

Naked mole-rats recruit colony mates to food sources

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Abstract. Naked mole-rats, *Heterocephalus glaber*, are eusocial, subterranean rodents that inhabit arid regions of northeastern Africa. They feed on bulbs and tubers that are patchily distributed. Nests are often located far from the nearest food source through a labyrinth of tunnels. Two captive colonies were studied to determine whether successful foragers recruit colony mates and, if so, how. Individuals that found a new food source typically gave a special vocalization on their way back to the nest and waved the food around once they got there. Colony mates preferentially visited the site where the initial forager had obtained food, often bypassing alternative sites containing the same type of food. Recruits preferred to use tunnels that had been traversed by the ‘scout’ rather than an alternative pathway to the same food, regardless of whether they had to turn in the same or the opposite direction from that of the scout to enter the previously used pathway. Recruits preferred tunnels that the scout had recently used over tunnels that were recently traversed by another colony mate carrying the same type of food. When tunnels traversed by the scout were replaced with clean substitutes or with tunnels that were recently traversed by another colony mate carrying the same type of food, recruits showed no pathway preferences. Results indicate that naked mole-rats follow each other’s (odour) trails to food. There are intriguing parallels between the foraging recruitment system of *H. glaber* and those of other social vertebrates and insects.

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Foragers in many species of social vertebrates and invertebrates face the dual challenges of locating patchy, unpredictable food sources and transmitting the information to other group members. Individuals advertise the locations of super-abundant food sources with special vocalizations in some birds (e.g. cliff swallows, *Hirundo pyrrhonota*: Brown et al. 1991; ravens, *Corvus corax*: Heinrich & Marzluff 1991) and mammals (e.g. chimpanzees, *Pan troglodytes*: Wrangham 1977; cotton-top tamarins, *Saguinus oedipus*: Cleveland & Snowdon 1982; Elowson et al. 1991; toque macaques, *Macaca sinica*: Dittus 1984; spider monkeys, *Ateles geoffroyi*: Chapman & Lefebvre 1990; and greater spear-nosed bats, *Phyllostomus hastatus*: Wilkinson & Boughman, in press), whereas Norway rats (*Rattus norvegicus*) leave odour trails to preferred food sources (Galef & Buckley, 1996).

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Foraging recruitment systems of social insects also take several forms. In many species of stingless bees (e.g. *Trigona cufira*: Michener 1974) and some ants (e.g. *Leptothorax acervorum*: Möglich 1978), foragers lead recruits to food. In many other ant species (reviewed by Gabba & Pavan 1970; Hölldobler & Wilson 1990, pp. 265–273; Hölldobler 1995), a few species of stingless bees (Michener 1974; Lindauer 1961) and most species of tent caterpillars (Fitzgerald 1995), foragers lay chemical trails to food. Finally of course, the dance language of honey bees, *Apis mellifera*, is legendary for its precision and accuracy (von Frisch 1967; Seeley 1995).

Naked mole-rats are eusocial, subterranean rodents that inhabit arid regions of northeastern Africa (Sherman et al. 1991; Jarvis et al. 1994). On average, colonies contain 70–80 mole-rats (range=2–295 or more: Braude 1991; Lacey & Sherman, 1996), among which only one female and one to three males breed (Lacey & Sherman 1991; Sherman et al. 1992). Colony mates are closely related owing to natal philopatry and

inbreeding (Faulkes et al. 1990; Reeve et al. 1990). Among non-breeders, there is a size-based division of labour: small males and females are the primary maintenance workers and foragers, and larger individuals of both sexes defend the colony against snakes and foreign mole-rats (Lacey & Sherman 1991; Jarvis et al. 1991; O'Riain & Jarvis, in press).

Naked mole-rats feed on a variety of succulent bulbs and tubers. In southeastern Kenya, large *Pyrenacantha kaurabassana* (Icacinaceae) tubers and small *Macrotyloma maranguense* (Leguminosae) roots are their major foods (Brett 1991). The large tubers and patches of small roots are widely and irregularly spaced, so the animals must tunnel extensively to reach them. Using radiotelemetry equipment, Brett (1991) discovered that the burrow system of one colony containing approximately 87 mole-rats was a maze-like labyrinth 3.6–4.0 km long that covered an area of roughly 105 000 m². This colony contained 11 nest chambers that were used at different times of the year, apparently depending on proximity to food; nests were often far from the nearest known food source, however. Nests sometimes contained tuber husks and root skins, suggesting that food may have been brought there for consumption and raising the question of how naked mole-rats harvest their food. The present study investigated whether workers discover new food sources independently or locate food using information obtained from colony mates.

