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## Research

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# Sex difference in travel is concentrated in adolescence and tracks reproductive interests

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Sexual selection theory suggests that the sex with a higher potential reproductive rate will compete more strongly for access to mates. Stronger intra-sexual competition for mates may explain why males travel more extensively than females in many terrestrial vertebrates. A male-bias in lifetime distance travelled is a purported human universal, although this claim is based primarily on anecdotes. Following sexual maturity, motivation to travel outside the natal territory may vary over the life course for both sexes. Here, we test whether travel behaviour among Tsimane forager–horticulturalists is associated with shifting reproductive priorities across the lifespan. Using structured interviews, we find that sex differences in travel peak during adolescence when men and women are most intensively searching for mates. Among married adults, we find that greater offspring dependency load is associated with reduced travel among women, but not men. Married men are more likely to travel alone than women, but only to the nearest market town and not to other Tsimane villages. We conclude that men’s and women’s travel behaviour reflects differential gains from mate search and parenting across the life course.

## 1. Introduction

Places have positive and negative attributes—attractors and repellents—and are separated by obstacles in the form of simple distance and specific risks. The balance of these valences and costs—which may differ among individuals and life stages—may explain human migration [1]. Here, we apply a similar perspective, viewed through the lens of sexual selection theory, to less permanent displacements: inter-village visits in a tribal Amazonian society. Such travel entails energetic, economic, injury and opportunity costs: individuals cannot defend territory, mate guard or maintain resources like crops while travelling. Given these costs, what motivates men and women to travel? Individuals who live far from kin may be pulled towards areas where family members are concentrated [2]. Valuable resources like salt, game, allies or refuges from disaster or disease may be patchily distributed, thus motivating travel to find and exploit them [3]. Individuals may also travel because there are few eligible mates in their natal community.

### (a) Sexual selection and human travel

Sex is an established predictor of animal travel across diverse taxa. According to sexual selection theory, the sex with the higher potential reproductive rate is expected to compete more strongly for mates [4]; males generally have higher potential reproductive rates than females in polygynous but not monogamous mating systems. Thus, in polygynous systems, males should be more willing to pay the costs of mate search, especially during periods of pair formation, because they benefit more than females from exposure to multiple mates. In line with this expectation, sex differences in home range are characteristic of polygynous but not monogamous voles [5]. In polygynous voles, the sex difference in home range is limited to reproductive individuals and to the mating season [5]. Studies of other rodents, carnivores and non-human primates are consistent with the

hypothesis (for review see [6]). A simulation found that, when ‘male’ robots had higher reproductive rates than ‘female’ robots, the males travelled more [7].

Humans are considered mildly polygynous (cf. [8]) and may manifest the predicted sex difference in travel. Pinker [9] includes greater male lifetime travel in his updated list of Brown’s human universals [10], yet most evidence for this purported human universal relies on anecdotal reports rather than systematic travel data. Such reports from hunter–gatherers, foragers and horticulturalists suggest a male-biased sex difference in travel (for review, see table 2 in [11]). In industrialized nations, women travel shorter distances daily than do men (e.g. [12]), although women’s travel does appear to be increasing (e.g. [13]) and potentially surpasses men’s in a few domains (e.g. [14]).

Two systematic studies have tested the hypothesis that male travel exceeds female travel throughout the lifespan. In a study of self-reported exploration ranges (defined as mean distance travelled) among Aka pygmies of the Central African Republic, Hewlett *et al.* [15] found a consistent male bias among unmarried adolescents, younger married adults with co-resident children and older married adults, although the sex difference was only significant for younger married adults [11]. However, sample size was very small and self-reports reflect lifetime travel, rather than specific life stages; the sex difference among young adults could result from travel either before or after marriage. Hewlett *et al.* [15] also calculated ‘half-ranges’ (median distance to non-natal communities visited at least once) for two groups of differentially acculturated Aka. The more acculturated group had high population densities, probably yielding higher encounter rates with potential mates. Consistent with this view, men travelled farther than women only in the less acculturated group [15]. In the other study, self-reported ‘home ranges’ from interviews and daily diaries are larger among Québécois men than women [16]. Again, due to insufficient data on the timing of travel across the lifespan, the extent to which the sex difference is due to mate search or other factors is unclear. While these two studies capture ends of the human ecological continuum—from foragers to post-industrialists—and agree that men often travel farther than women, a more precise evaluation of the sexual selection perspective on human travel is needed.

