

Electronic Supplementary Material

Title: Sun, age and test location affect spatial orientation in human foragers in rainforests.

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Ethics statement.

The field research on Mbendjele BaYaka people was conducted under all necessary permissions from the relevant authorities of the Republic of Congo (Ethics Approval Number: N°070/MRSIT/IRSEN/DG/DS from the Ministère de la Recherche Scientifique et de l'Innovation Technologique, the Republic of Congo). All study procedures complied with the national laws and regulations of the Republic of Congo, the ethical standards of the Max Planck Institute for Evolutionary Anthropology, and ethical guidelines of the Comité d'Ethique de la Recherche en Sciences de la Santé (N°095/MRSIT/IRSA/CERSSA) in Brazzaville. We obtained informed consent from each of all participants to participate in pointing tasks and to carry a hand-held Global Positioning System (GPS device) for three days. We obtained informed consent from focal children and women to follow them on their daily foraging trips.

Study population.

The Mbendjele have semi-nomadic lifestyles in which they move from camp to camp every few months, resulting in a large life-time range of up to 790 km² [1]. They also stay in the village from four to eight months per year to cultivate crops in gardens and trade forest foods with Bondongo fisher-farmers [2,3]. We conducted this study when the band was residing in one temporary camp in the forest near the Djoubé village. The Mbendjele society is largely egalitarian and both men and women actively engage in daily foraging activities including plant-gathering, fishing, hunting, and gardening [3,4]. The diet of the Mbendjele in this study comprises a mix of wild plants and animals and carbohydrate staples cultivated in gardens close to the village. The Mbendjele children start foraging independently from the age of around five and young boys around five often joined their fathers' long-distance hunting trips [5]. Some of the children in this study attended a Mbendjele school in the Djoubé village, but not regularly. We had information on the exact birth dates only for children who were born after we began our project in 2014. To estimate the ages of older children, we used inter-birth intervals (2 to 2.5 years for this population). For adults, we conducted detailed interviews with ten adult Mbendjele people of variable ages and two

Bondongo villagers, and estimated the Mbendjele's ages by comparing with the known ages of two villagers, 75 and 44 years. The Djoubé forest is flat lowland tropical rainforest with a tree density of 501 trees per ha [2] and visual detection range including garden areas is 55.4 m (median; range: 14.5 to 210.0 m) [2]. The Mbendjele people walk 90% of their daily travel distance on human-made trails [1].

Full details on statistical analyses.

To test which factors influence pointing accuracy, we used Bayesian multilevel regression models. Bayesian models were implemented in the Stan computational framework (<http://mc-stan.org/>) accessed with the function 'brm' of the brms package version 1.7.0 [6] in R version 3.5.0 [7]. We converted the absolute bearing differences between the pointed bearing and the actual bearing to fractions by dividing them by 180 degrees, which is the theoretical maximum bearing difference. Since this proportion of pointing errors was bound between 0.001 and 0.998, we fitted models with a beta error distribution and logit link function. We inspected the distributions of all quantitative predictors for being approximately symmetrically distributed. To achieve roughly symmetrically distributed predictors and avoid influential cases, we then log transformed age, distance from camp to test location, and distance from test to target location to achieve roughly symmetrical distributions and avoid influential cases. All quantitative predictors were then z-transformed to a mean of 0 and standard deviation of 1 before fitting the model [8]. To control for random variations on pointing errors within 1) participants, 2) test locations, 3) target locations, and 4) days as well as variation among 5) participants' performance across days, we included random effects of participant identity, test location identity, target location identity, day identity, and test identity (i.e., the combination of participant and day) (see Table S5 for the results regarding the random effect). Models included all theoretically identifiable random slopes for the fixed effects within random intercepts [9,10] (Table S2). We did not estimate parameters for correlations among random slopes and intercepts [11]. We specified mildly informative conservative priors to guard against overfitting [12]. We used weakly informative normal priors with a standard deviation of 5 on the regression coefficients of all fixed effects and Student's t priors with 3 degrees of freedom and a standard deviation of 5 for random effects. All