EXPERIMENT 1: RECRUITMENT TO SPECIFIC FOOD SOURCES

This experiment was conducted to see whether hungry naked mole-rats recruit specifically to a

food source that was recently discovered by a colony mate when other identical food sources are available nearby.

Methods

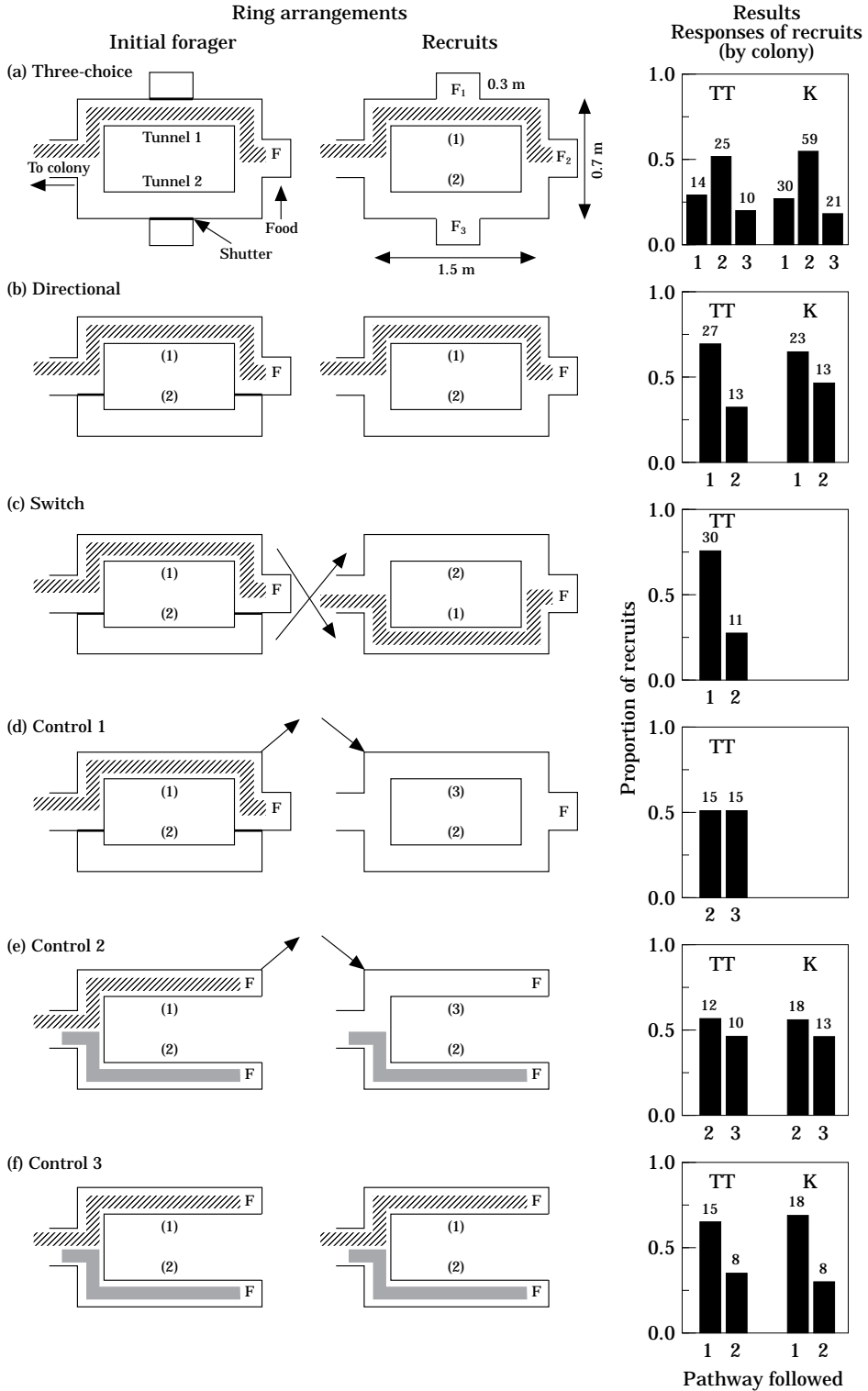
Subjects

We studied two captive colonies, designated TT ($N=34$ individuals) and K ($N=20$) from January 1992 to August 1993, and from August to December 1995. Colony founders were captured in southeastern Kenya in 1977 and 1980, respectively. We housed each colony in a separate room, within its own artificial tunnel system consisting of 20–30 m of clear Plexiglas tubes (see Lacey & Sherman 1991 for details of tunnel construction, husbandry and diet). To simulate the mole-rats' natural environment, we kept colony rooms quiet, warm (26–28°C) and humid (55–70%); dim illumination was provided by several lamps with 25-W red bulbs. Every mole-rat was uniquely tattooed on its back for individual identification; during experiments, we used a small flashlight to confirm tattoo marks.