## 2. Hypotheses

Here, we test four hypotheses about the travel-motivating effects of reproductive priorities among semi-sedentary Tsimane forager–horticulturalists. We focus on inter-village travel because it augments one’s potential mate pool. Our first hypothesis links to the existing literature by testing whether there is an overall sex difference in lifetime travel. Hence, *H1: Male lifetime travel exceeds female lifetime travel.*

Male travel may exceed female travel for a variety of reasons. Hunting mobile prey—a predominantly male activity—requires more extensive habitat knowledge and travel than the subsistence activities of women, which are largely focused on immobile plant resources. Wage-earning opportunities outside the natal community are differentially available to men. Men may conduct most business transactions, including travel to market crops or crafts. Given such possibilities, the remaining three hypotheses aim to more directly test sexual selection perspectives on human travel.

To address limitations of prior studies, we test whether the sex difference in travel peaks during the period of mate search. Thus, *H2: The male–female difference in travel will peak during adolescence.*

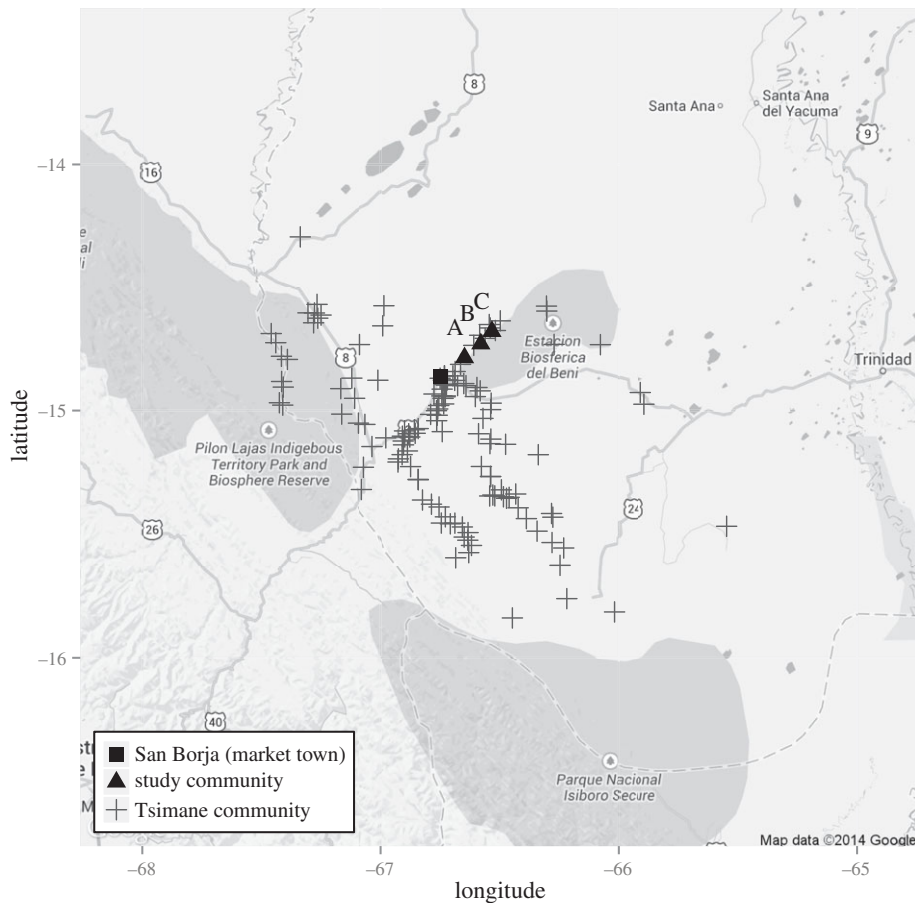
Shifting reproductive priorities due to marriage and child-rearing affect the opportunity costs of travel and mating effort. In the early years of marriage, individuals may continue to pursue other mates—as short-term mates or as additional long-term partners. Once individuals begin reproducing, their optimal balance of mating and parenting effort may shift; Tsimane men are less likely to have an affair as the number of dependent offspring increases [17]. We therefore predict a negative association between number of dependent offspring and travel. This relationship may differ for the two sexes because the women’s parental investment, which includes gestation and lactation, is less substitutable than men’s parental investment. Thus, *H3: Individuals with fewer dependent offspring will travel more per year than individuals with more dependent offspring.*

Husbands and wives may travel together or separately, and mating effort may be more feasible for the solo traveller. But the risk/reward ratio of travelling without one’s spouse may also differ by sex. Women may experience greater danger when unaccompanied by their spouse, and men may reap more mating advantages when travelling without their spouse. This may be particularly true for visits to local market towns where both risks and short-term mating opportunities may be concentrated. Thus, *H4: Men will be more likely than women to travel without their spouse, particularly to large market towns.*

