PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Jang H, Boesch C, Mundry R, Kandza V, Janmaat KRL. 2019 Sun, age and test location affect spatial orientation in human foragers in rainforests. *Proc. R. Soc. B* **286**: 20190934.
http://dx.doi.org/10.1098/rspb.2019.0934

Received: 20 April 2019
Accepted: 2 July 2019

Subject Category:
Behaviour

Subject Areas:
behaviour, cognition

Keywords:
spatial orientation, Mbendjele BaYaka people, pointing accuracy, sun navigation, spatial experience, rainforest

Author for correspondence:
Haneul Jang
e-mail: haneul_jang@eva.mpg.de

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4570976.

THE ROYAL SOCIETY
PUBLISHING

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

Haneul Jang[1], Christophe Boesch[1], Roger Mundry[1], Vidrich Kandza[1,2] and Karline R. L. Janmaat[1,3]

[1]Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
[2]Institut de Recherche en Sciences Exactes et Naturelles, Brazzaville, the Republic of Congo
[3]Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands

HJ, 0000-0001-5994-6413

The ability to know the direction of food sources is important for the foraging success of hunter–gatherers, especially in rainforests where dense vegetation limits visual detection distances. Besides sex and age, prior experience with the environment and the use of environmental cues are known to influence orientation abilities of humans. Among environmental cues, the position of the sun in the sky is important for orientation of diurnal animal species. However, whether or to what extent humans use the sun is largely unknown. Here, we investigated orientation abilities of the Mbendjele BaYaka people in the Republic of Congo, by conducting pointing tests ($N_{\text{participants}} = 54$, age: 6–76 years) in different locations in the rainforest. The Mbendjele were overall highly accurate at pointing to out-of-sight targets (median error: 6°). Pointing accuracy increased with age, but sex did not affect accuracy. Crucially, sun visibility increased pointing accuracy in young participants, especially when they were far from the camp. However, this effect became less apparent in older participants who exhibited high pointing accuracy, also when the sun was not visible. This study extends our understandings of orientation abilities of human foragers and provides the first behavioural evidence for sun compass use in humans.

1. Introduction

Spatial orientation is one of the most important cognitive abilities of mobile animal species for successful foraging [1]. The abilities to have a notion of direction of food locations and to find one's way from one food to another are especially expected to be beneficial when home ranges are large, as is the case for our own species [1–3]. To improve foraging success in large-scale and complex environments, foragers specifically need to know their current position in relation to a food location, and in which direction they should move to reach it [4–7]. The location of a known food source can be reached by following a set of landmarks that are connected to the food location (often referred to as topological knowledge) or by having metric information about distance and direction towards the food location (often referred to as Euclidean knowledge). These two types of spatial knowledge are generated from coding spatial information in relation to external objects in the environment (geocentric (or allocentric) ways of spatial coding) [8]. Contrary to egocentric ways of spatial coding, which rely on the perspective of a navigator, geocentric ways of spatial coding are 'environment-centred'. In other words, a navigator specifies a target location in relation to known external features in the environment, such as landmarks or celestial cues including the position of the sun and polarized light [9–11].

Researchers have investigated spatial orientation abilities of humans by using a wide variety of methods, also in comparison with non-human animal species including great apes [2,12]. Many behaviour and neuroscience studies have focused on identifying whether humans use topological versus Euclidean knowledge and egocentric versus geocentric ways of spatial coding [13–15]. However, how these different types of spatial knowledge and spatial coding are used for orientation by humans in real foraging contexts is not well understood yet. Classic developmental studies with Westernized human children suggest that children first use egocentric ways of spatial coding, and then subsequently develop the ability of using geocentric cues through self-locomotion which allows them to experience the surrounding environment [16,17]. However, Haun *et al.* [12] found that European 4-year-old children and great apes preferred geocentric spatial coding over egocentric and suggested that the human default is geocentric spatial coding which can be changed by the influence of culture and language. Studies from a broad range of cultures support this conclusion by showing that the ways of spatial coding can differ depending on ecological, cultural and social conditions [18–20]. Moreover, sex differences in orientation abilities may be also explained by different spatial experiences between sexes in various cultures, in terms of sex-specific activities and mobility patterns [21–23]. Trumble *et al.* [22] discussed that in studies on a variety of subsistence populations, male-biased orientation abilities appeared only in populations in which females engage less in foraging (e.g. the Temne [24], the settled Hadza [23], the Twe and Tjimba [25]), but not in populations in which both sexes actively travel away for extensive foraging (e.g. the Eskimo [24], mobile Hadza [23], the Tsimane [22]). Therefore, to better understand human orientation abilities, it seems to be important to consider the role of spatial experience in the development of orientation abilities and how this role relates to sex and age in different lifestyles and cultures.

In addition, differential spatial challenges that a navigator encounters in the environment can shape differential needs for orientation abilities and skills [7,13]. For example, the availability of spatial cues can vary between ecological conditions with different visibility and environmental geometry [23]. In an open environment unimpeded by vegetation, distant landmarks can be easily seen over longer distances, and a navigator can obtain a notion of direction easily in reference to the landmarks. By contrast, in a rainforest environment with closed canopy and heavy vegetation, a navigator would be challenged by low visibility as well as a lack of distant environmental cues. Through exploring the surrounding environment, a navigator can learn a wide range of geographical knowledge and environmental cues which are useful for orientation, which reinforces the development of orientation abilities [26]. Hence, assessing prior experience with the environment through mobility is also crucial for understanding orientation abilities. To date, a considerable number of studies have investigated human orientation abilities [5,15]. However, relatively few studies were conducted with information on individuals' mobility and prior experience with the environment. Moreover, most studies were conducted indoors lacking environmental cues and without involving self-movement over large areas. Thus, it is unclear how spatial experiences with the environment help human orientation performances, and how humans find their way by using environmental cues in a large-scale and real-life context [20].

