artificially inflating cognitive change over time (Rabbitt, Diggle, Smith, Holland, & McInnes, 2001). Recent evaluations confirm that cross-sectional studies with minimal cohort differences may offer more valid inferences about age-related changes than longitudinal studies biased by retest effects (Salthouse, 2009). Indeed, retesting among Tsimane has been shown to lead to improvement in at least one cognitive task (Ravens colored progressive matrices), especially among more educated individuals (Davis, 2014). Thus, our results concerning differential rates of cognitive decline from our one-shot cross-sectional design are at least consistent with those in cross-sectional studies in other human populations and in nonhuman populations where cohort differences are nonexistent (Herdon, Moss, Rosene, & Killiany, 1997; Salthouse, 2009). Here we argue that schooling plays an important role in the acquisition of cognitive skill at young ages; if older adults are less educated than their younger counterparts due to more limited access to educational opportunities, then naturally this raises concerns about the availability of formal schooling across communities and across ages. In the current sample, however, there is considerable community-level variability in access to schools and the duration of their establishment, and so schooling is not heavily confounded with the age cohort. Nevertheless, future research focused on documenting age-related differences in cognition in similar populations should take into consideration the potential reinforcing effects of education on performance, particularly among adolescents and young adults. It is also possible that cognitive buffering might require more schooling than the low levels observed in the Tsimane population.

Despite these limitations, the current results provide important information that will help improve our understanding of normative changes in cognition across the life course. Our results support existing patterns of cognitive aging across the life cycle in samples of healthy individuals and extend existing research by documenting the effects of educational attainment on both the acquisition of cognitive skills and the rate of cognitive declines with age. To our knowledge, the current study is among the first to replicate age-

related patterns of cognitive performance within a small-scale human society characterized by limited exposure to formalized schooling and is one of a few attempts to provide an evolutionary framework for the distinct age profiles of different cognitive abilities.

References

- Allen, J. S., Bruss, J., Brown, C. K., & Damasio, H. (2005). Normal neuroanatomical variation due to age: The major lobes and a parcellation of the temporal region. *Neurobiology of Aging*, *26*, 1245–1260. <http://dx.doi.org/10.1016/j.neurobiolaging.2005.05.023>
- Alley, D., Suthers, K., & Crimmins, E. (2007). Education and cognitive decline in older Americans: Results from the AHEAD sample. *Research on Aging*, *29*, 73–94. <http://dx.doi.org/10.1177/0164027506294245>
- Anstey, K., & Christensen, H. (2000). Education, activity, health, blood pressure and apolipoprotein E as predictors of cognitive change in old age: A review. *Gerontology*, *46*, 163–177. <http://dx.doi.org/10.1159/000022153>
- Ardila, A., Ostrosky-Solis, F., & Bernal, B. (2006). Cognitive testing toward the future: The example of Semantic Verbal Fluency (ANI-MALS). *International Journal of Psychology*, *41*, 324–332. <http://dx.doi.org/10.1080/00207590500345542>
- Ardila, A., Ostrosky-Solis, F., Rosselli, M., & Gómez, C. (2000). Age-related cognitive decline during normal aging: The complex effect of education. *Archives of Clinical Neuropsychology*, *15*, 495–513. [http://dx.doi.org/10.1016/S0887-6177\(99\)00040-2](http://dx.doi.org/10.1016/S0887-6177(99)00040-2)
- Ardila, A., & Rosselli, M. (2007). Illiterates and cognition: The impact of education. In B. Uzzell, M. Ponton, & A. Ardila (Eds.), *International handbook of cross-cultural neuropsychology* (pp. 181–198). Mahwah, NJ: Lawrence Erlbaum Associates.