## 3. Material and methods

This study examines travel by Tsimane, indigenous forager–horticulturalists living in the Beni Department, Bolivia, along the Maniqui River system. Tsimane reside in small villages (mean population  $\pm$  s.d. =  $124 \pm 98$ ) comprising extended family groups. The Tsimane are semi-sedentary, travelling frequently to fish and hunt, visit kin, socialize, gather fruits, and buy and sell goods [18]. The Tsimane notion of *sóbaqui* (‘to visit’) reflects a cultural tradition of social visitation within and among communities, often accompanied by communal drinking of *shocdye*, fermented manioc brew [18]. Tsimane post-marital residence patterns vary, although couples often live near the wife’s natal kin for the first few years of marriage [19]. Subsequently, the couple and their children may move to a community near the husband’s family. Although polygyny is not restricted, most Tsimane marriages are monogamous (90–95% [19]). Divorce is relatively uncommon, with less than 20% of marriages ending in divorce [20]. The variance in completed fertility is 57% higher among men than women [21], suggesting stronger sexual selection and mating competition among men [22,23]. Although Tsimane retain much of their traditional culture, economic and cultural change is occurring, allowing us to investigate the relationship between acculturation and travel [15].

The first author and three experienced Tsimane translators interviewed 53 adult men and 52 adult women from three communities (labelled A, B and C) from 2010 to 2011. Using maps, pilot interviews and past experience, we created a comprehensive list of 149 travel destinations, including all Tsimane communities (past and present) and any other settlements that Tsimane were known to have visited. Men sometimes work for wages on non-Tsimane ranches, whereas women rarely do. All analyses for H1–H3 are limited to visits to Tsimane communities, which are more likely to be socially and reproductively relevant. This restriction is conservative in relation to our hypotheses because men’s wage-labour ranch visits generate cash that could be



**Figure 1.** Map of Tsimane territory.

expended as mating effort. Visits to Tsimane communities and the local market town (San Borja) are included in analyses for H4. Each community was previously identified and located using GPS coordinates. Figure 1 is a map of the study area showing the local market town, the three study communities and all Tsimane communities visited by study participants.

To accommodate H2, the lives of participants were divided into three mutually exclusive periods: childhood (birth until puberty), adolescence (puberty to first marriage) and first marriage (from start to end of marriage or to the present if that first marriage was ongoing). We used two sex-specific Tsimane words to describe adolescents that have reached puberty but are still unmarried: *nanasi'* for females and *nanaty'i'* for males. All participants were adults and the interviews were retrospective, asking about travel during these three life periods. Our decision not to include adolescents was based on their frequent absence and a concern that those who were present might not be representative.

For each of the three time periods, individuals were asked where they had lived and whether they had visited each of the listed communities. For a subset of interviews ( $n = 44$ ), we also asked whether they had visited relatives, attended a party, drunk *shocdye'* (fermented manioc), fished and hunted (men only) during their visit to the particular community.

We also asked participants about travel during the previous month. For this period only, individuals reported the number of times they had visited each community.

We estimated period lengths for childhood, adolescence and first marriage (electronic supplementary material, §1). The average age at first marriage was 18.61 for men and 17.31 for women. Based on our specification, the adolescent period was shorter for men than it was for women ( $18.61 - 15 = 3.61$  and  $17.31 - 13 = 4.31$  years, respectively).

Censuses obtained from the Tsimane Health and Life History Project were used to determine the number of dependants less

than 5 years at the time of the interview. The number of dependants in each household was recoded to 0, 1 or 2+ dependants. To assess dependency, offspring age was calculated using the end date of each field season.

### (a) Exclusion criteria

Owing to some recall problems among older individuals, and hence possible bias, we excluded individuals older than 45. Age estimation methods are described elsewhere [24]. For a summary of exclusion criteria and resulting subsample sizes for each hypothesis, see the electronic supplementary material, table S1.

### (b) Data analyses

Although individuals may not report every reason for a visit, we conducted descriptive analyses,  $\chi^2$  and  $t$ -tests to understand why Tsimane visit other communities. For this analysis only, visits during childhood, adolescence and marriage were pooled; these conclusions therefore address reasons for travel throughout the lifespan.

To test H1 and facilitate comparison with other studies, we adopted travel measures commonly used in the literatures on human and non-human mobility (electronic supplementary material, §2). For comparison with the human literature, we calculated each participant's whole-life half-range and exploration range [11,15]. For comparison with the animal behaviour literature, we employed the two most common methods of home range estimation: the minimum convex polygon (MCP) [25] and the kernel utilization distribution (KUD) [26]. Thus, we test for whole-life sex differences via four separate independent-samples  $t$ -tests, one for each range-size measure. Log or square-root transformations were applied to approximate normality, allowing parametric tests.