Among many environmental cues, a navigator can correct their directional errors by using global cues such as distant landmarks (e.g. a mountain peak) or celestial cues (e.g. position of the sun, polarized light). Many diurnal animal species are known to use a sun compass in navigating towards distant goals [27] (e.g. desert ants [28,29], honeybees [30], monarch butterflies [31,32], dung beetles [33], fruit flies [34], pigeons [35], reef fish [36]). The position of the sun in the sky constantly changes from the East to the West across a day, and its daily movement trajectory varies with latitude and season. Therefore, a navigator needs to constantly correct time across the day as well as the progress of season [20]. Many insects and birds have precise internal clocks which allow them to use a time-compensated sun compass by incorporating spatial and temporal patterns of the sun's trajectory (e.g. [30,35]). Although it is unlikely that humans have internal clocks similar to ants and bees [20,37], a few studies and anecdotes suggest that humans also use a sun compass for orientation [38–40]. For example, Vikings are known to have navigated skillfully across the open sea using a sun compass with sunstones to determine the cardinal directions (north, south, east, west) [41]. Male undergraduate students self-reported that they use celestial cues to get a hint on cardinal directions [42]. Sanskrit and Hindi children aged from 11 to 15 years also reported that they compute cardinal directions with reference to the direction of sunrise [43]. However, there is no empirical and behavioural evidence yet for sun compass use throughout the day in humans, which raises the question about whether and to what extent humans use the sun for orientation.

Here, we aim to extend our understanding of orientation abilities of human foragers in a tropical lowland rainforest where dense vegetation hampers detection of landmarks, and whose orientation abilities are much less studied compared to those of human populations in savannah environments. We selected the Mbendjele BaYaka people (hereafter, 'the Mbendjele') in a rainforest of the Republic of Congo, who travel long distances in the forest for hunting and gathering on a daily basis without aid of navigational technology, such as maps or a compass [2]. We investigated their ability to point to important locations (e.g. camp, villages, food locations [22,25]). Pointing to a known but out-of-sight location has been applied as one sensitive measure of orientation abilities which encompass spatial memory and cognitive mapping abilities to mentally represent the spatial relationship between their current position and the target location [20,44–46]. Pointing performances rely on geocentric ways of spatial coding, especially with a Euclidean notion of direction with which individuals should be able to point directly to a target location, and not to the direction of the route that leads them there. The previous pointing tests with hunter–gatherer populations have been conducted mainly in participants' well-known and extremely familiar areas, such as their camp (e.g. [22,23,25,47]). Here, we elaborated on these studies by testing the effects of familiarity with the environment on participants' notion of direction in large-scale environments, as familiarity has been widely used as a proxy of spatial experience with the environment [48–50]. Thus, we varied pointing test locations, ranging from their camp to forest locations up to 6 km far from the camp.

We investigated the effects of (1) age, (2) sex, (3) distance from camp to test location as a proxy of familiarity with the environment and (4) sun visibility on the Mbendjele's pointing accuracy. First, we hypothesized that the Mbendjele people develop their notion of direction as they age, as a result of increasing spatial experience as well as brain development [51], and predicted that pointing accuracy increases with age. Second, we expected a higher pointing accuracy in the more mobile sex. If both sexes have similar mobility, we expected similar levels of spatial experience in both sexes, and thus no obvious sex differences in pointing accuracy. For this analysis, we additionally examined sex and age differences in the Mbendjele's ranging patterns, specifically daily travel distance and the maximum distance that they travelled from the camp during daily foraging trips. Third, we expected a higher pointing accuracy when participants are close to the camp, compared to when they are far from the camp. Fourth, we investigated whether the Mbendjele foragers use celestial cues for orientation, namely the position of the sun in the sky. The Mbendjele people live in flat lowland rainforests where distant landmarks (e.g. mountain peaks) and distinct environmental geometry (e.g. highland valleys) are absent. Thus, we expected that the Mbendjele people use the position of the sun to get a notion of cardinal direction. We expected a better pointing performance when the sun is visible compared to when the sun is not visible, especially in distant and less familiar areas.

2. Methods

(a) Study population

We conducted our study with one Mbendjele BaYaka band in the Djoubé village at the Motaba River in the department of Likouala of the north-western region of the Republic of Congo (2°28 N, 17°26 E). We collected data from March to August in 2015 and 2016. The band consisted of 47 individuals on average (range: 20–79) during the study period. The ethnography of this population is described in the electronic supplementary material.

(b) Pointing tests

(i) Procedures

We recruited a total of 54 participants including 31 females and 23 males from one band, including children, adolescents and adults (median estimated age: 29 years, range: 6–76 years). The youngest child in this study was 6 years old (see [52]). Each individual participated in pointing tests several times (mean ± s.d.: 12 ± 5 tests per individual, range: 3–22) in different test locations including their camp and random locations in the forest. We asked participants to point with their finger or with a wooden stick to a target location. At each test location, the participant pointed towards three to seven different target locations in sequence. The target locations included the camp, two adjacent villages and one distant village, a fishing pond, a hunting camp and a garden. The distance from the camp to these target locations ranged from 1.9 to 15.7 km (electronic supplementary material, table S1 for details). The distance from the test location to target location ranged from 71 m to 16.7 km, and the distance from the camp to test location ranged from 0 to 5.8 km. Before conducting a pointing test, we asked the participant whether he/she has ever visited the respective target location and if not, we removed the target location from the test. During each pointing test, we recorded whether (1) the researcher could see the sun in clear blue sky, (2) the sun was covered with clouds but the researcher was still able to know the position of the sun or (3) the position of the sun could not be recognized at all due to thick clouds. We defined the first two cases as ‘the sun was visible’, and only the last case as ‘the sun was not visible’. Pointing tests at camp were conducted outside of their huts where they could see the sky. To exclude social influence, we conducted pointing tests when a participant was alone in the forest or alone behind the researcher's tent at camp. We avoided conducting the pointing tests when there were obvious auditory cues, for example, on a day of a funeral ceremony in the village, and thus we could hear drumming sounds from the village. We measured the bearing pointed by the participant using a compass (Brunton ComPro Pocket Transit Compass’ or Suunto A–10) and noted the coordinates of the test location with a hand-held Global Positioning System (GPS) device (Garmin 62). The accuracy of the GPS was on average 7.56 m in Djoubé forests (see electronic supplementary material in [2]). We used the GPS coordinates of test and target locations to compute true bearings using Quantum-GIS (QGIS v. 2.18.1). We subtracted the participant's pointed bearings from the true bearings, and the absolute value of this difference was used as pointing error of each test. We had a total of 631 bearing measures at 66 different test locations. We conducted 264 pointing tests at their camp, and 367 tests in 65 random locations in the forest.