parameters were initialized to zero. To decrease the number of divergent transitions that could cause a bias in the obtained posterior samples, we adjusted the sampling behavior of Stan by increasing the value of ‘adapt_delta’ to 0.95 [6]. We dropped interactions of which we found no considerable influence on pointing errors from the full model and fitted a reduced model. We obtained posterior distributions of predictors from four independent MCMC chains each with 1000 warmup and 1000 sampling iterations. We checked for collinearity among predictors [13] by deriving variance inflation factors (VIFs) using the function ‘vif’ of the package ‘car’ [14], applied to a standard linear model including only the fixed effects (excluding interaction terms and random effects); no considerable collinearity was detected (maximum VIF=2.09). The main model was based on 631 pointing tests, and we included 49 day IDs, 109 test IDs, 54 participant IDs, 66 test location IDs, and 14 target location IDs. Three sub models were based on 367 pointing tests, with 48 day IDs, 75 test IDs, 50 participant IDs, 65 test location IDs, and 14 target location IDs.

Sub-models for different types of target locations.

Additionally, to infer about the effects of different types of target locations (see refs [15,16]) we fitted two sub-models using only data with pointing tests conducted outside the camp. For these specific models, we predicted that the participants would be more accurate at pointing to the camp compared to the other locations, as pointing to a distant location requires knowledge of the spatial relationship between the current position and the target location, which can be more challenging than pointing to their camp from which they started traveling to the test position. Hence, we categorized the target location into their current camp versus other locations. Second, we expected a positive influence of food-related locations on spatial memory and thus pointing accuracy, and categorized the target location type into food (a fishing lake, a hunting camp, a garden) versus non-food locations (villages, camps). For the sub-models, we dropped the interactions that had no considerable influence on pointing accuracy in the full model, but otherwise they were identical. As a result, we could not find any effects of the types of the target locations on pointing accuracy, either camp versus the others nor food locations versus non-food locations (Table S6).

Daily range patterns.

We investigated two parameters of daily range patterns of the Mbendjele: daily travel distance and maximum distance from the camp. We asked 26 adolescents and adults (15 males, 12 females; median estimated age: 34, range: 16.7 to 76) to wear a hand-held GPS (Garmin 62) for three non-consecutive days per individual from May to August in 2016. In addition, we conducted focal follows for five focal women (median estimated age: 27, range: 25.5 to 41) from March to August in 2015 and 2016, during which the mean number of observations per focal woman was 48 days (range: 41 to 53 days). We also conducted focal follows of 24 children (11 boys and 13 girls; median estimated age: 9.9, range: 6 to 15) from March to August in 2016, during which the mean number of observations per focal child was two days (range: one to three days). During focal follows the researchers wore a GPS and walked behind the focal individual (see Jang et al. for details on data collection). The GPS location was automatically recorded with a setting “as often as possible” (mean: every 8 seconds; range: 4 to 36). We included GPS ranging tracks from focal follows that were collected in the same period during which we collected GPS tracks of 29 adolescents and adults, to control for the potential effect of seasonality on their ranging patterns. We used a total 196 ranging tracks from 56 individuals (26 men, 30 women; median estimated age: 29; range: 6 to 76) to calculate daily travel distance and maximum travel distance from the camp. We removed outlier locations of GPS tracks that were derived from GPS inaccuracy (see ref [17] for details). We then used a program written by R.M. [17] to interpolate locations for one-minute time stamps, assuming a constant speed between known locations, for which the GPS could not record data due to satellite reception. We calculated total travel length per day by summing up the distances between the points that were each separated by one minute.