Recording vocalizations

To record vocalizations made by individuals that found food, we cut a slit (32 mm wide) along the entire length of a 1-m long Plexiglas tube. The slit was covered with clear tape to reduce air flow that might disturb the mole-rats; pin holes were punched through the tape down its entire length. We deprived colony K of food for 24 h, and then attached the recording tube to the colony's tunnel system; we baited the distal end of the tube with pea-size (ca 1 cm³) pieces of sweet potato. We allowed one mole-rat to enter the tube and find the food and then recorded its vocalizations using

Figure 1. Schematic diagram showing how the rectangular food ring was set up for (a) Experiment 1 (i.e. the three-choice test), and Experiment 2 (directional, switch and control tests 1–3; b–f respectively). In each row, the left-hand drawing depicts the way the apparatus looked when the initial forager (scout) entered and exited, and the centre drawing shows the set-up when recruits were permitted to enter one at a time; the right-hand histograms indicate the number of recruits that arrived at each food goal (a) or that followed each numbered pathway to the food goal (b–f) before the scout or a previously successful recruit returned to the food ring. For clarity of presentation, in (a) F_2 is depicted as the food goal visited by the initial forager; in the actual trials, however, the 'correct' goal was randomized. Hatched pathways represent (schematically) the route taken by the initial forager, grey pathways represent the route taken by a successful forager that was removed before it could communicate its find to colony mates, 'F' indicates the location of food goals, and bars across pathways indicate the locations of shutters. The two main tunnels in the food ring (a–d) and the Y-maze (e, f) are numbered to clarify the differences between experiments and results.



a Nagra IV-L tape-recorder (tape speed=38 cm/s) and a Sennheiser directional condenser microphone (Model MKH-416) held 1–2 cm from the slit and positioned over the head of the mole-rat as it moved through the tunnel. Sound spectrograms (Fig. 2) were made using SoundEditPro, and the image was edited for publication by removing extraneous noise.

Experimental procedures

We attached a rectangular ring of Plexiglas tunnels to the colony's main burrow system by a single tunnel (Fig. 1a, left). Access to the ring was controlled with a plastic shutter. Three short tunnel extensions, spaced evenly in the ring, served as 'food goals'. Each food goal could be isolated with a shutter, enabling us to restrict access to that goal or to trap any mole-rat that entered it.

We conducted observations 24–28 h after a colony was last fed. To equalize hunger levels among colony members, we removed all uneaten food 6 h after a feeding; no new food was added for the next 18–22 h. There was always uneaten food left at 6 h, implying that individuals were satiated at that point. We assumed that colony members were equally hungry 18–22 h later.

To start a three-choice trial, we randomly selected one food goal (by drawing numbers out of a hat) and placed 16–20 pea-sized pieces of sweet potato at its distal end; the other two goals were shuttered closed (Fig. 1a, left). We allowed a single mole-rat to enter the ring and closed the main shutter behind it. The forager usually explored the ring for several minutes before discovering the food; then it took a piece and immediately headed back the way it had come. If the forager failed to take food before attempting to exit the ring we stopped the trial and cleaned the tunnels thoroughly with soap and hot water.

When the initial forager (or 'scout') returned to the ring entrance with a piece of food in its mouth, we raised the main access shutter just long enough to allow it to leave; we then quickly placed 16–20 identically-sized pieces cut from the same sweet potato in the other two food goals, and removed all goal shutters (Fig. 1a, centre). We allowed mole-rats to enter the food ring one at a time and recorded the first goal each one entered.

To eliminate the possibility that naive colony mates could receive information about alternative food sources from secondary foragers, whenever an individual entered one of the 'wrong' goals (i.e. a goal not visited by the scout) we removed it from the tunnel system until the end of that trial. To focus on the behaviour pattern of the scout and reduce possible confounding effects of information transmitted by subsequent recruits, we did not allow individuals that had already visited a goal once during that trial (including the scout) to return to the ring.