**Table 1.** Percentage of visits in which activity was reported, tabulated by sex. Participants could report multiple activities per community visited, so percentages do not sum to 100%. Significant differences ( $p < 0.05$ ) indicated in *italic*.

|       | <i>n</i> | drinking <i>shocdye'</i> (%) | visiting a relative (%) | attending a party (%) | hunting (%) | fishing (%) |
|-------|----------|------------------------------|-------------------------|-----------------------|-------------|-------------|
| women | 16       | 49.8                         | <i>67.6</i>             | 47.8                  | —           | 27.9        |
| men   | 21       | 57.9                         | 43.6                    | 46.6                  | 28.4        | 36.3        |

Two measures were used to test H2. For each visit, we calculated the straight-line distance (km) between the home and the visited community (electronic supplementary material, §3), and then summed these distances by life period. In addition, we also tallied the number of communities visited by life period, a calculation that does not rely on the median-distance correction for unidentifiable home communities. We divided both the distance and tally measures by the individual-specific duration of the relevant period to yield the sum distance travelled, or number of communities visited, per period-year. Our travel measures are underestimates because each 'visit' may represent multiple visits to a given community during that period (information about the frequency of visits to each community was not elicited, except for the previous-month data). Both the distance and tally measures are highly skewed, so both were log-transformed before use in the statistical models.

To test H2, a linear model was fitted for each of these two outcome measures. Each model included main effects for sex (male = 1, female = 0), time period (childhood, adolescence and marriage), age, interview community (A, B and C), and all two-way interaction terms for sex, time period and age. H2 predicts a significant two-way interaction between sex and period, with male travel most exceeding female travel during adolescence. Participant age is included in the models as a control for possible age-related differences in travel recall. Interview community is included because communities vary in population size, distance from the market town and levels of acculturation.

To test H3–H4, frequency of visits to each community in the previous month was elicited from detailed interviews. Using frequency counts and intercommunity distances (above), we computed the total distance travelled during the prior month. Because these two hypotheses examine the effects of dependants and compare spouses, unmarried individuals ( $n = 3$ ) were excluded. To test H3, a linear model was fitted for each sex using the number of dependent children and current age to predict total distance travelled in the last month. Current age is included as an alternative explanation: older individuals may travel less, regardless of their number of dependent children.

The 43 married individuals reporting on travel during the prior month included 13 couples. Thus, for these 26 individuals, any visit *not* mentioned in the separate interviews of both spouses was assumed to be travel without their spouse. (Visits during the last month that were mentioned in both interviews were assumed to be travel with the spouse.) To test H4, we calculated a series of directional paired-samples *t*-tests using sex to predict (i) the proportion of monthly visits to Tsimane communities, (ii) the proportion of monthly distance travelled to Tsimane communities and (iii) the number of monthly visits to the local market town of San Borja without their spouse.

All models and analyses were run in R v. 3.0.1 [27].

## 4. Results

### (a) Reported reasons for travel

The most frequently reported visiting behaviours were socializing with relatives and drinking *shocdye'* (table 1). Women were more likely to report the former ( $\chi^2(1, n = 1033) = 42.26$ ,

$p < 0.001$ ) and men were more likely to report the latter ( $\chi^2(1, n = 1033) = 4.67, p < 0.05$ ); men were also more likely to report fishing during a visit ( $\chi^2(1, n = 1033) = 5.42, p < 0.05$ ). There was no sex difference in reported attendance at parties ( $\chi^2(1, N = 1033) = 0.07, p = 0.80$ ).

Average travel distances were not uniform across reported activities: visits that involved hunting or fishing activity were to more distant villages (30.6 and 31.1 km, respectively). Hunting is traditionally a male-only activity. A two-sample *t*-test on log-transformed distances showed a non-significant sex difference in travel distances for visits that included fishing ( $p = 0.18$ ). However, two-sample *t*-tests on log-transformed distances showed that male travel distances are significantly greater for visits that included all other behaviours (drinking *shocdye'*, visiting relatives and attending a party; all  $p < 0.05$ ).

*H1: Male lifetime travel will exceed female lifetime travel.* We find no significant sex difference in whole-life half-range, exploration range or KUD home range (table 2). However, whole-life MCP home ranges are 2.6 times larger for men than for women. Even excluding the 5% of locations that were the farthest away from the centroid of the home range before calculating MCPs, whole-life MCP home ranges are 2.4 times larger for men than for women ( $t_{44} = 2.47, p < 0.05$ ).