To investigate the sex and age differences in daily travel distance and maximum distance from the camp, we fitted two linear mixed models (LMM) [18] with a Gaussian error structure and identity link function. LMMs were implemented using the function ‘lmer’ of the package ‘lme4’ [19] (version 1.1-19) in R version 3.5.2 [7]. The two models were based on 196 tracks and included the two-way interaction between sex and age and the random effects of participant identity and day identity. We compared each full

model with a respective null model [10] lacking sex and age and the interaction between them but being otherwise identical. We used a likelihood ratio test (R function ‘anova’ [20]) for this comparison. Only when a full-null model comparison revealed a significance ($P < 0.05$), did we discuss the results of the model with respect to individual test predictors [10,21]. We determined the significance of individual effects by dropping them one at a time and comparing the resulting models with the full model using a likelihood ratio test [9] (R function ‘drop1’). We removed non-significant interactions from the models and fitted the reduced models with only the main effects of sex and age. All p-values were two-tailed. We determined 95% confidence intervals using the function ‘bootMer’ of the ‘lme4’[19].

Supplementary Figures

(a)

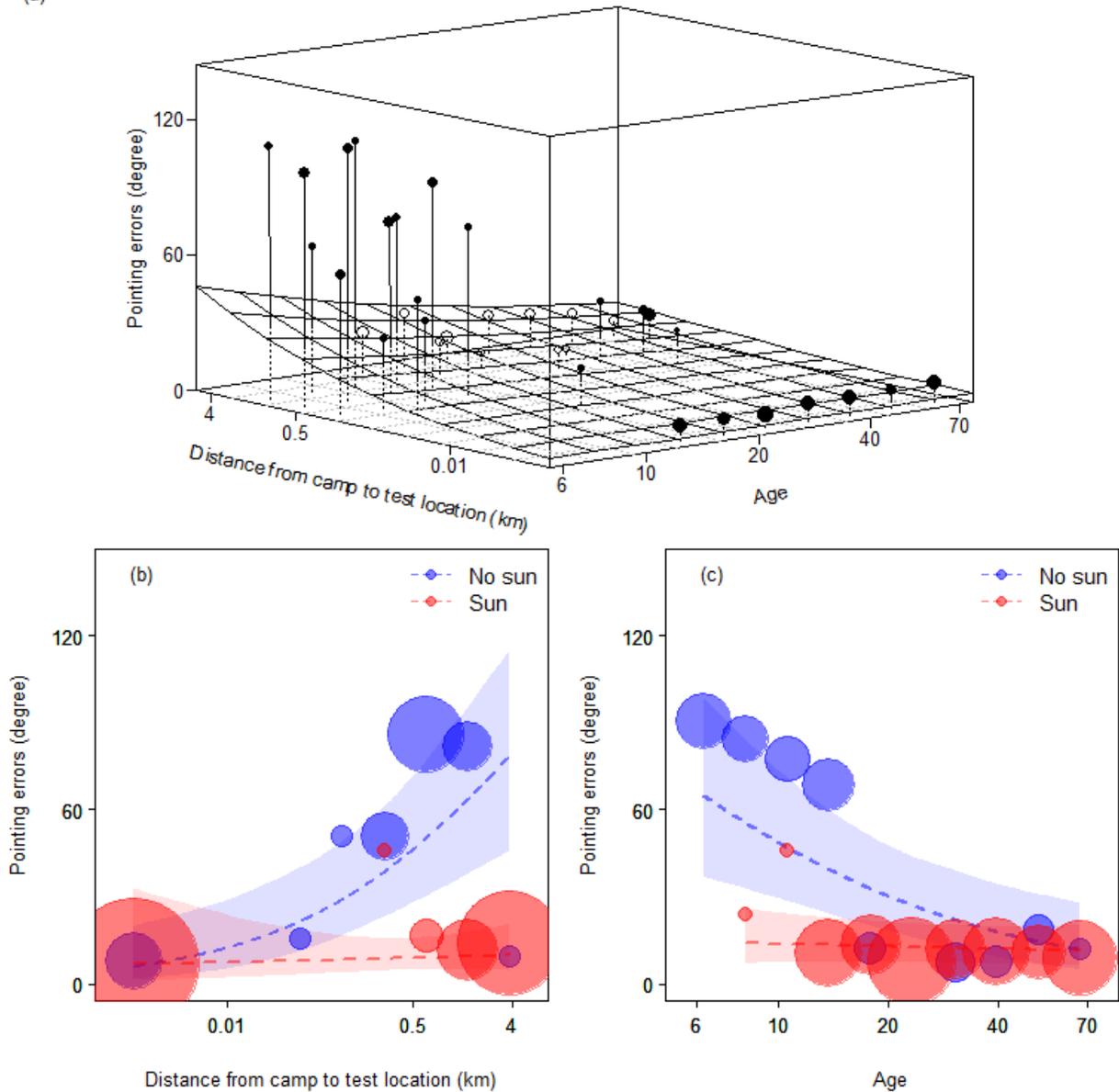


Figure S1. Interactive effects of (a) age and distance from camp to test location, (b) sun visibility and distance from camp to test location, and (c) age and sun visibility on pointing errors. (a) Pointing errors increased when the test location was farther away from the camp, but this effect disappeared as age increased. The surface represents the fitted model; *spheres* represent the averaged pointing errors per cell of the surface, and their ‘volume’ corresponds to the relative number of pointing tests in the respective cell (N: 3 to 53 per cell). *Filled spheres* fall above the fitted surface, indicated by *solid vertical lines*; *open spheres* fall below the surface, indicated by *dashed vertical lines*. (b) When the sun was not visible, the pointing errors increased as the participants were far from the camp. However, when the sun was visible, the pointing errors remained the same. (c) When the sun was not visible, the pointing errors increased especially in young ages. However, when the sun was visible, the pointing errors remained low across ages. The *dashed lines* represent the fitted model (with all other predictors being centered); *dots* represent the averaged pointing errors per binned group size (12 bins with equal widths in log-transformed group size), and their area corresponds to the relative number of pointing tests in the respective bin (N = 3 to 222 per bin). *Shaded areas* represent 95% credible intervals of the fitted model. The deviations of data from the respective model are in part explained by other terms present in the model.