- Arslan, R. C., & Penke, L. (2015). Zeroing in on the Genetics of Intelligence. *Journal of Intelligence*, *3*, 41–45. <http://dx.doi.org/10.3390/jintelligence3020041>
- Atkinson, H. H., Rosano, C., Simonsick, E. M., Williamson, J. D., Davis, C., Ambrosius, W. T., . . . the Health ABC study. (2007). Cognitive function, gait speed decline, and comorbidities: The health, aging and body composition study. *The Journals of Gerontology: Series A: Biological Sciences and Medical Sciences*, *62*, 844–850. <http://dx.doi.org/10.1093/gerona/62.8.844>
- Auyeung, T. W., Lee, S. W. J., Leung, J., Kwok, T., & Woo, J. (2014). Age-associated decline of muscle mass, grip strength and gait speed: A 4-year longitudinal study of 3018 community-dwelling older Chinese. *Geriatrics & Gerontology International*, *14*(Suppl. 1), 76–84. <http://dx.doi.org/10.1111/ggi.12213>
- Baker, D. P., Eslinger, P. J., Benavides, M., Peters, E., Dieckmann, N. F., & Leon, J. (2015). The cognitive impact of the education revolution: A possible cause of the Flynn Effect on population IQ. *Intelligence*, *49*, 144–158. <http://dx.doi.org/10.1016/j.intell.2015.01.003>
- Baltes, P. B., & Lindenberger, U. (1997). Emergence of a powerful connection between sensory and cognitive functions across the adult life span: A new window to the study of cognitive aging? *Psychology and Aging*, *12*, 12–21. <http://dx.doi.org/10.1037/0882-7974.12.1.12>
- Barulli, D., & Stern, Y. (2013). Efficiency, capacity, compensation, maintenance, plasticity: Emerging concepts in cognitive reserve. *Trends in Cognitive Sciences*, *17*, 502–509. <http://dx.doi.org/10.1016/j.tics.2013.08.012>
- Blair, C., & Raver, C. C. (2014). Closing the achievement gap through modification of neurocognitive and neuroendocrine function: Results from a cluster randomized controlled trial of an innovative approach to the education of children in kindergarten. *PLoS ONE*, *9*, e112393. <http://dx.doi.org/10.1371/journal.pone.0112393>
- Bock, J. (2002a). Evolutionary demography and intrahousehold time allocation: School attendance and child labor among the Okavango Delta

- Peoples of Botswana. *American Journal of Human Biology*, 14, 206–221. <http://dx.doi.org/10.1002/ajhb.10040>
- Bock, J. (2002b). Learning, life history, and productivity: Children's lives in the Okavango Delta, Botswana. *Human Nature*, 13, 161–197. <http://dx.doi.org/10.1007/s12110-002-1007-4>
- Briley, D. A., & Tucker-Drob, E. M. (2015). Comparing the developmental genetics of cognition and personality over the life span. *Journal of Personality*. Advance online publication. <http://dx.doi.org/10.1111/jopy.12186>
- Brinch, C. N., & Galloway, T. A. (2012). Schooling in adolescence raises IQ scores. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 425–430. <http://dx.doi.org/10.1073/pnas.1106077109>
- Bugg, J. M., Zook, N. A., DeLosh, E. L., Davalos, D. B., & Davis, H. P. (2006). Age differences in fluid intelligence: Contributions of general slowing and frontal decline. *Brain and Cognition*, 62, 9–16. <http://dx.doi.org/10.1016/j.bandc.2006.02.006>
- Bull, R., & Scerif, G. (2001). Executive functioning as a predictor of children's mathematics ability: Inhibition, switching, and working memory. *Developmental Neuropsychology*, 19, 273–293. http://dx.doi.org/10.1207/S15326942DN1903_3
- Butler, S. M., Ashford, J. W., & Snowdon, D. A. (1996). Age, education, and changes in the Mini-Mental State Exam scores of older women: Findings from the Nun Study. *Journal of the American Geriatrics Society*, 44, 675–681. <http://dx.doi.org/10.1111/j.1532-5415.1996.tb01831.x>
- Carlsson, M., Dahl, G. B., Öckert, B., & Rooth, D.-O. (2015). The effect of schooling on cognitive skills. *The Review of Economics and Statistics*, 97, 533–547. http://dx.doi.org/10.1162/REST_a_00501
- Carroll, J. B. (1993). *Human cognitive abilities: A survey of factor-analytic studies*. New York, NY: Cambridge University Press. <http://dx.doi.org/10.1017/CBO9780511571312>
- Cattell, R. B. (1971). *Abilities: Their structure, growth, and action*. Oxford, England: Houghton Mifflin.
- Cavanaugh, J. C., & Blanchard-Fields, F. (2006). *Adult development and aging*. Belmont, CA: Thomson Learning.