(ii) Model explanation

We predicted that pointing accuracy increases as age increases, and age differences in pointing accuracy become larger when the participants are (1) far from the camp and (2) pointing at a target far away from the current test location. We also predicted that if there were sex differences in pointing accuracy, the differences would become more pronounced with increasing age and when participants are (1) far from the camp and (2) pointing at a distant target. Lastly, we predicted that sun visibility would increase pointing accuracy, but more markedly when participants are far from the camp. We furthermore expected that the effects of sun visibility depend on age, as the children need to learn how to use the position of the sun for orientation. Hence, we included seven two-way interactions between (1) age and distance from camp to test location, (2) age and distance from test to target location, (3) sex and distance from camp to test location, (4) sex and distance from test to target location, (5) sex and age, (6) sun visibility and distance from camp to test location, and (7) sun visibility and age in the full model. We controlled for whether a test was conducted on-trail or off-trail, as a trail itself can be a conspicuous landmark which could guide their orientation. After we checked the result of the main model, we fitted a *post hoc* model with a three-way interaction and all contained two-way interactions between age, distance from the camp to test location and sun visibility.

(iii) Statistical analyses of pointing tests

We used Bayesian multilevel regression models in the Stan computational framework (http://mc-stan.org/), accessed with the function ‘brm’ of the brms package v. 1.7.0 [53] in R v. 3.5.0 [54]. We converted the absolute bearing differences between the pointed bearing and the actual bearing to fractions by dividing them by 180° which is the theoretical maximum bearing difference. We fitted models with a beta error distribution and logit link function. We log-transformed age, distance from camp to test location, and distance from test to target location. All quantitative predictors were then z-transformed to a mean of 0 and standard deviation of 1 before fitting the model [55]. We included random effects of participant, test location, target location, day and test identities (i.e. the combination of participant and day) (electronic supplementary material, table S5). Models included all theoretically identifiable random slopes for the fixed effects within random intercepts [56,57] (electronic supplementary material, table S2). We used weakly informative normal priors to guard against overfitting [58]. We dropped interactions of which we found no considerable influence on

Table 1. Absolute degree differences between actual bearing and the Mbendjele's pointed bearing. See electronic supplementary material, table S3 for mean values.

		median pointing error (quartiles; range)
overall pointing error[a]		6° (2°, 27°; 1° to 179°)
sex[b]	female	6° (2°, 23°; 1° to 176°)
	male	7° (2°, 31°; 1° to 179°)
sun compass[c]	sun visible	4° (1°, 13°; 1° to 88°)
	sun not visible	27° (8°, 113°; 1° to 179°)

[a] Total 631 pointing tests of 54 participants.

[b] $N_{\text{females}} = 31$ (366 pointing tests), $N_{\text{males}} = 23$ (265 pointing tests).

[c] $N_{\text{sun}} = 432$, $N_{\text{no sun}} = 199$.

pointing errors from the full model and fitted a reduced model. We obtained posterior distributions of predictors' effects from four independent MCMC chains each with 1000 warmup and 1000 sampling iterations. The main model was based on 631 pointing tests with 49 day IDs, 109 test IDs, 54 participant IDs, 66 test location IDs and 14 target location IDs (see the electronic supplementary material for full details).

(c) Daily range patterns

We further investigated sex and age differences in Mbendjele's daily range patterns, in terms of daily travel distance and maximum distance that they travelled from the camp during daily foraging trips. We used a total 196 ranging tracks from 56 individuals (26 males, 30 females; median estimated age: 29; range: 6–76) to calculate daily travel distance and maximum distance from the camp (see the electronic supplementary material for data collection methods). We calculated both measures by using cleaned tracks after removing outliers. For statistical analyses, we fitted two linear mixed models [59] with a Gaussian error structure and identity link function, using the function 'lmer' of the package 'lme4' [60] (v. 1.1–19) in R v. 3.5.0 [54]. The two models included a two-way interaction between sex and age because we expected that daily travel distance and maximum distance would increase with age, but more apparently for males (e.g. [21]). We included the random effects of participant identity and day identity. We compared each full model with a respective null model [57] lacking sex and age and the interaction between them but being otherwise identical. 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 [56]. All *p*-values were two-tailed.

3. Results

(a) Pointing accuracy tests

As an overall result, median pointing error of the Mbendjele people was only 6° (first, third quartile: 2°, 27°; range: 1–179°; table 1). Pointing errors of the Mbendjele were similar in females (median = 6°) and males (median = 7°; table 1). Pointing errors were much lower when the sun was visible (median = 4°) compared with when the sun was not visible (median = 27°; table 1). As a model result, after removing interactions without considerable influence on pointing errors (electronic supplementary material, table S4 for the full model result), we found considerable effects of interactions between (1) age and distance from the camp to the test location, (2) sun visibility and distance from the camp to test location, and (3) age and sun visibility on pointing errors (table 2). Pointing errors increased as the test location was farther from camp in young participants, but this effect disappeared as age increased (electronic supplementary material, figure S1a). Pointing errors increased as the test location was farther from camp, but only when the sun was not visible (electronic supplementary material, figure S1b). Pointing errors were larger in younger participants, but only when the sun was not visible (electronic supplementary material, figure S1c). After we checked the results of the main model, we fitted a *post hoc* model with a three-way interaction between age, distance from the camp to test location, and sun visibility, and we found a trend for the three-way interaction (table 2). This result implied that when the sun was visible, pointing errors were overall low across ages (figure 1*a*). Pointing errors in young ages increased when the test locations were increasingly farther away from the camp, but this effect was very weak when the sun was visible (figure 1*a*). However, when the sun was not visible, pointing errors substantially increased when the test location was increasingly farther away from the camp, especially in young participants (figure 1*b*). We did not find any evidence for sex differences in pointing errors (table 2).

(b) Sex and age differences in daily range patterns

There were clear effects of sex and age on the Mbendjele's daily travel distance (full-null model comparison $\chi^2 = 27.131$, d.f. = 3, $p < 0.001$), and effects of age on the maximum distance from camp ($\chi^2 = 25.105$, d.f. = 3, $p < 0.001$). Daily travel distance tended to be longer in the Mbendjele men than women, but only as age increased (table 3*a*; electronic supplementary material, figure S2). After removing a non-significant interaction between sex and age, we found that the Mbendjele travelled farther from the camp as age increased, without obvious sex differences (table 3*b* and figure 2).