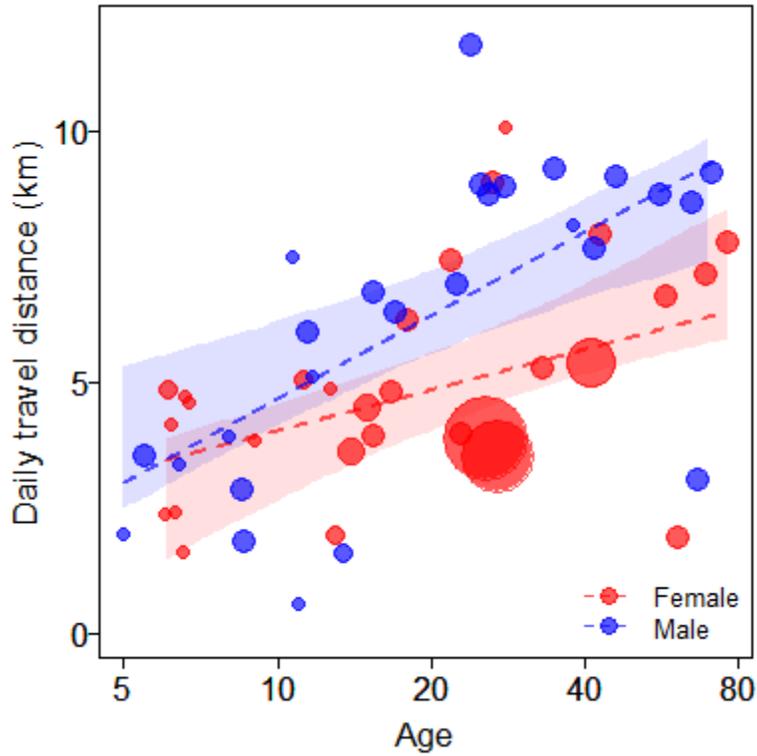


Figure S2. Sex and age differences in daily travel distance. Daily travel distance increased as age increased, and males tended to travel longer distance than females, which became more apparent as age increased. Each dot represents one individual. The area of dots represents the number of days used to calculate daily travel distance (N: 1 to 26 days, 56 individuals including children, adolescents, and adults). Dashed lines are fitted values of as a function of age for females (red line) and males (blue line), and shaded areas show the confidence interval of the fitted model.

Supplementary Tables

Table S1. Target locations used in the pointing tests with distance from the camp.

Pointed target location	Distance from the camp to target (km)
Camp	0
Djoubé village	4.2
Monsanda village	2.9
Bangui Motaba village	15.7
Ndongó fishing pond	5
Bimbamboko hunting camp	9.5
Bondongo farmer's garden	1.9

The distance of different test locations in the forest to the target ranged from 71 m to 16.7 km.

Table S2. Random slopes in full and reduced model. The effect of a fixed effect that appears in the table allows that its effect randomly varies among levels of a random effect.

Random effects	Estimated effects
Main full model*	
Participant ID	Intercept Distance from test to target location Type of test location
Target location ID	Intercept Sex Age Sun visibility Distance from camp to test location Distance from test to target location Type of test location Sex: Age Sex: Distance from camp to test location Sex: Distance from test to target location Age: Distance from camp to test location Age: Distance from test to target location Sun visibility: Distance from camp to test location
Test location ID	Intercept Distance from test to target location
Test ID (participant and day)	Intercept Distance from test to target location
Day ID	Intercept Distance from test to target location
Main reduced model	
Participant ID	Intercept Distance from camp to target location Type of test location
Target location ID	Intercept Sex Age Sun visibility Distance from camp to test location Distance from test to target location Type of test location Age: Distance from camp to test location Sun visibility: Distance from camp to test location
Test location ID	Intercept Distance from test to target location
Test ID (participant and day)	Intercept Distance from test to target location
Day ID	Intercept Distance from test to target location

*see Table S5 for the results of estimated variance components (standard deviations) for the random effects in the main full model

Table S3. Absolute degree differences between actual bearing and the Mbendjele's pointed bearing.

		Mean \pm SD off-target
Overall pointing error¹		25 \pm 42 °
Sex²	Female	23 \pm 39 °
	Male	28 \pm 44 °
Sun compass³	Sun visible	10 \pm 15 °
	Sun not visible	58 \pm 58 °

Note that mean and standard deviation are no sensitive descriptors of distributions which are very skewed; here we reported them nevertheless for reasons of comparability with previous studies

¹ Total 631 pointing tests of 54 participants

² N_{females}= 31 (366 pointing tests), N_{males}= 23 (265 pointing tests)

³ N_{sun}= 432 pointing tests, N_{no sun}= 199 pointing tests

Table S4. Mean posterior estimates and 95% credible intervals for each of the model parameters estimated in the main full model, reduced model, and a post-hoc model including the 3-way interaction between age, distance from camp to test location, and sun visibility.