- Ceci, S. J. (1991). How much does schooling influence general intelligence and its cognitive components? A reassessment of the evidence. *Developmental Psychology*, 27, 703–722. <http://dx.doi.org/10.1037/0012-1649.27.5.703>
- Cheng, H., & Furnham, A. (2012). Childhood cognitive ability, education, and personality traits predict attainment in adult occupational prestige over 17 years. *Journal of Vocational Behavior*, 81, 218–226. <http://dx.doi.org/10.1016/j.jvb.2012.07.005>
- Christensen, H., Mackinnon, A. J., Korten, A., & Jorm, A. F. (2001). The “common cause hypothesis” of cognitive aging: Evidence for not only a common factor but also specific associations of age with vision and grip strength in a cross-sectional analysis. *Psychology and Aging*, 16, 588–599. <http://dx.doi.org/10.1037/0882-7974.16.4.588>
- Clouston, S. A. P., Brewster, P., Kuh, D., Richards, M., Cooper, R., Hardy, R., . . . Hofer, S. M. (2013). The dynamic relationship between physical function and cognition in longitudinal aging cohorts. *Epidemiologic Reviews*, 35, 33–50. <http://dx.doi.org/10.1093/epirev/mxs004>
- Cooper, R., Hardy, R., Aihie Sayer, A., Ben-Shlomo, Y., Birnie, K., Cooper, C., . . . the HALCYON Study Team. (2011). Age and gender differences in physical capability levels from mid-life onwards: The harmonisation and meta-analysis of data from eight UK cohort studies. *PLoS ONE*, 6, e27899. <http://dx.doi.org/10.1371/journal.pone.0027899>
- Craik, F. I., & Bialystok, E. (2006). Cognition through the lifespan: Mechanisms of change. *Trends in Cognitive Sciences*, 10, 131–138. <http://dx.doi.org/10.1016/j.tics.2006.01.007>
- Davis, H. E. (2014). *Variable doctoral exposure and cognitive task performance* (Unpublished doctoral dissertation). University of New Mexico, Albuquerque.
- Deary, I. J., Strand, S., Smith, P., & Fernandes, C. (2007). Intelligence and educational achievement. *Intelligence*, 35, 13–21. <http://dx.doi.org/10.1016/j.intell.2006.02.001>
- Duckworth, A. L., Peterson, C., Matthews, M. D., & Kelly, D. R. (2007). Grit: Perseverance and passion for long-term goals. *Journal of Personality and Social Psychology*, 92, 1087–1101. <http://dx.doi.org/10.1037/0022-3514.92.6.1087>
- Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science*, 317, 1344–1347. <http://dx.doi.org/10.1126/science.1145463>
- Eklöf, H. (2010). Skill and will: Test-taking motivation and assessment quality. *Assessment in Education: Principles, Policy & Practice*, 17, 345–356. <http://dx.doi.org/10.1080/0969594X.2010.516569>
- Ekstrom, R. B., French, J. W., & Harman, H. H. (1976). *Manual for kit of factor-referenced cognitive tests*. Princeton, NJ: Educational Testing Service.
- Farmer, M. E., Kittner, S. J., Rae, D. S., Bartko, J. J., & Regier, D. A. (1995). Education and change in cognitive function. The Epidemiologic Catchment Area Study. *Annals of Epidemiology*, 5, 1–7. [http://dx.doi.org/10.1016/1047-2797\(94\)00047-W](http://dx.doi.org/10.1016/1047-2797(94)00047-W)
- Feinstein, L., & Bynner, J. (2004). The importance of cognitive development in middle childhood for adulthood socioeconomic status, mental health, and problem behavior. *Child Development*, 75, 1329–1339. <http://dx.doi.org/10.1111/j.1467-8624.2004.00743.x>
- Fortenbaugh, F. C., DeGutis, J., Germine, L., Wilmer, J. B., Grosso, M., Russo, K., & Esterman, M. (2015). Sustained attention across the life span in a sample of 10,000: Dissociating ability and strategy. *Psychological Science*, 26, 1497–1510. <http://dx.doi.org/10.1177/0956797615594896>
- Furnham, A., & Cheng, H. (2013). Factors influencing adult earnings: Findings from a nationally representative sample. *The Journal of Socio-Economics*, 44, 120–125. <http://dx.doi.org/10.1016/j.socec.2013.02.008>
- Germine, L. T., Duchaine, B., & Nakayama, K. (2011). Where cognitive development and aging meet: Face learning ability peaks after age 30. *Cognition*, 118, 201–210. <http://dx.doi.org/10.1016/j.cognition.2010.11.002>
- Glosser, G., Wolfe, N., Albert, M. L., Lavine, L., Steele, J. C., Calne, D. B., & Schoenberg, B. S. (1993). Cross-cultural cognitive examination: Validation of a dementia screening instrument for neuroepidemiological research. *Journal of the American Geriatrics Society*, 41, 931–939. <http://dx.doi.org/10.1111/j.1532-5415.1993.tb06758.x>
- Godoy, R., Seyfried, C., Reyes-García, V., Huanca, T., Leonard, W. R., McDade, T., . . . Vadez, V. (2007). Schooling's contribution to social capital: Study from a native Amazonian society in Bolivia. *Comparative Education*, 43, 137–163. <http://dx.doi.org/10.1080/03050060601162677>
- Gurven, M. (2012). Human survival and life history in evolutionary perspective. In J. Mitani, J. Call, P. Kappeler, R. Palombit, & J. B. Silk (Eds.), *The evolution of primate societies* (pp. 293–314). Chicago, IL: University of Chicago Press.