*H2: The male–female difference in travel will peak during adolescence.* Our models use sex, period, age and community to predict either sum distance travelled or number of communities visited per period year (log-transformed values in table 3; untransformed values in the text). The grand mean for sum distance travelled per period year was 67.08 km (s.d. = 156.11) and for the number of communities visited per period year was 3.01 (s.d. = 6.69).

There is no main effect of sex on either of these travel measures, supporting most tests of H1: men are not travelling more than women across the whole lifespan. Main effects of community were significant with individuals living in community C travelling the most, followed by individuals in community A.

During adolescence, men's yearly travel exceeds women's, as evidenced by the positive and significant sex-by-adolescence interactions (table 3). Adolescent men travel 5.26 km farther to visit 3.67 more communities per year than adolescent women (for visualization, see electronic supplementary material, §4 and figures S2 and S3). The age-by-marriage interaction was also significant: older adults report travelling less per year of marriage than do younger adults, whereas adults of all ages report similar travel during childhood. Each of the models used to test H2 (one per travel measure) explains approximately 50% of the variance, and the pattern of effects is consistent across the two models. The model of sum distances travelled from table 3 is graphed by age and sex in figure 2.

To test whether our results depend on excluding the 13 individuals missing period length information, we ran parallel linear regression models for each travel measure without

**Table 2.** Results of between-sex, independent-samples *t*-tests for half-range, exploration range, MCP home range and KUD home range. Statistical significance in probability tests is indicated by asterisks. Untransformed standard deviations appear in parentheses beside untransformed means.

|  | women           | men             | <i>t</i> | d.f. |
|--|-----------------|-----------------|----------|------|
| half-range (km) <sup>a</sup>                   | 18.3 (9.6)      | 22.1 (11.3)     | 1.22     | 45   |
| exploration range (km)                         | 20.39 (7.92)    | 25.05 (9.65)    | 1.81     | 45   |
| MCP home range (km <sup>2</sup> ) <sup>a</sup> | 938.8 (1351.4)  | 2447.0 (2861.7) | 2.48*    | 44   |
| KUD home range (km <sup>2</sup> ) <sup>b</sup> | 4476.4 (3603.2) | 5880.3 (3623.6) | 1.51     | 44   |

<sup>a</sup>Measures were log-transformed prior to *t*-tests as indicated.

<sup>b</sup>Measures were square-root-transformed prior to *t*-tests as indicated.

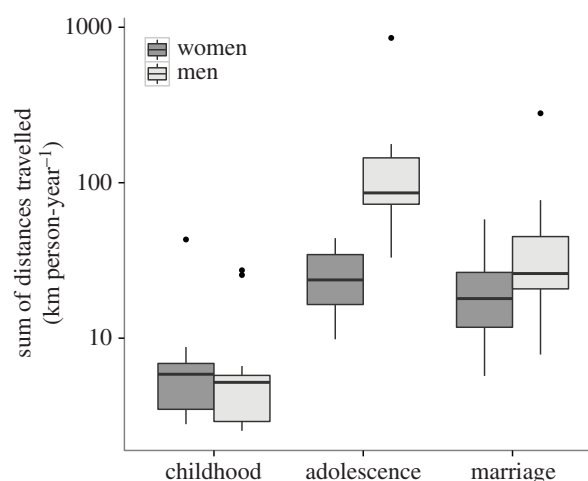
\**p* < 0.05.

**Table 3.** Unstandardized coefficients and summary statistics from linear multiple regression models using sex, time period, age and interview community, and their two-way interactions, to predict log-transformed sum of distance travelled and number of communities visited per period year. Intercept: sex, female; period, childhood; community, community A; age, 0. Statistical significance in probability tests is indicated by asterisks.