Parameter	Estimate	Est. Error	Lower CI	Upper CI	Eff. sample	Rhat ¹
<i>Full model</i>						
Intercept	-2.37	0.45	-3.26	-1.45	2356	1.00
Sex (male) ²	-0.08	0.19	-0.44	0.28	2380	1.00
Age ³	-0.41	0.26	-0.90	0.12	1682	1.00
Sun visibility (yes) ⁴	-0.90	0.38	-1.62	-0.13	2147	1.00
Distance from camp to test location ⁵	1.34	0.43	0.49	2.15	1322	1.00
Distance from test to target location ⁶	0.27	0.42	-0.53	1.14	1396	1.00
Type of test location (on-trail) ⁷	0.17	0.34	-0.48	0.87	2157	1.00
Sex : Age	0.07	0.16	-0.26	0.36	2586	1.00
Sex : Distance from test to target location	0.03	0.22	-0.36	0.56	1899	1.00
Sex : Distance from camp to test location	0.12	0.15	-0.17	0.42	3537	1.00
Age : Distance from test to target location	-0.12	0.26	-0.64	0.41	1917	1.00
Age : Distance from camp to test location	-0.21	0.11	-0.40	0.01	2068	1.00
Sun visibility (yes) : Distance from camp to test location	-0.86	0.52	-2.04	0.00	962	1.00
Age: Sun visibility (yes)	0.52	0.19	0.15	0.90	1872	1.00
<i>Reduced model</i>						
Intercept	-2.32	0.44	-3.19	-1.50	2039	1.00
Sex (male) ²	-0.10	0.11	-0.32	0.13	4082	1.00
Age ³	-0.52	0.20	-0.90	-0.12	1600	1.00
Sun visibility (yes) ⁴	-0.90	0.37	-1.61	-0.13	2212	1.00
Distance from camp to test location ⁵	1.32	0.42	0.49	2.12	1454	1.00
Distance from test to target location ⁶	0.32	0.30	-0.23	0.94	1894	1.00
Type of test location (on-trail) ⁷	0.13	0.34	-0.52	0.80	1808	1.00
Age: Distance from camp to test location	-0.19	0.10	-0.38	-0.04	2195	1.00
Sun visibility (yes): Distance from camp to test location	-0.82	0.50	-1.97	-0.00	901	1.00
Age: Sun visibility (yes)	0.47	0.18	0.11	0.83	2257	1.00
<i>Post-hoc model with a 3-way interaction</i>						
Intercept	-2.37	0.42	-3.20	-1.57	3246	1.00
Sex (male) ²	-0.06	0.15	-0.34	0.26	4799	1.00
Age ³	-0.44	0.21	-0.84	-0.01	2745	1.00
Sun visibility (yes) ⁴	-0.84	0.38	-1.55	-0.06	2554	1.00
Distance from camp to test location ⁵	1.26	0.39	0.45	1.99	1265	1.00
Distance from test to target location ⁶	0.34	0.30	-0.23	0.95	2180	1.00
Type of test location (on-trail) ⁷	0.14	0.32	-0.49	0.76	2847	1.00
Age: Distance from camp to test location	-0.52	0.23	-0.94	-0.06	2457	1.00
Sun visibility (yes): Distance from camp to test location	-0.81	0.50	-1.94	0.08	901	1.00
Age: Sun visibility (yes)	0.40	0.19	0.03	0.77	1990	1.00
Age: Distance from camp to test location: Sun visibility (yes)	0.40	0.23	-0.02	0.84	2457	1.00

¹ An Rhat value being one indicates the model converged

² Sex was dummy coded with the reference category 'female'; N_{females} = 31 (366 tests), N_{male} = 23 (265 tests)

^{3, 5, 6} Log- and then z-transformed; mean ± SD of log-transformed values: ³ 3.17 ± 0.69, ⁵ 4.15 ± 3.59, ⁶ 7.33 ± 2.48

⁴ Sun visibility was dummy coded with the reference category 'no'; N_{sun} = 432, N_{no sun} = 199

⁷ Type of test locations was dummy coded with the reference category 'off-trail'; N_{on-trail} = 374, N_{off-trail} = 257

Table S5. Random slopes and estimated variance components (standard deviations) for the random effects from the main full model.