- Gurven, M. D., & Kaplan, H. S. (2006). Determinants of time allocation across the lifespan: A theoretical model and an application to the Machiguenga and Piro of Peru. *Human Nature*, 17, 1–49. <http://dx.doi.org/10.1007/s12110-006-1019-6>
- Gurven, M., Kaplan, H., & Gutierrez, M. (2006). How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span. *Journal of Human Evolution*, 51, 454–470. <http://dx.doi.org/10.1016/j.jhevol.2006.05.003>
- Gurven, M., Kaplan, H., & Supa, A. Z. (2007). Mortality experience of Tsimane Amerindians of Bolivia: Regional variation and temporal trends. *American Journal of Human Biology*, 19, 376–398. <http://dx.doi.org/10.1002/ajhb.20600>
- Gurven, M., Stieglitz, J., Hooper, P. L., Gomes, C., & Kaplan, H. (2012). From the womb to the tomb: The role of transfers in shaping the evolved human life history. *Experimental Gerontology*, 47, 807–813. <http://dx.doi.org/10.1016/j.exger.2012.05.006>

- Halberda, J., Ly, R., Wilmer, J. B., Naiman, D. Q., & Germine, L. (2012). Number sense across the lifespan as revealed by a massive Internet-based sample. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 11116–11120. <http://dx.doi.org/10.1073/pnas.1200196109>
- Hamilton, W. D. (1966). The moulding of senescence by natural selection. *Journal of Theoretical Biology*, *12*, 12–45. [http://dx.doi.org/10.1016/0022-5193\(66\)90184-6](http://dx.doi.org/10.1016/0022-5193(66)90184-6)
- Harada, C. N., Natelson Love, M. C., & Triebel, K. L. (2013). Normal cognitive aging. *Clinics in Geriatric Medicine*, *29*, 737–752. <http://dx.doi.org/10.1016/j.cger.2013.07.002>
- Hartshorne, J. K., & Germine, L. T. (2015). When does cognitive functioning peak? The asynchronous rise and fall of different cognitive abilities across the life span. *Psychological Science*, *26*, 433–443. <http://dx.doi.org/10.1177/0956797614567339>
- Hedden, T., & Gabrieli, J. D. E. (2004). Insights into the ageing mind: A view from cognitive neuroscience. *Nature Reviews Neuroscience*, *5*, 87–96. <http://dx.doi.org/10.1038/nrn1323>
- Hedden, T., Park, D. C., Nisbett, R., Ji, L.-J., Jing, Q., & Jiao, S. (2002). Cultural variation in verbal versus spatial neuropsychological function across the life span. *Neuropsychology*, *16*, 65–73. <http://dx.doi.org/10.1037/0894-4105.16.1.65>
- Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences*, *33*, 61–83. <http://dx.doi.org/10.1017/S0140525X0999152X>
- Herdon, J. G., Moss, M. B., Rosene, D. L., & Killiany, R. J. (1997). Patterns of cognitive decline in aged rhesus monkeys. *Behavioural Brain Research*, *87*, 25–34. [http://dx.doi.org/10.1016/S0166-4328\(96\)02256-5](http://dx.doi.org/10.1016/S0166-4328(96)02256-5)
- Horn, J. L., & Cattell, R. B. (1967). Age differences in fluid and crystallized intelligence. *Acta Psychologica*, *26*, 107–129. [http://dx.doi.org/10.1016/0001-6918\(67\)90011-X](http://dx.doi.org/10.1016/0001-6918(67)90011-X)
- Kaplan, H., Hill, K., Lancaster, J. B., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology*, *9*, 156–185. [http://dx.doi.org/10.1002/1520-6505\(2000\)9:4<156::AID-EVAN5>3.0.CO;2-7](http://dx.doi.org/10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.0.CO;2-7)
- Kaplan, H. S., & Robson, A. J. (2002). The emergence of humans: The coevolution of intelligence and longevity with intergenerational transfers. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 10221–10226. <http://dx.doi.org/10.1073/pnas.152502899>
- Karlamangla, A. S., Miller-Martinez, D., Aneshensel, C. S., Seeman, T. E., Wight, R. G., & Chodosh, J. (2009). Trajectories of cognitive function in late life in the United States: Demographic and socioeconomic predictors. *American Journal of Epidemiology*, *170*, 331–342. <http://dx.doi.org/10.1093/aje/kwp154>