4. Discussion

There are several published studies on pointing errors of other subsistence populations (mean ± s.d. pointing errors of the Hadza in Tanzania: men 14.5 ± 5.5°, women 16.9 ± 5.7° [23]; the Twe and Himba in Namibia: men 15.2 ± 7.5°, women 19.2 ± 9.3° [47]; the Hai||om in Namibia: 16.4° [61]; the Tsimane in Bolivia: 25.1 ± 17.8° [22]). However, as each study included different age ranges of the participants and conducted pointing tests with different test and target locations, comparison between populations is not straightforward, and thus it remains elusive which populations have superior orientation abilities. Nevertheless, our study shows that Mbendjele people were overall very accurate at pointing to target locations (table 1), which might be related to their hunting and gathering lifestyles in a rainforest environment where low visibility and lack of distant landmarks requires them to have a good sense of direction. Crucially, we found no sex differences in pointing accuracy, but clear positive effects of age and sun visibility on their pointing performances, depending on the test locations (table 2).

The absence of sex differences in pointing accuracy (table 2) corresponds with the results of our analyses on the

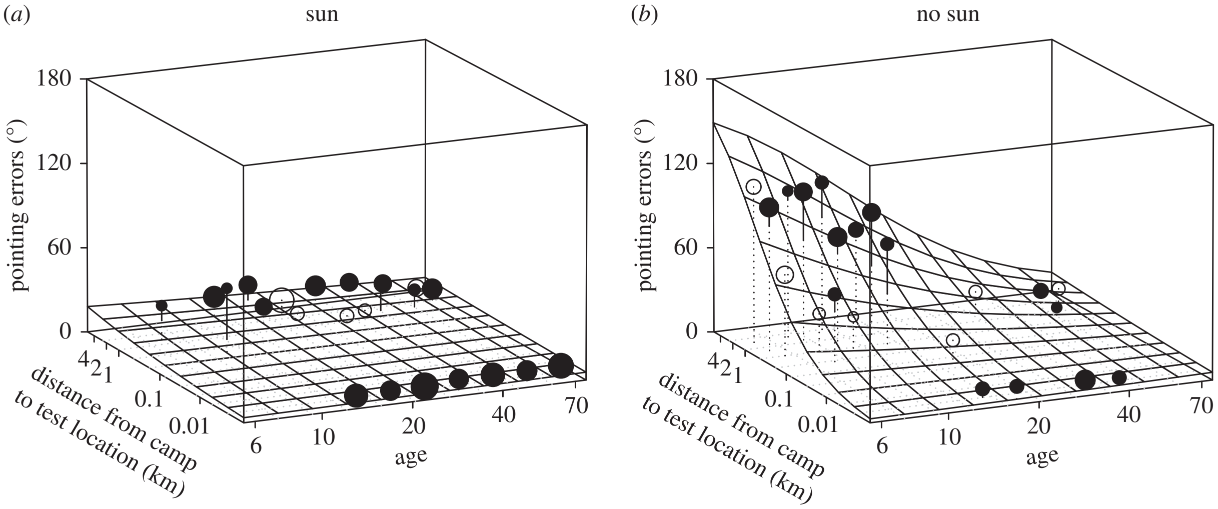

Figure 1. *Post hoc* model results with a three-way interaction between age, distance from camp to the test location, and sun visibility on pointing errors (*a*) when the sun was visible and (*b*) when the sun was not visible. (*a*) Pointing errors remained low across ages. In young ages, pointing errors increased when the test location was farther away from the camp, but this effect was very weak when the sun was visible. (*b*) When the sun was not visible, pointing errors substantially increased when the test location was farther away from the camp, especially in young ages. 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; total 631 pointing tests; 54 participants). *Filled spheres* fall above the fitted surface, indicated by *solid vertical lines*; *open spheres* fall below the surface, indicated by *dashed vertical lines*.

Table 2. Results of the main model: mean posterior estimates and 95% credible intervals for each of the model parameters. See electronic supplementary material, table S4 for the results of the main full model and the number of effective samples. All predictors had the Rhat value being one which indicates the model converged. Results with statistically considerable influence appear in *italics*.

parameter	estimate	est. error	lower CI	upper CI
main reduced model				
intercept	−2.32	0.44	−3.19	−1.50
sex (male)[a]	−0.10	0.11	−0.32	0.13
age[b]	−0.52	0.20	−0.90	−0.12
sun visibility (yes)[e]	−0.90	0.37	−1.61	−0.13
distance from camp to test location[c]	1.32	0.42	0.49	2.12
distance from test to target location[d]	0.32	0.30	−0.23	0.94
type of test location (on-trail)[f]	0.13	0.34	−0.52	0.80
age: distance from camp to test location	*−0.19*	*0.10*	*−0.38*	*−0.04*
sun visibility (yes): distance from camp to test location	*−0.82*	*0.50*	*−1.97*	*−0.00*
age: sun visibility (yes)	*0.47*	*0.18*	*0.11*	*0.83*
post hoc model with a three-way interaction				
intercept	−2.37	0.42	−3.20	−1.57
sex (male)[a]	−0.06	0.15	−0.34	0.26
age[b]	−0.44	0.21	−0.84	−0.01
sun visibility (yes)[e]	−0.84	0.38	−1.55	−0.06
distance from camp to test location[c]	1.26	0.39	0.45	1.99
distance from test to target location[d]	0.34	0.30	−0.23	0.95
type of test location (on-trail)[f]	0.14	0.32	−0.49	0.76
age: distance from camp to test location	−0.52	0.23	−0.94	−0.06
sun visibility (yes): distance from camp to test location	−0.81	0.50	−1.94	0.08
age: sun visibility (yes)	0.40	0.19	0.03	0.77
age: distance from camp to test location: sun visibility (yes)	*0.40*	*0.23*	*−0.02*	*0.84*

[a] Sex was dummy coded with the reference category 'female'; $N_{\text{females}} = 31$ (366 pointing tests), $N_{\text{males}} = 23$ (265 pointing tests).