Random effects	Term ²	Estimate	Lower CI	Upper CI	Rhat
Day ID	(Intercept)	0.46	0.02	0.98	1.00
Day ID	Distance from test to target location	0.40	0.04	0.83	1.00
Test ID	(Intercept)	0.11	0.01	0.29	1.00
Test ID	Distance from test to target location	0.07	0.00	0.19	1.00
Participant ID	(Intercept)	0.09	0.00	0.23	1.00
Participant ID	Distance from test to target location	0.07	0.00	0.20	1.00
Participant ID	Type of test location	0.42	0.04	0.76	1.00
Test location ID	(Intercept)	0.73	0.36	1.06	1.00
Test location ID	Distance from test to target location	0.81	0.54	1.11	1.00
Target location ID	(Intercept)	0.29	0.05	0.69	1.00
Target location ID	Distance from camp to test location	0.10	0.00	0.31	1.00
Target location ID	Distance from test to target location	0.61	0.18	1.20	1.00
Target location ID	Age	0.41	0.02	1.05	1.00
Target location ID	Type of test location	0.48	0.13	1.02	1.00
Target location ID	Sex	0.25	0.01	0.81	1.00
Target location ID	Sun visibility	0.37	0.04	0.94	1.00
Target location ID	Sex: Distance from camp to test location	0.13	0.00	0.43	1.00
Target location ID	Sex: Distance from test to target location	0.28	0.01	0.92	1.00
Target location ID	Sex: Age	0.19	0.01	0.63	1.00
Target location ID	Age: Distance from camp to test location	0.11	0.00	0.47	1.00
Target location ID	Age: Distance from test to target location	0.63	0.19	1.26	1.00
Target location ID	Sun visibility: Distance from camp to test location	0.44	0.05	1.07	1.00

¹Number of observations = 631; number of levels of random effects: Day IDs = 49; Test IDs = 109; Participant IDs= 54; Test location IDs = 66, Target location IDs = 14

²The column 'term' specifies whether the row refers to a random intercept or random slope component.

Table S6. Results of the two sub-models with types of target locations (camp versus others, food versus non-food): mean posterior estimates and 95% credible intervals for each of the model parameters estimated.

Parameter	Estimate	Est. Error	Lower CI	Upper CI	Eff. sample	Rhat ¹
Sub-model 1: target location type (camp versus others)						
<i>full model</i>						
Intercept	-0.88	0.50	-1.86	0.14	2907	1.00
Sex (male) ²	0.02	0.21	-0.39	0.44	2602	1.00
Age ³	-0.59	0.34	-1.23	0.11	1970	1.00
Sun visibility (yes) ⁴	-1.51	0.42	-2.35	-0.66	2402	1.00
Distance from camp to test location ⁵	0.34	0.23	-0.12	0.78	1745	1.00
Distance from test to target location ⁶	0.36	0.23	-0.06	0.83	2422	1.00
Type of target location (others) ⁷	-0.04	0.44	-0.94	0.83	2308	1.00
Age : Distance from camp to test location	-0.14	0.25	-0.61	0.38	2581	1.00
Age : Sun visibility (yes)	0.95	0.29	0.38	1.50	2398	1.00
Age : Type of target location (others)	-0.52	0.35	-1.24	0.13	2256	1.00
Sun visibility (yes) : Distance from camp to test location	-0.51	0.41	-1.29	0.33	2447	1.00
<i>reduced model</i>						
Intercept	-0.85	0.48	-1.79	0.10	1522	1.00
Sex (male) ²	0.03	0.20	-0.36	0.44	2299	1.00
Age ³	-0.93	0.25	-1.41	-0.44	1825	1.00
Sun visibility (yes) ⁴	-1.61	0.36	-2.32	-0.90	1476	1.00
Distance from camp to test location ⁵	0.23	0.21	-0.18	0.63	2236	1.00
Distance from test to target location ⁶	0.33	0.24	-0.12	0.82	2323	1.00
Type of target location (others) ⁷	-0.09	0.41	-0.94	0.71	1500	1.00
Age : Sun visibility (yes)	0.90	0.27	0.38	1.44	2179	1.00
Sub-model 2: target location type (food versus non-food)						
<i>full model</i>						
Intercept	-0.75	0.36	-1.46	-0.04	2674	1.00
Sex (male) ²	0.02	0.20	-0.38	0.43	3129	1.00
Age ³	-1.16	0.28	-1.72	-0.59	1749	1.00
Sun visibility (yes) ⁴	-1.56	0.40	-2.32	-0.78	2241	1.00
Distance from camp to test location ⁵	0.35	0.21	-0.08	0.76	2558	1.00
Distance from test to target location ⁶	0.30	0.21	-0.12	0.73	2119	1.00
Type of target location (non-food) ⁸	-0.25	0.27	-0.76	0.31	2041	1.00
Age : Distance from camp to test location	-0.14	0.24	-0.59	0.35	2425	1.00
Age : Sun visibility (yes)	0.93	0.28	0.37	1.50	2420	1.00
Age : Type of target location (others)	0.30	0.27	-0.22	0.87	2149	1.00
Sun visibility (yes) : Distance from camp to test location	-0.52	0.41	-1.32	0.26	1873	1.00
<i>reduced model</i>						
Intercept	-0.80	0.34	-1.48	-0.16	2010	1.00
Sex (male) ²	0.03	0.20	-0.36	0.43	3420	1.00
Age ³	-0.92	0.24	-1.40	-0.44	2257	1.00
Sun visibility (yes) ⁴	-1.63	0.36	-2.36	-0.93	1880	1.00
Distance from camp to test location ⁵	0.27	0.19	-0.12	0.63	1530	1.00
Distance from test to target location ⁶	0.29	0.24	-0.19	0.77	2511	1.00
Type of target location (non-food) ⁸	-0.26	0.28	-0.76	0.35	1771	1.00
Age : Sun visibility (yes)	0.89	0.27	0.36	1.43	2245	1.00