- Kline, M. A. (2014). How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals. *Behavioral and Brain Sciences*, *38*, e31. <http://dx.doi.org/10.1017/S0140525X14000090>
- Komaraju, M., Ramsey, A., & Rinella, V. (2013). Cognitive and non-cognitive predictors of college readiness and performance: Role of academic discipline. *Learning and Individual Differences*, *24*, 103–109. <http://dx.doi.org/10.1016/j.lindif.2012.12.007>
- Krall, J. R., Carlson, M. C., Fried, L. P., & Xue, Q.-L. (2014). Examining the dynamic, bidirectional associations between cognitive and physical functioning in older adults. *American Journal of Epidemiology*, *180*, 838–846. <http://dx.doi.org/10.1093/aje/kwu198>
- Lam, M., Eng, G. K., Rapisarda, A., Subramaniam, M., Kraus, M., Keefe, R. S. E., & Collinson, S. L. (2013). Formulation of the age-education index: Measuring age and education effects in neuropsychological performance. *Psychological Assessment*, *25*, 61–70. <http://dx.doi.org/10.1037/a0030548>
- Le Carret, N., Lafont, S., Letenneur, L., Dartigues, J.-F., Mayo, W., & Fabrigoule, C. (2003). The effect of education on cognitive performances and its implication for the constitution of the cognitive reserve. *Developmental Neuropsychology*, *23*, 317–337. http://dx.doi.org/10.1207/S15326942DN2303_1
- Lee, R. D. (2003). Rethinking the evolutionary theory of aging: Transfers, not births, shape senescence in social species. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 9637–9642. <http://dx.doi.org/10.1073/pnas.1530303100>
- Leibovici, D., Ritchie, K., Ledéser, B., & Touchon, J. (1996). Does education level determine the course of cognitive decline? *Age and Ageing*, *25*, 392–397. <http://dx.doi.org/10.1093/ageing/25.5.392>
- Lemaitre, H., Goldman, A. L., Sambataro, F., Verchinski, B. A., Meyer-Lindenberg, A., Weinberger, D. R., & Mattay, V. S. (2012). Normal age-related brain morphometric changes: Nonuniformity across cortical thickness, surface area and grey matter volume? *Neurobiology of Aging*, *33*, 1–15. <http://dx.doi.org/10.1016/j.neurobiolaging.2010.07.013>
- Lyketsos, C. G., Chen, L.-S., & Anthony, J. C. (1999). Cognitive decline in adulthood: An 11.5-year follow-up of the Baltimore Epidemiologic Catchment Area study. *The American Journal of Psychiatry*, *156*, 58–65. <http://dx.doi.org/10.1176/ajp.156.1.58>
- Martin, M. A., Lassek, W. D., Gaulin, S. J., Evans, R. W., Woo, J. G., Geraghty, S. R., . . . Gurven, M. D. (2012). Fatty acid composition in the mature milk of Bolivian forager-horticulturalists: Controlled comparisons with a US sample. *Maternal and Child Nutrition*, *8*, 404–418. <http://dx.doi.org/10.1111/j.1740-8709.2012.00412.x>
- May, A. (2011). Experience-dependent structural plasticity in the adult human brain. *Trends in Cognitive Sciences*, *15*, 475–482. <http://dx.doi.org/10.1016/j.tics.2011.08.002>
- Maylor, E. A., Vousden, J. I., & Brown, G. D. A. (1999). Adult age differences in short term memory for serial order: Data and a model. *Psychology and Aging*, *14*, 572–594. <http://dx.doi.org/10.1037/0882-7974.14.4.572>
- McAllister, L., Gurven, M., Kaplan, H., & Stieglitz, J. (2012). Why do women have more children than they want? Understanding differences in women's ideal and actual family size in a natural fertility population. *American Journal of Human Biology*, *24*, 786–799. <http://dx.doi.org/10.1002/ajhb.22316>
- McArdle, J. J., Ferrer-Caja, E., Hamagami, F., & Woodcock, R. W. (2002). Comparative longitudinal structural analyses of the growth and decline of multiple intellectual abilities over the life span. *Developmental Psychology*, *38*, 115–142. <http://dx.doi.org/10.1037/0012-1649.38.1.115>
- Mejía-Arango, S., Wong, R., & Michaels-Obregón, A. (2015). Normative and standardized data for cognitive measures in the Mexican Health and Aging Study. *Salud Pública de México*, *57*(Suppl. 1), S90–S96.