|                                | log sum of distances travelled per person-year | log no. communities visited per person-year |
|--------------------------------|--|---|
|                                | $\beta \pm \text{s.e.}$                        | $\beta \pm \text{s.e.}$                     |
| intercept                      | 1.39 ± 0.68*                                   | −0.77 ± 0.50                                |
| sex                            | 0.04 ± 0.75                                    | −0.14 ± 0.55                                |
| adolescence                    | 2.81 ± 0.84**                                  | 2.43 ± 0.61***                              |
| marriage                       | 2.79 ± 0.85**                                  | 2.62 ± 0.62***                              |
| age                            | 0.02 ± 0.03                                    | −0.01 ± 0.02                                |
| community C                    | 1.61 ± 0.47***                                 | 1.23 ± 0.34***                              |
| community B                    | −0.71 ± 0.19***                                | −0.47 ± 0.14***                             |
| sex-by-adolescence             | 1.66 ± 0.46***                                 | 1.30 ± 0.34***                              |
| sex-by-marriage                | 0.82 ± 0.46                                    | 0.47 ± 0.33                                 |
| sex-by-age                     | −0.01 ± 0.03                                   | 0.00 ± 0.02                                 |
| age-by-adolescence             | −0.05 ± 0.03                                   | −0.03 ± 0.02                                |
| age-by-marriage                | −0.06 ± 0.03*                                  | −0.05 ± 0.02*                               |
| <i>F</i>                       | 14.69***                                       | 22.29***                                    |
| d.f.                           | (11, 163)                                      | (11, 164)                                   |
| <i>R</i> <sup>2</sup>          | 0.4978   | 0.5992                                      |
| adjusted <i>R</i> <sup>2</sup> | 0.4639   | 0.5724                                      |

\**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001.

controlling for period length. In this more inclusive analysis, the sex-by-adolescence effect remains significant for both sum distance travelled and number of communities. To account for the repeated nature of the data (electronic supplementary material, §5), we also ran parallel mixed-effects models for each travel measure including the individual as a random effect (electronic supplementary material, table S2)



**Figure 2.** Box plot of predicted sum distances travelled per person-year, by sex and period. Predicted sum distances are based on the regression presented in table 3.

and including both the individual and the community as random effects (electronic supplementary material, table S3). In all cases, the overall pattern of effects remains consistent with the results of the linear regression in table 3.

*H3: Individuals with fewer dependent offspring will travel more per year than individuals with more dependent offspring.* H3 is supported only among women (table 4). Controlling for current age, married men with fewer dependent children did not travel a greater total distance during the last month than those with more dependent offspring ( $\beta = 0.0089$ ,  $p = 0.97$ ). There was no effect of the control variable, age ( $\beta = 0.059$ ,  $p = 0.77$ ). Dependent children and age together did not significantly explain men's monthly travel distance ( $R^2 = 0.00$ ,  $F_{2,23} = 0.04$ ,  $p = 0.96$ ).

By contrast, married women with fewer dependent children travelled a greater total distance in the previous month than those with more dependants ( $\beta = -0.50$ ,  $p < 0.01$ ). There was a significant effect of age ( $\beta = 0.89$ ,  $p < 0.001$ ). Dependent children and age together explain a large proportion of variance in total monthly travel distance for women, ( $R^2 = 0.74$ ,  $F_{2,17} = 24.38$ ,  $p < 0.001$ ).

These divergent results for men and women hold when dependants are defined as 'under 10' rather than 'under 5'. The models of previous-month travel distances (above and table 4) are graphed by sex and dependency load in figure 3.

*H4: Men will be more likely than women to travel without their spouse, particularly to large market towns.* We found partial support for H4. The proportion of monthly distance travelled

**Table 4.** Unstandardized coefficients and summary statistics from linear multiple regression models using age and number of dependent children to predict log-transformed distance travelled in the previous month, separately for men and women. Intercept: dependent children, 0; age, 0. Statistical significance in probability tests is indicated in asterisks.

|                                | natural log of distance travelled in previous month by women | natural log of distance travelled in previous month by men |
|--------------------------------|--|--|
|                                | $\beta \pm \text{s.e.}$                                      | $\beta \pm \text{s.e.}$                                    |
| intercept                      | $-0.069 \pm 0.12$  | $0.00 \pm 0.20$  |
| dependent children under 5     | $-0.50 \pm 0.13^{**}$  | $0.01 \pm 0.21$  |
| age                            | $0.89 \pm 0.13^{***}$  | $-0.06 \pm 0.21$   |
| <i>F</i>                       | 24.38 <sup>***</sup>   | 0.04   |
| d.f.                           | (2, 17)  | (2, 23)  |
| <i>R</i> <sup>2</sup>          | 0.74   | 0.00   |
| adjusted <i>R</i> <sup>2</sup> | 0.71   | -0.08  |

