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In many parts of Africa, people searching for honey are led to bees' nests by the greater honeyguide (*Indicator indicator* Sparrman). The Boran people of Kenya claim that they can deduce the direction and the distance to the nest as well as their own arrival at the nest from the bird's flight pattern, perching height, and calls. Analyses of the behavior of guiding birds confirmed these claims.

ACCORDING TO ROCK PAINTINGS from the central Sahara, Zimbabwe, and South Africa, man has collected honey in Africa for 20,000 years (*1, 2*). Even today, honey contributes significantly to the diets of many African people (*2–5*). When searching for honey, Africans are often joined by the greater honeyguide (*Indicator indicator*), which leads them to bee colonies (*Apis mellifira*) located in large trees, rock crevices, or termite mounds. After the gatherers have opened and left the nest, the bird feeds on pieces of honeycomb left behind. From these it extracts mainly the larvae and the wax to supplement its normal diet of insects (*5–7*). The earliest written accounts of this bird-man interaction date back to the 17th century (*6*). Because of the anecdotal nature of most of these reports, however,

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many consider this interaction to be a myth. Soon, it may no longer be possible to prove them wrong, because in many areas honey is more and more being obtained from beekeepers or is even being replaced by commercial food, sugar, drugs, and alcohol. In these areas, the birds no longer guide (*5, 6*).

A 3-year field study of the greater honeyguide was carried out near Sololo and Marsabit in northern Kenya (*5*). The area, dry bush country, is the home of the nomadic Boran people who still follow the honeyguide regularly. In unfamiliar areas, their search time per bees' nest was, on average, 8.9 hours when not guided and 3.2 hours when guided (n = 329 hours and 238 hours, respectively). This 64% reduction in time is a conservative estimate, because it includes only those days during which at least one nest was found. Because many days without guiding lead to no nest detection at all, the acutal benefit to the humans is even more substantial (*5*). The honeyguide benefits as well. The Borans' use of smoky fire reduces the bird's risk of being stung, and their use of tools increases the amount of food, because 96% of all nests (n = 186) are accessible to the birds only after humans have opened them.

In view of this mutual benefit, it is not surprising that humans and the honeyguide have developed an elaborate interspecific communication system. To draw the attention of the bird, the Borans use a penetrating whistle that can be heard from a distance of over 1 km on our study sites. This whistle, known in Boran language as "*Fuulido*," is produced by blowing air into clasped fists, modified snail shells, or hollowed-out doum palm nuts (*Hyphaene coriacea* Gaertn.). Shouting and knocking on dry wood are also used to draw the bird's attention. Such noise doubles the encounter rate with the bird ($P < 0.02$, Mann-Whitney U test).

The greater honeyguide draws the attention of a human by flying close to him, moving restlessly between perches around him, and emitting a double-noted, persistent call, which sounds like "tirr-tirr-tirr-tirr" (Fig. 1A). Thereafter, it often performs a directional flight above the tree tops and may disappear for a minute or more (here termed first disappearance). Upon returning, the bird perches again on a conspicuous tree or bush. If approached to within 5 to 15 m, the bird takes off, still calling. After a short undulating flight, during which the white outer tail feathers are displayed, it perches again and continues calling. As the Borans follow, they whistle, bang on wood, and talk loudly to the bird to keep it interested in the guiding. When they get close to it, the bird flies to another perch. This pattern of leading and following is repeated until the bee colony is reached.

Professional honey gatherers (interviewed by H.A.I., a Boran) said that, through its guiding pattern, the bird informs them about the direction of, the distance to, and their arrival at the colony.

Direction. The direction in which the bird flies is said to indicate the direction of the colony. We plotted several guiding routes (Fig. 2B) and found a clear directional preference toward the nest (Fig. 2A; $P <$ 0.01, Rayleigh test) (*8*). The mean bearing of the closely clustered guiding vectors deviated only 0.5° from the nest direction; the large mean length of the vectors (0.834) indicates that this direction was maintained with a high consistency. As the variance in the direction of the last three sections was lower than in previous ones (F = 5.476, ν_1 = 38, ν_2 = 56, $P < 0.001$), the directional precision seems to increase as the colony is approached. Once the location of a colony was known to us, we could elicit repeated guidings to the same nest by not destroying it. When we attracted the bird to the same starting point, we were led via more or less the same route (Fig. 2C). From different compass points, the bird led us via different, but again fairly direct routes (Fig. 2D). When more than one colony was present in an area, the nest to which we were guided first was closer to the point of first encounter than subsequent ones in 88% of the cases (Fig. 2E) (n = 25 trips). These experiments and data suggest that the directionality exhibited by the bird is a reflection of its prior knowledge of the nest locality.