- Minoshima, S., Giordani, B., Berent, S., Frey, K. A., Foster, N. L., & Kuhl, D. E. (1997). Metabolic reduction in the posterior cingulate cortex in very early Alzheimer's disease. *Annals of Neurology*, *42*, 85–94. <http://dx.doi.org/10.1002/ana.410420114>
- Murre, J. M. J., Janssen, S. M. J., Rouw, R., & Meeter, M. (2013). The rise and fall of immediate and delayed memory for verbal and visuospatial information from late childhood to late adulthood. *Acta Psychologica*, *142*, 96–107. <http://dx.doi.org/10.1016/j.actpsy.2012.10.005>
- Nyberg, L., Lövdén, M., Riklund, K., Lindenberg, U., & Bäckman, L. (2012). Memory aging and brain maintenance. *Trends in Cognitive Sciences*, *16*, 292–305. <http://dx.doi.org/10.1016/j.tics.2012.04.005>
- Pakkenberg, B., Pelvig, D., Marné, L., Bundgaard, M. J., Gundersen, H. J. G., Nyengaard, J. R., & Regeur, L. (2003). Aging and the human neocortex. *Experimental Gerontology*, *38*, 95–99. [http://dx.doi.org/10.1016/S0531-5565\(02\)00151-1](http://dx.doi.org/10.1016/S0531-5565(02)00151-1)
- Park, D., & Gutches, A. (2006). The cognitive neuroscience of aging and culture. *Current Directions in Psychological Science*, *15*, 105–108. <http://dx.doi.org/10.1111/j.0963-7214.2006.00416.x>

- Park, D. C., Lautenschlager, G., Hedden, T., Davidson, N. S., Smith, A. D., & Smith, P. K. (2002). Models of visuospatial and verbal memory across the adult life span. *Psychology and Aging, 17*, 299–320. <http://dx.doi.org/10.1037/0882-7974.17.2.299>
- Penke, L., & Jokela, M. (2016). The evolutionary genetics of personality revisited. *Current Opinion in Psychology, 7*, 104–109. <http://dx.doi.org/10.1016/j.copsyc.2015.08.021>
- Poletti, M., Emre, M., & Bonuccelli, U. (2011). Mild cognitive impairment and cognitive reserve in Parkinson's disease. *Parkinsonism & Related Disorders, 17*, 579–586. <http://dx.doi.org/10.1016/j.parkreidis.2011.03.013>
- Rabbitt, P., Diggle, P., Smith, D., Holland, F., & McInnes, L. (2001). Identifying and separating the effects of practice and of cognitive ageing during a large longitudinal study of elderly community residents. *Neuropsychologia, 39*, 532–543. [http://dx.doi.org/10.1016/S0028-3932\(00\)00099-3](http://dx.doi.org/10.1016/S0028-3932(00)00099-3)
- Reser, J. E. (2009). Alzheimer's disease and natural cognitive aging may represent adaptive metabolism reduction programs. *Behavioral and Brain Functions, 5*, 13. <http://dx.doi.org/10.1186/1744-9081-5-13>
- Reyes-García, V., Broesch, J., Calvet-Mir, L., Fuentes-Peláez, N., McDade, T. W., Parsa, S., . . . Martínez-Rodríguez, M. R. (2009). Cultural transmission of ethnobotanical knowledge and skills: An empirical analysis from an Amerindian society. *Evolution and Human Behavior, 30*, 274–285. <http://dx.doi.org/10.1016/j.evolhumbehav.2009.02.001>
- Rosano, C., Simonsick, E. M., Harris, T. B., Kritchevsky, S. B., Brach, J., Visser, M., . . . Newman, A. B. (2004). Association between physical and cognitive function in healthy elderly: The health, aging and body composition study. *Neuroepidemiology, 24*, 8–14. <http://dx.doi.org/10.1159/000081043>
- Ruchkin, D. S., Grafman, J., Cameron, K., & Berndt, R. S. (2003). Working memory retention systems: A state of activated long-term memory. *Behavioral and Brain Sciences, 26*, 709–728. <http://dx.doi.org/10.1017/S0140525X03000165>
- Salthouse, T. (2004). What and when of cognitive aging. *Current Directions in Psychological Science, 13*, 140–144. <http://dx.doi.org/10.1111/j.0963-7214.2004.00293.x>