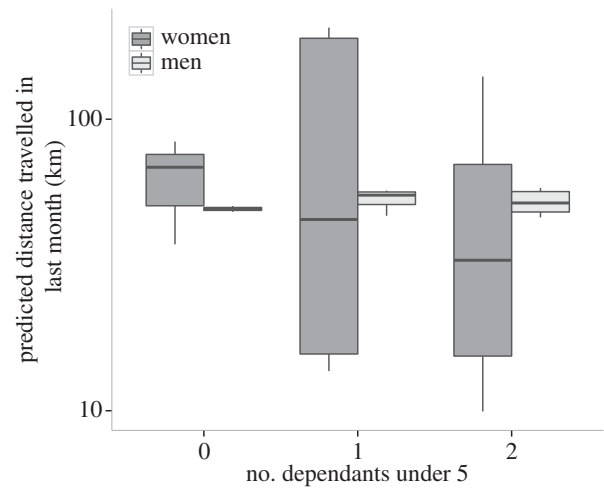
\*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

to Tsimane communities without their spouse was not significantly higher for men (mean  $\pm$  s.d. =  $0.70 \pm 0.36$ ) than for women ( $0.59 \pm 0.28$ ;  $t_{12} = 0.84$ ,  $p = 0.21$ ). Similarly, the proportion of monthly visits to Tsimane communities without their spouse was not significantly higher for men than for women ( $0.67 \pm 0.34$  versus  $0.55 \pm 0.27$ ;  $t_{12} = 0.99$ ,  $p = 0.17$ ). However, men took significantly more trips without their spouse to San Borja, the local market town, in the past month than did women ( $1.69 \pm 2.18$  versus  $0.15 \pm 0.38$ ;  $t_{12} = 2.38$ ,  $p < 0.05$ ).

## 5. Discussion

We find only weak support for the simple sex-difference hypothesis of H1. Half-ranges, exploration ranges and KUD ranges were not significantly larger for men, but there is a sex difference in MCP home range (table 2). Moreover, the main effect for sex is non-significant for both travel measures used to test H2 (table 3). Half-ranges and exploration ranges are linear travel measures; of the two areal measures, the MCP calculation is more sensitive to visits to distant, orthogonal locations (electronic supplementary material, figures S4–S6 compare the various home range calculations), and thus may better reflect scramble-type mate search. Because all four home range measures indicate greater male travel (with the MCP reaching significance), greater statistical power might indicate a lifelong sex difference in range size: men may realize greater pay-offs from mate search (regardless of marital status) throughout their lives. Nevertheless, the use of whole-life measures is not the most nuanced test of the sexual-selection hypothesis: sex differences should peak during the life stages when mating competition is maximal.

In support of this expectation, H2 is strongly supported: a highly significant sex-by-period interaction indicates that



**Figure 3.** Box plot of predicted total distances travelled in the last month by sex and dependency load. Predicted total distances are based on the regression presented in the text and in table 4.

men travel more than women during adolescence. This result is robust across diverse measures of travel and inclusion criteria. Sum distance travelled per period year includes visits where the distance between the home and visited community was conservatively estimated because the home community at the time of the visit was unknown. Conversely, number of communities visited per period year neglects the spatial aspects of the data. Yet both measures of travel show a significant sex difference during adolescence, and do so whether or not we control for the length of the adolescent period.

This pattern, with the sex difference in travel peaking in adolescence, is not explained by male-biased activities such as hunting or wage labour. Adolescent men spend about 50% less time hunting than do adult men [28], and thus hunting's effect on travel should peak in adulthood, not adolescence. Wage labour increases during late adolescence, but visits to non-Tsimane ranches were excluded from all analyses.

Might this sex difference instead be influenced by factors that keep adolescent females at home, rather than factors that promote male travel? Just as the mother's parental investment is less substitutable than the father's, adolescent females may reap greater reproductive benefits from care of siblings than do their male counterparts. This hypothesis cannot be ruled out by our data, and any contribution it makes to sex differences in adolescent travel patterns would be another manifestation of divergent male and female reproductive strategies. Another possible barrier to female travel is that adolescent females suffer greater risks of violence when they travel than do adolescent males. This is plausible, but it should be emphasized that travelling companions can be chosen to reduce such risks; thus one's own sex is not the key determinant of vulnerability.

There is no sex difference in travel during childhood. Previous research among English children found that boys range farther than girls, but focused on ranging around the child's home, which is often possible without parental accompaniment [29]. Our study only considered travel beyond the residential village, and thus largely reflects the decisions of parents.

We included the individual's home community as a control variable because acculturation and population of the home community may influence travel [11]. Acculturated villages are more likely to have large populations, to engage in cash

cropping, and to have schools and other attractors that collectively reduce the need to travel [1,15]. Consistent with its small population, community C's members travelled the most. Communities A and B had similar population sizes but different travel opportunities. Community A is located on a road that connects to the local market town (San Borja) and several other villages; community B is accessible only by forest trails or by river. Thus, probably due to lower transportation costs and greater density of nearby villages, community A's members travelled more than community B's.