Results with statistically considerable influence appear in bold

¹ Rhat value being one indicates the model converged

² Sex was dummy coded with the reference category 'female'; N_{females} = 27 (192 tests), N_{male} = 23 (175 tests)

^{3, 5, 6} Log- and then z-transformed; mean ± SD of log-transformed values: ³ 3.00 ± 0.75, ⁵ 7.13 ± 0.96, ⁶ 8.11 ± 0.98

⁴ Sun visibility was dummy coded with the reference category 'no'; N_{sun} = 210, N_{no_sun} = 157

⁷ Type of target locations was dummy coded with the reference category 'camp'; N_{camp} = 84, N_{others} = 283

⁸ Type of target locations was dummy coded with the reference category 'food'; N_{food} = 146, N_{non-food} = 221

Table S7. Average daily travel distance and maximum distance from camp.

	Median daily travel distance (km)	Median maximum distance from camp (km)
Overall ¹	4.83 (range: 0.23 to 16.74)	1.54 (range: 0.04 to 4.39)
Sex ²		
Female	4.27 (range: 0.23 to 11.12)	1.33 (range: 0.04 to 4.39)
Male	6.86 (range: 0.45 to 16.74)	2.09 (range: 0.12 to 4.23)

¹Total 196 tracks of 56 individuals, age range: 6 to 76 years old

² N_{female}= 26, N_{males}= 30

Table S8. Results of the full model for sex and age differences in maximum distance from the camp.

Response	Effect	Estimate	SE	χ^2	df	Pr (Chi)
	(Intercept)	37.460	1.793			-
Maximum distance from the camp ¹	Age ²	4.154	1.548			-
	Sex (male) ³	4.457	2.657			-
	Age: Sex (male)	3.053	2.200	1.894	1	0.169

- Values not shown due to having a very limited interpretation

¹Total 196 tracks of 56 individuals: N_{females} = 26, N_{males} = 30

² Log- and then z-transformed; mean \pm SD of log-transformed values: 3.17 \pm 0.63

³ Sex was dummy coded with the reference category 'female'

Supplementary references

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