[b,c,d] Log- and then *z*-transformed; mean ± s.d. of log-transformed values: [b]3.17 ± 0.69, [c]4.15 ± 3.59, [d]7.33 ± 2.48.

[e] Sun visibility was dummy coded with the reference category 'no'; $N_{\text{sun}} = 432$, $N_{\text{no sun}} = 199$.

[f] Type of test locations was dummy coded with the reference category 'off-trail'; $N_{\text{on-trail}} = 374$, $N_{\text{off-trail}} = 257$.

Table 3. Sex and age differences in (a) daily travel distance and (b) maximum distance from the camp. Statistically significant results appear in *italics*. See electronic supplementary material, table S8 for the result of full model of maximum distance from the camp. Dashes denote values not shown due to having a very limited interpretation.

response	effect	estimate	s.e.	CI_{lower}	CI_{upper}	χ^2	d.f.	*p* (chi)
(a) daily travel distance[a]	(intercept)	5.042	0.371	4.314	5.781			—
	age[b]	0.731	0.324	0.100	1.401			—
	sex (male)[c]	1.708	0.552	0.650	2.878			—
	age: sex (male)	*0.771*	*0.460*	*−0.187*	*1.605*	*2.737*	*1*	*0.098**
(b) maximum distance from the camp[a]	(intercept)	37.752	1.815	34.128	41.258			—
	age[b]	*5.673*	*1.117*	*3.404*	*7.726*	*21.948*	*1*	*<0.001****
	sex (male)[c]	3.858	2.672	−1.704	9.108	1.983	1	0.159

[a] Total 196 tracks of 56 individuals: $N_{\text{females}} = 26$, $N_{\text{males}} = 30$.

[b] Log- and then *z*-transformed; mean ± s.d. of log-transformed values: 3.17 ± 0.63.

[c] Sex was dummy coded with the reference category ‘female’.

Mbendjele’s daily range patterns in which we did not find any sex differences in the maximum distance that they travelled away from the camp (table 3 and figure 2). The Mbendjele adult men tended to travel longer distance than women (table 3, electronic supplementary material, figure S2). However, the longer travel distance in men does not necessarily mean that the men travelled farther to the forest, because the men might repeatedly visit the village or walk around in proximate areas from the camp during their search for prey or honey trees. We indeed found that the Mbendjele women travelled as far away from camp into the forest as did men (table 3 and figure 2), which could enable women to have similar levels of spatial experience as men in distant areas. We are aware that these ranging pattern analyses did not contain long-distance hunting trips or travels between camps, as participants were asked to return the GPS to the researcher within the same day. However, the results were still consistent with our adlib observations in which the Mbendjele women travelled long distances of up to 10 km in a day with their husbands for fishing, hunting and visiting kin in distant villages (H.J. & K.R.L.J. 2015, unpublished data). In addition, a combination of interview and GPS data revealed that the Mbendjele women have extensive lifetime travel ranges up to 790 km^2 (based on a minimum convex polygon; see [2]). We suggest that the gender equality in the Mbendjele population may result in the Mbendjele women’s long-distance foraging for fishing and hunting [62] as well as the women’s engagement in strength-based activities such as digging, planting, clearing forest and carrying heavy items [63].

Our result is consistent with previous studies that found no sex differences in orientation abilities in human populations where both sexes actively travelled away from home (e.g. Eskimo [24], mobile Hadza [23], Tsimane [22]). This result is in contrast to the sex differences in orientation abilities found in hunter–gatherer societies where women engage less in foraging (e.g. the Temne [24], the settled Hadza [23], the Twe and Tjimba [25]), and in Westernized societies where women are more likely to work at home or closer to home compared with men (e.g. USA [64,65], Israel [66], the Netherlands [67], Korea [68], Italy [69]). The studies from various cultures suggest that sex differences in orientation abilities may indeed result from sex-specific mobility, and our findings build on this growing body of evidence. Future studies still need to investigate whether the sex differences in the Mbendjele people emerge in different spatial tasks, such as a mental rotation task (see [23]).

Previous studies suggested that 3–10-year-old children develop their ability to combine both egocentric and geocentric ways of spatial coding, and show adult-level performance in cognitive map tasks around the age of 12 years [15]. Our findings suggest that the young Mbendjele children at around six years performed as accurately as adults in the pointing tests when they were close to the camp. However, their pointing accuracy decreased when they were far away from the camp (figure 1*b*). Crucially, in distant areas, the Mbendjele children substantially improved their pointing accuracy when the sun was visible (figure 1*a*). This result suggests that the Mbendjele children are able to understand the position of the sun in the sky in terms of cardinal directions and to use it to infer the direction of distant locations. The positive effect of the sun on pointing accuracy could not be explained by better visibility on sunny days of distant landmarks which served as global cues from a large distance [70], because our study was conducted in a dense rainforest environment where distant landmarks are absent [2]. Therefore, we instead suggest that the children who were unable to identify the directions of sunrise and sunset due to a cloudy sky were generating errors in finding other directions, which caused large pointing errors. Our results suggest that the Mbendjele children learn how to use celestial cues such as the position of the sun in the sky to correct their directional errors at an early age, at least before six years old.

The positive effect of sun visibility on pointing accuracy became less apparent as age increased (figure 1), which can be explained by higher pointing accuracy of the older participants in distant test locations, also on very cloudy days when the sun position was not be able to recognized (figure 1*b*). This result is consistent with our finding that the Mbendjele people explore more distant areas as age increases, and may thus become more familiar with these areas (table 3 and figure 2), which may enable them to have an accurate sense of direction in distant test locations in our study. Thus, there might have been relatively little effect of using a sun compass on pointing performances in adults. However, this result does not imply that only children use