H3 was supported only among women: women with fewer dependent children travelled more than women with more dependent children. This is consistent with Tsimane sexual division of labour, where women face greater constraints on their time and mobility due to breastfeeding and childcare. Alternatively, men may maintain investment in travel (and potential mating effort) as their dependency rises: men's direct care of offspring is minimal, so their visiting investment may be 'price-inelastic'. Visits to more acculturated communities may even increase when men have young children, not because of mating effort, but to seek medical care. The null result for men may indicate that additional variables should be included to reflect their shift from mating effort to parenting effort. For instance, if men live with their wife's family until their first child is born, their mating effort (and travel) might be damped until couples move elsewhere.

Despite the sex differences documented here, Tsimane men and women both report travelling to obtain scattered food resources (e.g. fish and game) and to socialize, especially with kin. However, Tsimane women were more likely to report visiting relatives than were men. In the present sample, there was no tendency for one sex versus the other to live away from their natal community; nevertheless, men travelled farther to visit relatives than did women. Because Tsimane practise cross-cousin marriage, visiting distant relatives may represent mate search and men may invest more in this strategy. At least 15% of Tsimane men report seeking a spouse and obtaining permission from future in-laws, often through protracted visitation ( $n = 137$ ; M. Gurven 2002–2005, unpublished data).

Other possible influences on travel patterns merit future consideration. In parallel with the logic of H2, travel may increase after divorce. Alternatively, men who travel more may be at greater risk of divorce. In fact, Tsimane wives often perceive increased travel, especially to town, as mate search, leading to more marital conflict [30]. Travel patterns may also reflect investment opportunities in kin other than children. For example, the birth of grandchildren elsewhere may motivate additional travel; Hadza grandmothers relocate to maximize the utility of their investments in grandchildren [31].

Consistent with the results of our systematic retrospective analyses, family members often reported that their adolescent male relatives were away travelling, visiting kin or working on ranches (approx. 25% of adolescent men away at a time, as compared with approx. 10% of adolescent women); hence *current* adolescents were not included in our samples.

We found some support for H4, that men travel without their spouse more than women. There was no sex difference in such travel for visits to Tsimane communities, but men were more likely than women to travel without their spouse to the local market town, San Borja. Although men occasionally meet their eventual wives in San Borja (four couples in the current analysis met there), married men may pursue extramarital affairs in San Borja because affairs may be harder to detect or

easier to achieve there than in Tsimane communities. Living in a community near San Borja is associated with a 1.7 times greater probability of infidelity [32]. Alternatively, women may be less able to visit San Borja without their spouse out of concerns about safety or the acceptability of travelling alone outside their ethnic communities. On the other hand, travelling without a spouse does not necessarily mean travelling alone—individuals may travel with parents, siblings, cousins or any other non-spouse individual.

## 6. Conclusion

With the exception of studies of residence patterns (e.g. [33–35]), information about human travel patterns in preindustrial populations is limited. This study quantifies intercommunity visitation in a natural-fertility population of forager–horticulturalists and tests specific hypotheses about the effects of reproductive priorities on travel. A variety of site-specific positive and negative factors as well as various costs associated with travel may tally differently for men and women at different life stages [1]. If women are more vulnerable to violence when they travel or their parenting effort is less substitutable, there may be stronger forces keeping them home. Our tests of H3 seem to support the latter factor; women with more dependent children travel less, and this dependency is plausibly a better measure of the demand for the parenting effort than a measure of their physical vulnerability. In populations like the Tsimane, where men have higher reproductive variance than women, their impetus to travel may be greater. Because the observed sex difference in travel peaks during the primary period of pair formation, our results suggest that the search for mates is one factor motivating travel away from the home community. The models presented in table 3 explain more than half of the variance in travel, indicating that both sex and reproductive status are key variables for understanding travel patterns. There was not robust support across travel measures for the purported human universal sex difference in lifetime travel. Instead, male travel most exceeds female travel during adolescence, consistent with the prediction that this sex difference should be maximal during periods of mate search. A similar pattern is expected in other populations (and species) to the extent that males have higher variance in reproductive success and female parental investment is less substitutable than that of the male.

**Ethics statement.** The study and consent procedures were approved by the Institutional Review Boards (IRB) of the University of California, Santa Barbara, and the University of New Mexico. In Bolivia, all procedures were approved by the Tsimane Government (Gran Consejo Tsimane), by village leaders and by study participants. Because many Tsimane do not read or write, participant permission was verbal and it was obtained twice: an initial affirmation to participate and a second confirmation once all procedures had been explained.

**Data accessibility.** Because of the centrality of residential GPS coordinates the data could not be adequately anonymized. Researchers with a targeted Human Subjects clearance may request the data from the corresponding author.

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