- Salthouse, T. A. (2009). When does age-related cognitive decline begin? *Neurobiology of Aging, 30*, 507–514. <http://dx.doi.org/10.1016/j.neurobiolaging.2008.09.023>
- Salthouse, T. A. (2010). Selective review of cognitive aging. *Journal of the International Neuropsychological Society, 16*, 754–760. <http://dx.doi.org/10.1017/S1355617710000706>
- Satz, P. (1993). Brain reserve capacity on symptom onset after brain injury: A formulation and review of evidence for threshold theory. *Neuropsychology, 7*, 273–295. <http://dx.doi.org/10.1037/0894-4105.7.3.273>
- Schaie, K. W. (1989). Perceptual speed in adulthood: Cross-sectional and longitudinal studies. *Psychology and Aging, 4*, 443–453. <http://dx.doi.org/10.1037/0882-7974.4.4.443>
- Schaie, K. W. (2005). What Can We Learn From Longitudinal Studies of Adult Development? *Research in Human Development, 2*, 133–158. http://dx.doi.org/10.1207/s15427617rhd0203_4
- Schmidt, F. L., & Hunter, J. (2004). General mental ability in the world of work: Occupational attainment and job performance. *Journal of Personality and Social Psychology, 86*, 162–173. <http://dx.doi.org/10.1037/0022-3514.86.1.162>
- Schniter, E., Gurven, M., Kaplan, H. S., Wilcox, N. T., & Hooper, P. L. (2015). Skill ontogeny among Tsimane forager-horticulturalists. *American Journal of Physical Anthropology, 158*, 3–18. <http://dx.doi.org/10.1002/ajpa.22757>
- Schoon, I. (2010). Childhood cognitive ability and adult academic attainment: Evidence from three British cohort studies. *Longitudinal and Life Course Studies, 1*, 241–258. <http://dx.doi.org/10.14301/llcs.v1i3.93>
- Schwarz, F., Springer, S. A., Altheide, T. K., Varki, N. M., Gagneux, P., & Varki, A. (2016). Human-specific derived alleles of CD33 and other genes protect against postreproductive cognitive decline. *Proceedings of the National Academy of Sciences of the United States of America, 113*, 74–79. <http://dx.doi.org/10.1073/pnas.1517951112>
- Singh-Manoux, A., Kivimaki, M., Glymour, M. M., Elbaz, A., Berr, C., Ebmeier, K. P., . . . Dugravot, A. (2012). Timing of onset of cognitive decline: Results from Whitehall II prospective cohort study. *BMJ: British Medical Journal, 344*, d7622. <http://dx.doi.org/10.1136/bmj.d7622>
- Skirbekk, V. (2004). Age and individual productivity: A literature survey. In G. Fiechter (Ed.), *Vienna yearbook of population research* (Vol. 2, pp. 133–154). Vienna, Austria: Austrian Academy of Sciences.
- Skirbekk, V. (2008). Age and productivity potential: A new approach based on ability levels and industry-wide task demand. *Population and Development Review, 34*, 191–207. <http://www.jstor.org/stable/25434764>
- Stern, Y. (2002). What is cognitive reserve? Theory and research application of the reserve concept. *Journal of the International Neuropsychological Society, 8*, 448–460. <http://dx.doi.org/10.1017/S1355617702813248>
- Stieglitz, J., Gurven, M., Kaplan, H., & Hooper, P. L. (2013). Household task delegation among high-fertility forager-horticulturalists of lowland Bolivia. *Current Anthropology, 54*, 232–241. <http://dx.doi.org/10.1086/669708>
- Stieglitz, J., Schniter, E., Von Rueden, C., Kaplan, H., & Gurven, M. (2015). Functional disability and social conflict increase risk of depression in older adulthood among Bolivian forager-farmers. *The Journals of Gerontology: Series B: Psychological Sciences and Social Sciences, 70*, 948–956.