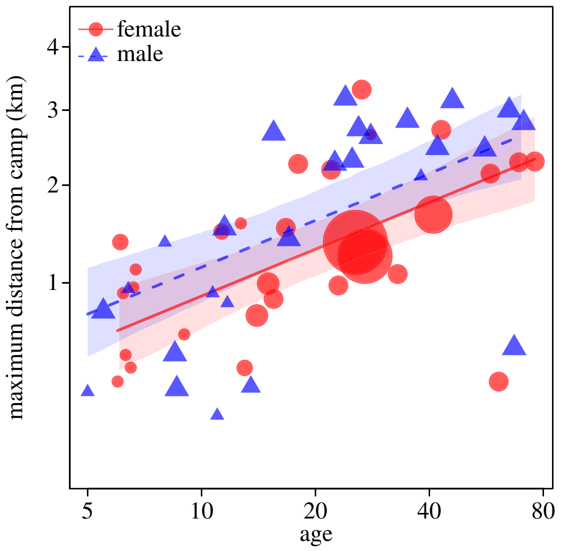

Figure 2. Sex and age differences in the maximum distance from the camp. The maximum distance from the camp increased as age increased, without obvious sex differences. Each dot represents one female and each triangle represents one male. The area of dots and triangles represents the number of days used to calculate the maximum distance from the camp (*N*: 1 to 26 days, 56 individuals including children, adolescents and adults). Lines are fitted values as a function of age for females (solid line) and males (dashed line) and shaded areas depict the model's confidence intervals.

a sun compass, because adult men reported that navigation is difficult in unfamiliar areas if the sun is not visible, in our anecdotal interviews ($N = 5$). Therefore, to better understand the effects of sun visibility on orientation abilities in adults, further studies should be conducted in unfamiliar areas where the adults also have large pointing errors. Moreover, we need follow-up studies to investigate the relative effects of time of a day on pointing accuracy. As dung beetles and desert ants decrease their orientation precision in the middle of day with higher solar elevations [33,71], we expect that humans would be worse at orientation in the middle of the day when the sun is at its highest point, compared with the early morning or late in the day when the sun is closer to the horizon of the east or west. Such findings would give us a better clue to understanding sun compass use in humans.

In sum, our study found evidence that the Mbendjele children of at least 6 years old have already developed a geocentric frame of reference to specify the direction of locations, and that their directional accuracy is sensitive to familiarity with their environment, as well as the sun visibility. We found that the spatial range in which they have developed the notion of direction becomes larger over the course of their life, without obvious effects of their sex. Crucially, the Mbendjele seemed to correct their directional errors by using the position of the sun in the sky, suggesting their sophisticated understandings of the spatial relationships between their current position, the target location, and the cardinal direction inferred from the sun position. To better understand the Mbendjele's ability to use a Euclidean knowledge which consists of both distance and direction, their notion of distance should also be studied, especially in children of different ages. Moreover, studies on the Mbendjele's spatial language will provide a better clue to explain their geocentric ways of spatial coding from early age, for example, whether they describe the space as being 'environment-centred' (e.g. north, south, east and west) rather than 'ego-centred' (e.g. left, right) [19,20]. Finally, our study provides the first behavioural evidence for the potential use of sun compass in human rainforest foragers from a very early age. This study allows us to increase our understanding of how humans have survived in rainforest environments in which orientation is challenging due to a lack of visibility and distant landmarks, by using celestial cues, such as the sun compass.

Ethics. This study was conducted under all necessary permissions and ethical guidelines from the relevant authorities of the Republic of Congo and the Max Planck Institute for Evolutionary Anthropology. We obtained informed consent from all participants (see the electronic supplementary material for full Ethics statement).

Data accessibility. The data supporting this article can be found in the electronic supplementary material.

Authors' contributions. H.J., C.B. and K.R.L.J. conceived the study. H.J. and K.R.L.J. designed the data collection strategy, and H.J., C.B., R.M. and K.R.L.J. designed the analysis strategy. H.J., V.K. and K.R.L.J. conducted pointing tests with the Mbendjele people and obtained permits for research. H.J. and R.M. analysed data and prepared tables and figures. H.J., C.B., R.M. and K.R.L.J. wrote the manuscript.

Competing interests. We declare we have no competing interests.

Funding. This work was supported by the Max Planck Institute for Evolutionary Anthropology and Leakey Foundation.

Acknowledgements. We thank the Ministère de la Recherche Scientifique et de l'Innovation Technologique, the Comité d'Ethique de la Recherche en Sciences de la Santé, and Institut de Recherche en Sciences Exactes et Naturelles (IRSEN) for their permission to execute our studies. We gratefully acknowledge Prof. C. Bouka-Biona and Prof. J. M. Moutsambote at IRSEN and M. J. Dzabatou in Makao for logistic support of our studies. We thank D. Bombjaková for introducing us to the Mbendjele family in Djoube. We thank R. McElreath for helpful advice on Bayesian modelling. We thank N. Newcombe and R. Byrne for helpful discussion on sun compass use in humans. We are especially grateful to the Mbendjele people participating in pointing tests and allowing us to follow them on their daily foraging trips.

References

1. Shettleworth SJ. 2010 Getting around: spatial cognition. In *Cognition, evolution, and behavior*, pp. 261–312. Oxford, UK: Oxford University Press.
2. Jang H, Boesch C, Mundry R, Ban SD, Janmaat KRL. In press. Travel linearity and speed of human foragers and chimpanzees during their daily search for food in tropical rainforests. *Sci. Rep.*
3. Milton K, May ML. 1976 Body weight, diet and home range area in primates. *Nature* **259**, 459–462. (doi:10.1038/259459a0)
4. Gallistel CR. 2017 Navigation: whence our sense of direction? *Current Biology* **27**, R108–R110. (doi:10.1016/j.cub.2016.11.044)
5. Golledge. 1999 *Wayfinding behavior: cognitive mapping and other spatial processes*. Baltimore, MD: JHU Press.
6. Janson CH. 2019 Foraging benefits of ecological cognition in fruit-eating primates: results from field experiments and computer simulations. *Front. Ecol. Evol.* **7**, 125. (doi:10.3389/fevo.2019.00125)
7. Wolbers T, Hegarty M. 2010 What determines our navigational abilities? *Trends Cogn. Sci.* **14**, 138–146. (doi:10.1016/j.tics.2010.01.001)
8. Newcombe N, Huttenlocher J, Drummey AB, Wiley JG. 1998 The development of spatial location coding: place learning and dead reckoning in the second and third years. *Cogn. Dev.* **13**, 185–200. (doi:10.1016/S0885-2014(98)90038-7)
9. Klatzky RL. 1998 Allocentric and egocentric spatial representations: definitions, distinctions, and

interconnections. In *Spatial cognition* (eds C Freksa, C Habel, KF Wender), pp. 1–17. Berlin, Germany: Springer.