We conducted 36 trials in colony K and 16 trials in colony TT. Each trial lasted at least 30 min and was terminated when no new recruits attempted to enter the ring for 3 min. At the end of each trial, we scrubbed the entire ring with soap and hot water. To minimize habituation, we conducted no more than one trial per day and skipped a day between trials every 2–3 days. Mole-rats could not enter the ring except during a food trial.

Data analyses

We analysed our data using binomial tests (Lehmann 1975). Under the null (random) hypothesis $P=0.333$, because recruits could choose between three food goals. First, we counted each mole-rat once in each trial in which it recruited (even though some individuals recruited in more than 1 trial), pooled data from multiple trials on the same colony and tested the distribution of food goals visited against the binomial null expectation. Second, for each trial in each colony, we computed the proportion of recruits that visited the 'correct' food goal (i.e. the goal the scout had visited). We tested whether these 'composite scores' differed between colonies; because they did not ($P=0.65$, G -test), we combined the data. Then we fitted composite scores from all trials in both colonies to a generalized linear model with overdispersion (McCullagh & Nelder 1989) using the GLENMOD procedure (SAS 1993), and computed 99% confidence intervals for the probability that recruits entered the single correct goal. Third, to eliminate pseudo-replication, we counted the food goal choice of each individual mole-rat only once in the entire experiment (i.e. only in the first trial in which it recruited). This analysis is extremely conservative, and it drastically reduced our sample size because not all mole-rats in a colony foraged.

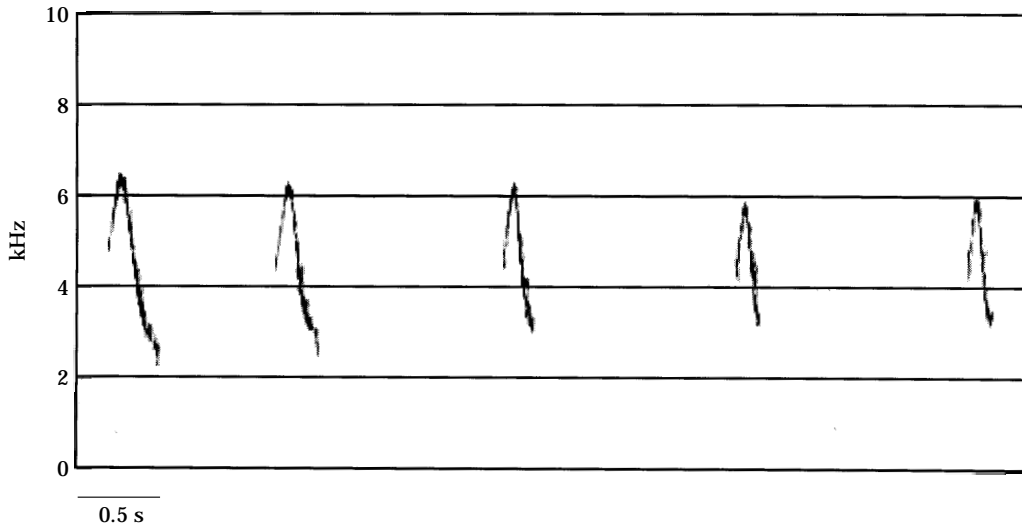


Figure 2. Sound spectrogram of a 'recruitment call' produced by a naked mole-rat that discovered a new food source and was carrying a piece of food back to the colony's nest.

Results

Recruitment behaviour

When the initial forager arrived at the first T-junction in the food ring, it usually spent 1–2 min sniffing and repeatedly turning one way and then the other before entering a tunnel. It moved slowly and hesitantly, stopping often to sniff, and frequently crouched and backed up before proceeding. Once the scout found the baited food goal, it thoroughly sniffed the sweet potato, took a piece in its incisors, spun around, ran unhesitatingly back along the pathway it had come with the food held aloft in its jaws and exited the ring when the shutter was raised. On 34 of 46 occasions (74%) the scout gave a chirp-like vocalization at a constant rate on the return trip (Fig. 2), only stopping when it reached the nest. We never heard this call before the scout found food ($N > 50$ observations), and unsuccessful foragers never gave this call as they returned to the nest ($N = 37$). The call was given on just 3 of 28 (11%) occasions when a forager returned to the nest from a food source that had already been discovered by a colony mate.