Distance. According to Boran honey collectors, three features decrease with diminishing distance to the nest (Nestdist): the duration for which the bird disappears after the first encounter (Disdur); the distance between the perches where it waits until the follower has caught up (Stopdist) (*9*); and the height of the perch (Perch). During several guiding tours we recorded these four variables plus the number of stops (Stopno)

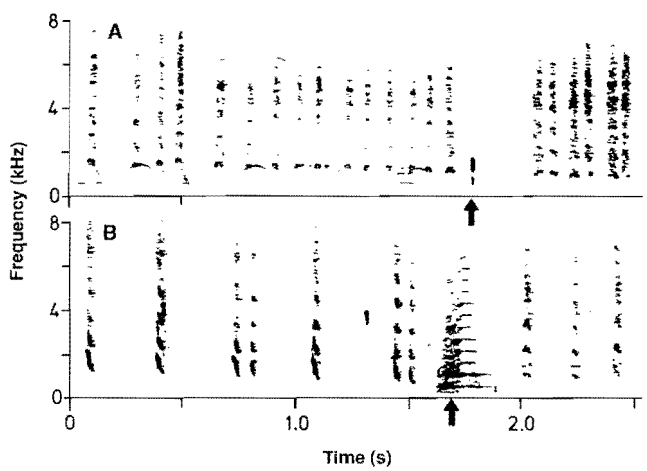

Fig. 1. Sonograms (**A**) of a typical guiding call emitted by the honeyguide on the route and (**B**) of an indication call emitted after the bird has reached the colony. Arrows indicate the input of human sound, which increased the repetition rate markedly in (A) but not in (B).

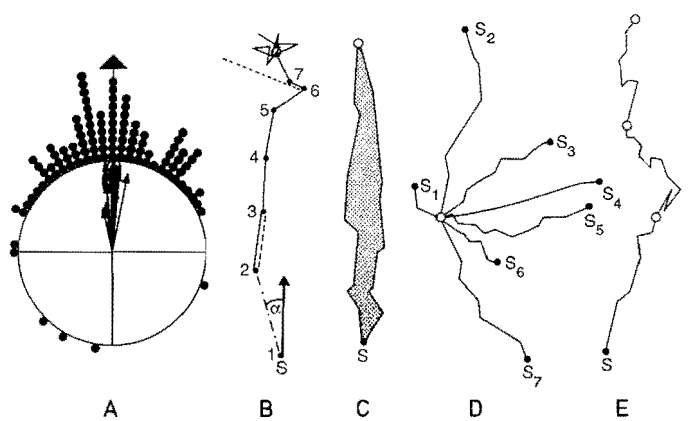

Fig. 2. (**A**) Orientation of 16 guiding routes in relation to nest direction (0°, large arrow). Black dots at the periphery give the pooled bearings of all guiding sections. Arrows originating in the center represent the vectors, calculated as the mean bearing of all sections in a particular guiding route. The overall bivariate means of the single vectors correspond to the centers of the ellipse, which indicates their 99% confidence limits (according to Hotelling's T^2 test) (*8*). (**B–E**) Sketches of guiding patterns from the first encounter (S) to the nest (O): (B) Typical fairly straight course, also showing the variables used in the distance analysis: Stopno (1 through 7), Stopdist (-----) (here between Stopno 2 and 3), and the corresponding Nestdist (———) and Distflown (–·–·–); α is the angle between any one section of the guiding and the straight direction to the nest (arrow). The dotted line originating from Stopno 6 shows an overshooting. (C) Area of five guiding courses between the same starting point and the same nest. (D) Routes to the same nest starting from different points (S_1 through S_7). (E) Consecutive guidings to three nests.

and the distance already covered (Distflown) from the start of the tour to the present perch (see Fig. 3A for an illustrative example) (*10*).