10. Levinson SC. 1996 Language and space. *Annu. Rev. Anthropol.* **25**, 353–382. (doi:10.1146/annurev.anthro.25.1.353)
11. Nadel L, Hardt O. 2004 The spatial brain. *Neuropsychology* **18**, 473–476. (doi:10.1037/0894-4105.18.3.473)
12. Haun DBM, Rapold CJ, Call J, Janzen G, Levinson SC. 2006 Cognitive cladistics and cultural override in Hominid spatial cognition. *Proc. Natl Acad. Sci. USA* **103**, 17 568–17 573. (doi:10.1073/pnas.0607999103)
13. Burgess N. 2006 Spatial memory: how egocentric and allocentric combine. *Trends Cogn. Sci.* **10**, 551–557. (doi:10.1016/j.tics.2006.10.005)
14. Filimon F. 2015 Are all spatial reference frames egocentric? Reinterpreting evidence for allocentric, object-centered, or world-centered reference frames. *Front. Hum. Neurosci.* **9**, 648. (doi:10.3389/fnhum.2015.00648)
15. Newcombe N. 2019 Navigation and the developing brain. *J. Exp. Biol.* **222**, jeb186460. (doi:10.1242/jeb.186460)
16. Piaget J, Inhelder B. 1967 *The child's conception of space*. New York, NY: WW Norton.
17. Siegel A, White S. 1975 The development of spatial representations of large-scale environments. *Adv. Child Dev. Behav.* **10**, 9–55. (doi:10.1016/S0065-2407(08)60007-5)
18. Dasen PR. 1984 The cross-cultural study of intelligence: Piaget and the Baoule. *Int. J. Psychol.* **19**, 407–434. (doi:10.1080/00207598408247539)
19. Haun DBM, Rapold CJ, Janzen G, Levinson SC. 2011 Plasticity of human spatial cognition: spatial language and cognition covary across cultures. *Cognition* **119**, 70–80. (doi:10.1016/j.cognition.2010.12.009)
20. Levinson SC. 2003 *Space in language and cognition: explorations in cognitive diversity*. Cambridge, UK: Cambridge University Press.
21. Cashdan E, Gaulin SJC. 2016 Why go there? Evolution of mobility and spatial cognition in women and men. *Hum. Nat.* **27**, 1–15. (doi:10.1007/s12110-015-9253-4)
22. Trumble BC, Gaulin SJC, Dunbar MD, Kaplan H, Gurven M. 2016 No sex or age difference in dead-reckoning ability among Tsimane forager-horticulturalists. *Hum. Nat.* **27**, 51–67. (doi:10.1007/s12110-015-9246-3)
23. Cashdan E, Marlowe FW, Crittenden A, Porter C, Wood BM. 2012 Sex differences in spatial cognition among Hadza foragers. *Evol. Hum. Behav.* **33**, 274–284. (doi:10.1016/j.evolhumbehav.2011.10.005)
24. Berry JW. 1966 Temne and Eskimo perceptual skills. *Int. J. Psychol.* **1**, 207–229. (doi:10.1080/00207596608247156)
25. Vashro L, Cashdan E. 2015 Spatial cognition, mobility, and reproductive success in northwestern Namibia. *Evol. Hum. Behav.* **36**, 123–129. (doi:10.1016/j.evolhumbehav.2014.09.009)
26. Vasilyeva M, Lourenco SF. 2012 Development of spatial cognition: development of spatial cognition. *Wiley Interdiscip. Rev. Cogn. Sci.* **3**, 349–362. (doi:10.1002/wcs.1171)
27. Gallistel CR. 1990 *The organization of learning*. Cambridge, MA: The MIT Press.
28. Wehner R, Hoinville T, Cruse H, Cheng K. 2016 Steering intermediate courses: desert ants combine information from various navigational routines. *J. Comp. Physiol. A* **202**, 459–472. (doi:10.1007/s00359-016-1094-z)
29. Wehner R, Müller M. 2006 The significance of direct sunlight and polarized skylight in the ant's celestial system of navigation. *Proc. Natl Acad. Sci. USA* **103**, 12 575–12 579. (doi:10.1073/pnas.0604430103)
30. Dyer FC, Dickinson JA. 1994 Development of sun compensation by honeybees: how partially experienced bees estimate the sun's course. *Proc. Natl Acad. Sci. USA* **91**, 4471–4474. (doi:10.1073/pnas.91.10.4471)
31. Merlin C, Gegear RJ, Reppert SM. 2009 Antennal circadian clocks coordinate sun compass orientation in migratory monarch butterflies. *Science* **325**, 1700–1704. (doi:10.1126/science.1176221)
32. Mouritsen H, Frost BJ. 2002 Virtual migration in tethered flying monarch butterflies reveals their orientation mechanisms. *Proc. Natl Acad. Sci. USA* **99**, 10 162–10 166. (doi:10.1073/pnas.152137299)
33. Dacke M, Jundi B el, Smolka J, Byrne M, Baird E. 2014 The role of the sun in the celestial compass of dung beetles. *Phil. Trans. R. Soc. B* **369**, 20130036. (doi:10.1098/rstb.2013.0036)
34. Warren TL, Giraldo YM, Dickinson MH. 2019 Celestial navigation in *Drosophila*. *J. Exp. Biol.* **222**, jeb186148. (doi:10.1242/jeb.186148)
35. Wiltschko R, Walker M, Wiltschko W. 2000 Sun-compass orientation in homing pigeons: compensation for different rates of change in azimuth? *J. Exp. Biol.* **203**, 889–894.
36. Mouritsen H, Atema J, Kingsford MJ, Gerlach G. 2013 Sun compass orientation helps coral reef fish larvae return to their natal reef. *PLoS ONE* **8**, e66039. (doi:10.1371/journal.pone.0066039)
37. Ekstrom AD, Spiers HJ, Bohbot VD, Rosenbaum RS. 2018 *Human spatial navigation*. Princeton, NJ: Princeton University Press.
38. Ammarell G. 1999 *Bugis navigation*. New Haven, CT: Yale University Southeast Asia Studies.
39. Gladwin T. 1970 *East is a big bird: navigation and logic on Puluwat Atoll*. Cambridge, MA: Harvard University Press.
40. Lewis D. 1994 *We, the navigators: The ancient Art of landfinding in the pacific*. Honolulu, HI: University of Hawaii Press.
41. Bernáth B, Blahó M, Egri Á, Barta A, Kriska G, Horváth G. 2013 Orientation with a Viking sun-compass, a shadow-stick, and two calcite sunstones under various weather conditions. *Appl. Opt.* **52**, 6185–6194. (doi:10.1364/ao.52.006185)
42. Lawton CA. 1994 Gender differences in way-finding strategies: relationship to spatial ability and spatial anxiety. *Sex Roles* **30**, 765–779. (doi:10.1007/BF01544230)
43. Mishra RC, Singh S, Dasen PR. 2009 Geocentric dead reckoning in Sanskrit- and Hindi-medium school children. *Cult. Psychol.* **15**, 386–408. (doi:10.1177/1354067X09343330)
44. Jeanne Sholl M. 1988 The relation between sense of direction and mental geographic updating. *Intelligence* **12**, 299–314. (doi:10.1016/0160-2896(88)90028-1)
45. Lawton CA. 1996 Strategies for indoor wayfinding: the role of orientation. *J. Environ. Psychol.* **16**, 137–145. (doi:10.1006/jevp.1996.0011)
46. Montello DR. 1991 Spatial orientation and the angularity of urban routes: a field study. *Environ. Behav.* **23**, 47–69. (doi:10.1177/0013916591231003)
47. Vashro L, Padilla L, Cashdan E. 2016 Sex differences in mobility and spatial cognition: a test of the fertility and parental care hypothesis in northwestern Namibia. *Hum. Nat.* **27**, 16–34. (doi:10.1007/s12110-015-9247-2)
48. Acredolo LP. 1982 The familiarity factor in spatial research. *New Dir. Child Adolesc. Dev.* **1982**, 19–30. (doi:10.1002/cd.23219821504)
49. Gale N, Golledge RG, Halperin WC, Couclelis H. 1990 Exploring spatial familiarity. *Prof. Geogr.* **42**, 299–313. (doi:10.1111/j.0033-0124.1990.00299.x)
50. Iachini T, Ruotolo F, Ruggiero G. 2009 The effects of familiarity and gender on spatial representation. *J. Environ. Psychol.* **29**, 227–234. (doi:10.1016/j.jenvp.2008.07.001)
51. Lingwood J, Blades M, Farran EK, Courbois Y, Matthews D. 2015 The development of wayfinding abilities in children: Learning routes with and without landmarks. *J. Environ. Psychol.* **41**, 74–80. (doi:10.1016/j.jenvp.2014.11.008)
52. Riggins T, Blankenship SL, Mulligan E, Rice K, Redcay E. 2015 Developmental differences in relations between episodic memory and hippocampal subregion volume during early childhood. *Child Dev.* **86**, 1710–1718. (doi:10.1111/cdev.12445)
53. Bürkner P-C. 2017 Advanced Bayesian multilevel modeling with the R package brms. *arXiv:1705.11123 [stat]*.
54. R Core Team. 2018 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
55. Schielzeth H. 2010 Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**, 103–113. (doi:10.1111/j.2041-210X.2010.00012.x)
56. Barr DJ, Levy R, Scheepers C, Tily HJ. 2013 Random effects structure for confirmatory hypothesis testing: keep it maximal. *J. Mem. Lang.* **68**, 255–278. (doi:10.1016/j.jml.2012.11.001)
57. Forstmeier W, Schielzeth H. 2011 Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behav. Ecol. Sociobiol.* **65**, 47–55. (doi:10.1007/s00265-010-1038-5)
58. McElreath R, Smaldino PE. 2015 Replication, communication, and the population dynamics of