- Tisserand, D. J., & Jolles, J. (2003). On the involvement of prefrontal networks in cognitive ageing. *Cortex, 39*, 1107–1128. [http://dx.doi.org/10.1016/S0010-9452\(08\)70880-3](http://dx.doi.org/10.1016/S0010-9452(08)70880-3)
- Trollor, J. N., Sachdev, P. S., Haindl, W., Brodaty, H., Wen, W., & Walker, B. M. (2005). Regional cerebral blood flow deficits in mild Alzheimer's disease using high resolution single photon emission computerized tomography. *Psychiatry and Clinical Neurosciences, 59*, 280–290. <http://dx.doi.org/10.1111/j.1440-1819.2005.01372.x>
- Trumble, B. C., Stieglitz, J., Thompson, M. E., Fuerstenberg, E., Kaplan, H., & Gurven, M. (2015). Testosterone and male cognitive performance in Tsimane forager-horticulturalists. *American Journal of Human Biology, 27*, 582–586. <http://dx.doi.org/10.1002/ajhb.22665>
- Tucker-Drob, E. M. (2009). Differentiation of cognitive abilities across the life span. *Developmental Psychology, 45*, 1097–1118. <http://dx.doi.org/10.1037/a0015864>
- Tucker-Drob, E. M. (2011). Global and domain-specific changes in cognition throughout adulthood. *Developmental Psychology, 47*, 331–343. <http://dx.doi.org/10.1037/a0021361>
- Tucker-Drob, E. M., Johnson, K. E., & Jones, R. N. (2009). The cognitive reserve hypothesis: A longitudinal examination of age-associated declines in reasoning and processing speed. *Developmental Psychology, 45*, 431–446. <http://dx.doi.org/10.1037/a0014012>
- Tucker-Drob, E. M., & Salthouse, T. A. (2011). Individual differences in cognitive aging. In T. Chamorro-Premuzic, S. von Stumm, & A. Furnham (Eds.), *The Wiley-Blackwell handbook of individual differences* (Vol. 2, p. 242). Hoboken, NJ: Wiley-Blackwell.
- Unsworth, N., Redick, T. S., Heitz, R. P., Broadway, J. M., & Engle, R. W. (2009). Complex working memory span tasks and higher-order cognition: A latent-variable analysis of the relationship between processing and storage. *Memory, 17*, 635–654. <http://dx.doi.org/10.1080/09658210902998047>
- Van Dijk, K. R., Van Gerven, P. W. M., Van Boxtel, M. P. J., Van der Elst, W., & Jolles, J. (2008). No protective effects of education during normal cognitive aging: Results from the 6-year follow-up of the Maastricht Aging Study. *Psychology and Aging, 23*, 119–130. <http://dx.doi.org/10.1037/0882-7974.23.1.119>

- Walker, R., & Hill, K. (2003). Modeling growth and senescence in physical performance among the ache of eastern Paraguay. *American Journal of Human Biology, 15*, 196–208. <http://dx.doi.org/10.1002/ajhb.10135>
- Wang, J., & Kaufman, A. S. (1993). Changes in fluid and crystallized intelligence across the 20- to 90-year age range on the K-Bit. *Journal of Psychoeducational Assessment, 11*, 29–37. <http://dx.doi.org/10.1177/073428299301100104>
- Whiten, A., & Byrne, R. W. (Eds.). (1997). *Machiavellian intelligence II: Extensions and evaluations*. New York, NY: Cambridge University Press. <http://dx.doi.org/10.1017/CBO9780511525636>
- Wilson, R. S., Beckett, L. A., Bennett, D. A., Albert, M. S., & Evans, D. A. (1999). Change in cognitive function in older persons from a community population: Relation to age and Alzheimer disease. *Archives of Neurology, 56*, 1274–1279. <http://dx.doi.org/10.1001/archneur.56.10.1274>
- Zahodne, L. B., Glymour, M. M., Sparks, C., Bontempo, D., Dixon, R. A., MacDonald, S. W., & Manly, J. J. (2011). Education does not slow cognitive decline with aging: 12-year evidence from the victoria longitudinal study. *Journal of the International Neuropsychological Society, 17*, 1039–1046. <http://dx.doi.org/10.1017/S1355617711001044>
- Zimprich, D., & Mascherek, A. (2010). Five views of a secret: Does cognition change during middle adulthood? *European Journal of Ageing, 7*, 135–146. <http://dx.doi.org/10.1007/s10433-010-0161-5>

Received February 13, 2016

Revision received May 24, 2016

Accepted May 25, 2016 ■