We found all three Boran statements to be true. The closer the nest, the shorter the duration of the first disappearance (Fig. 3A). When disappearing, the bird probably flies toward the nest to confirm its position before starting a guiding tour. Whether it covers the whole distance or only flies until it finds a conspicuous landmark, we cannot tell.

Also, the closer we approached the nest, the shorter the distance between stops, especially during the last 200 m (Fig. 3B) ($P = 0.011$, Wilcoxon test; *11*). Stopdist was not significantly related, however, to Distflown and Stopno (both $P > 0.180$). Thus, first disappearance and stopping distance reflect the remaining distance to the nest. Conversely, perching height reflects the number of stops and the distance already covered since the tour started. Perch decreased with Stopno (Fig. 3C) and Distflown (not shown in Fig. 3; $b = -0.002 \pm 0.001$, $P = 0.015$) (*12*). As guiding is fairly direct (Fig. 2, B through E), an increase in Stopno and Distflown normally leads to a decrease in Nestdist. Thus, our results confirm the honey gatherers' observation that the bird perches lower as it gets closer to the colony. The results do not, however, confirm their interpretation that perching height indicates the distance to the nest; Perch was not significantly related to Nestdist ($P = 0.275$).

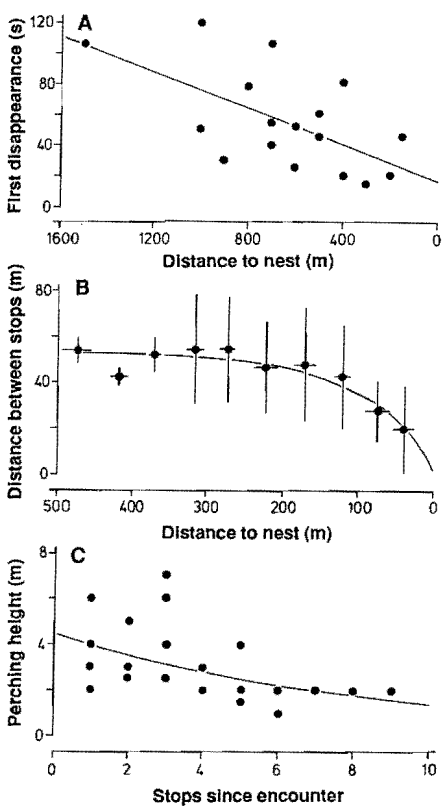

Fig. 3. (**A**) Duration of first disappearance, (**B**) stopping distance, and (**C**) perching height in relation to nest distance (A and B) and number of the stop (C), respectively. Shown in (B) are the means and standard deviations calculated from pooling data within the same 50-m category of nest distance (1 to 50, 51 to 100, . . ., 451 to 500 m). (A) and (C) give the original data together with the respective regression lines. Their slopes ($b \pm$ SE) are 0.059 ± 0.019, $P = 0.007$ [(A), linear model] and -0.115 ± 0.034, $P = 0.002$ [(C), exponential model].

Arrival. Boran honey gatherers maintain that they can tell from changes in the bird's behavior when it has reached its goal. We found two behavioral changes to support this statement; one is related to the call, the other to the flight pattern. On arrival at the nest, the bird perches close to it and emits the "indication call" (Fig. 1B). This call differs from the previous guiding call in that it has a softer tone, with longer intervals between successive notes. There is also a diminished response, if any at all, to whistling and shouting by humans. After a few indication calls, the bird remains silent. When approached by the searching gatherer, it flies to another perch close by, sometimes after circling around the nest. The resulting flight path (Fig. 2B) finally reveals the location of the colony to the gatherer. If the honey collector does not (or pretends not to) detect the nest, the bird gives up after a while. It may then leave the area either silently or start a guiding session to another colony. In the latter case, it switches from the indication call to the guiding call and resumes a fairly direct flight pattern.