scientific discovery. *PLoS ONE* **10**, e0136088. (doi:10.1371/journal.pone.0136088)

59. Baayen RH. 2008 *Analyzing linguistic data: a practical introduction to statistics using R*. Cambridge, UK: Cambridge University Press.
60. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
61. Widlok T. 1997 Orientation in the wild: the shared cognition of Hai||om bushpeople. *J. R. Anthropol. Inst.* **3**, 317–332. (doi:10.2307/3035022)
62. Lewis J. 2002 Forest hunter-gatherers and their world: a study of the Mbendjele Yaka pygmies of Congo-Brazzaville and their secular and religious activities and representations. PhD dissertation, London School of Economics and Political Science, University of London.
63. Boyette A, LeHanka A, Sarma M, Lew-Levy S, Gettler L, Miegakanda V. In press. BaYaka foragers' daily strength-requiring activities and physically intensive demands: variation by sex but few anthropometric correlates. *Am. J. Hum. Biol.* **31**.
64. Hanson S, Johnston I. 1985 Gender differences in work-trip length: explanations and implications. *Urban Geogr.* **6**, 193–219. (doi:10.2747/0272-3638.6.3.193)
65. Rosenbloom S. 2006 Understanding women's and men's travel patterns: The research challenge. In *Research on women's issues in transportation: conference proceedings* 35, pp. 7–28. Washington, DC: National Research Council.
66. Blumen O, Kellerman A. 1990 Gender differences in commuting distance, residence, and employment location: metropolitan Haifa 1972 and 1983. *Prof. Geogr.* **42**, 54–71. (doi:10.1111/j.0033-0124.1990.00054.x)
67. Schwanen T, Dijst M, Dieleman FM. 2002 A microlevel analysis of residential context and travel time. *Environ. Plan A* **34**, 1487–1507. (doi:10.1068/a34159)
68. Lee BS, McDonald JF. 2003 Determinants of commuting time and distance for seoul residents: the impact of family status on the commuting of women. *Urban Stud.* **40**, 1283–1302. (doi:10.1080/0042098032000084604)
69. Cristaldi F. 2005 Commuting and gender in Italy: a methodological issue. *Prof. Geogr.* **57**, 268–284. (doi:10.1111/j.0033-0124.2005.00477.x)
70. Steck SD, Mallot HA. 2000 The role of global and local landmarks in virtual environment navigation. *Presence: Teleoperators Virtual Environ.* **9**, 69–83. (doi:10.1162/105474600566628)
71. Müller M, Wehner R. 2007 Wind and sky as compass cues in desert ant navigation. *Naturwissenschaften* **94**, 589–594. (doi:10.1007/s00114-007-0232-4)