Although a few investigators (*7*) have assumed that greater honeyguides know the location of one or more bee colonies in a particular area, the prevailing opinion still is that the bird does not know where it is taking a person but rather "leads in a most erratic course" until the sight and sound of incidentally encountered bees brings the guiding to a halt (*6, 13*). The very first discovery of a colony may indeed depend on such signs; but thereafter the birds (regularly?) monitor the nests even when no guiding is taking place. From camouflaged observing positions occupied before dawn, we observed several marked and unmarked honeyguides visiting a nest. They always appeared singly, stayed for only about a minute, and then flew away. When the bees were still docile, as on cloudy and cool mornings, the bird would fly straight into the entrance of the nest and peer into it.

The information gathered during such visits enables the bird to engage in its goal-oriented guiding behavior. Our finding that native people are able to interpret this pattern reliably is, however, not equivalent to saying that every aspect of the bird's guiding behavior is meant to inform them. The changes in call and flight pattern after the arrival (Figs. 1 and 2B) probably are informative; but there are more parsimonious explanations for other aspects of the bird's behavior. The directional flight (Fig. 2A) and the duration of the first disappearance (Fig. 3A) are inevitable results of a bird flying to a nest that it knows. The reduction in perching height (Fig. 3C) could be due to the honeyguide's gradual loss of fear of the follower. Similar cases of distances decreasing over time are known from mobbing birds and other animals interacting with predators (*14, 15*). Decreasing risk and fear, however, are unlikely to account for the reduced distance between stops (Fig. 3B), because Stopdist decreased neither with Distflown nor with the frequency with which the bird had been approached (Stopno). Also, the bird allows people to approach to within 5 to 15 m of its perch, much closer than even the shortest average stopping distance of 20 m (Fig. 3B).

We suggest that the decreasing Stopdist represents an "area-restricted search" (*16*) that is performed by many animals when close to their goal, be it food, hosts, or homes (*17–19*). One common characteristic of this search pattern is reduced step length and thus speed. Consequently, the animal spends more time scanning the promising area and is more likely to detect signs of the goal, such as swarming bees or specific landmarks. This will enable it to correct directional errors (compare the smaller directional variance toward the end) to avoid an overshooting or even missing (dotted line in Fig. 2B). Farther away from the nest, longer stopping distances may be more economical because they reduce the number of energetically expensive maneuvers associated with takeoff and landing. According to this interpretation, distances between the final stops should decrease when any feature impedes detection of the nest (for example, dense vegetation). Unfortunately, our present data do not allow us to test this prediction, but the high variation in stopping distances may have resulted partly from such differences in visibility. This high variation also makes it unlikely that the bird "deliberately" tells the follower where to look precisely for the nest.

Our data also do not yet allow us to test the following two claims of Boran honey gatherers: (i) that a bird, flying lower than the tree tops, will guide to a colony close to the ground, and (ii) that when nest distances become very long (about 2 km or more), the birds "deceive" the gatherers about the real distance by stopping at shorter intervals. However, having found all the other Boran

observations to be true, we see no reason to doubt the statements of these excellent "ethologists."

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9. The observation that stopping distances decrease as the bees' nest is approached was also reported by G. W. Stow [*The Native Races of South Africa* (Swan Sonnenschein, London, 1905)].
10. We measured distances by counting paces and later converting them into meters. Perching heights were estimated to the nearest 0.5 m. In cases of skewed distribution, original data were log-transformed.
11. The relation between Stopdist and Stopno was tested within guidings, yielding one regression coefficient (b) for each tour. The relations between Stopdist and Nestdist and Distflown, respectively, were tested across guidings. In the case of Nestdist, separate regressions were calculated for each Stopno, whereas, in the case of Distflown, separate regressions were calculated for each 50-m category of Nestdist. In all cases, the regression coefficients were then tested against the 0 hypothesis of no relation ($b = 0$) by means of a Wilcoxon matched-pairs, signed-ranks test.
12. The small sample size did not allow us to calculate separate regressions as in the case of Stopdist. Therefore, Perch data from all guidings were pooled.
13. Our reanalysis of Friedmann's data (*6*) indicates that even his birds showed directional guiding and probably had prior knowledge of the hive location (H. A. Isack and H.-U. Reyer, in preparation).
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