Individual notes of the call (Fig. 2) had a mean (\pm SD) starting frequency of 4.30 ± 0.35 kHz (range = 3.6–5.0 kHz; $N = 51$ calls from 12 animals), a mean maximum frequency of 5.29 ± 0.51 kHz (4.40–6.10 kHz; $N = 55$ calls from 12

animals), a mean minimum frequency of 2.71 ± 0.32 kHz (2.20–3.50 kHz; $N = 53$ calls from 12 animals), and a mean duration of 0.16 ± 0.03 s (0.10–0.28 s; $N = 41$ calls from 10 animals).

The initial forager usually carried the food piece back to the nest intact rather than stopping to gnaw on it. Aside from calling, it showed no special marking behaviours such as urination, rubbing against tunnel walls or ano-genital dragging. Once the scout reached the nest, it often held the food piece aloft in its jaws and waved it around (for up to 30 s). Sometimes it appeared that the scout was simply attempting to keep the food away from others. If a colony mate succeeded in seizing hold of the food, a tugging contest sometimes ensued and usually the larger individual prevailed, particularly if it was a breeder (Schieffelin & Sherman 1995). Even when scouts were not pursued by hungry colony mates, however, they often waved the food around, then dropped it in a corner without consuming it themselves. Sometimes the scout was the first to attempt to return to the food ring, but more often the ring was visited by multiple colony mates before the scout returned.

Three-choice tests

As the initial forager was returning to the nest carrying a piece of sweet potato, it often

encountered colony mates. Some of these individuals spontaneously followed the scout's path in the reverse direction and, unlike the scout, they entered the food ring with little or no hesitation. These recruits went to the same food goal that the scout had visited more often than to the other two food goals in colony K ($N=110$ observations on 19 different recruits, $P<0.023$) and colony TT ($N=59$ observations on 20 recruits, $P<0.007$; Fig. 1a, histograms). Using the generalized linear model approach, the 99% confidence interval for the proportion of correct choices (colonies combined) was 0.480–0.630, which is well above the binomial null probability. Counting each individual only once in the experiment (i.e. only the first time it recruited), 12 recruits in colony K went to the 'correct' goal and seven went to one of the two 'incorrect' goals ($P=0.007$); in colony TT, 12 went to the correct goal and nine went to one of the incorrect goals ($P=0.026$); for the two colonies combined, $P=0.006$.

Identities of recruits changed in the course of the experiment. During the first few trials, colony members of all sizes entered the ring. As trials proceeded, however, larger mole-rats in both colonies (including the breeders) stopped foraging. Apparently they disliked being trapped and, because food was consistently brought to the nest for them by smaller colony mates, they did not need to forage for themselves.

Discussion

Recruitment calls

Because successful initial foragers called after but never before they found food, whereas unsuccessful foragers and recruits rarely called, it seems reasonable to label the vocalization (Fig. 2) a 'recruitment call.' Individual notes of the recruitment call were structurally similar to those of the 'loud chirp' and, especially, the 'soft chirp' recorded by Pepper et al. (1991). The most obvious difference is that the recruitment call was always given repetitively, but soft chirps were usually given once or twice (e.g. when colony mates bumped into each other), and loud chirps were generally given in short bouts (e.g. during conflicts over food or digging opportunities).

Individual recruitment call notes sounded more like soft than loud chirps, but inspection of spectrograms indicated that their peak frequency was higher than soft chirp notes (6–7 kHz versus 4 kHz) and that their frequency range was greater (2–6 kHz versus 2–4 kHz). Recruitment call notes peaked at about the same frequency as loud chirp notes, but their frequency range was narrower than that of loud chirps (1–7 kHz).

Moreover, Pepper et al. (1991) recorded several harmonics of loud chirp notes in the 8–14 kHz range, but we did not detect any high frequency harmonics of recruitment call notes. These differences, along with the special circumstances under which the call was given, suggest that the recruitment call is a previously undescribed element of the naked mole-rat's vocal repertoire. If so, it brings to 18 the total number of different vocalization types in this species, by far the largest vocal repertoire of any known rodent.

Pepper et al. (1991) suggested that soft chirps may be individually distinctive, and soft chirp notes of different-sized individuals in the same colony indeed differ in maximum frequency, frequency range, and duration (P. Sherman, unpublished data). D. Polakow & S. Telford (unpublished data) confirmed that soft chirps are individual-specific using discriminant analyses and suggested that an individual's soft chirps represent its unique vocal 'signature'. Structural similarities between recruitment call notes and soft chirps raise the possibility that the former advertise not only the presence of food but also the identity of the scout who discovered it.

Three-choice tests

Naked mole-rats could locate a food source that was recently discovered by a colony mate. Recruits chose the food goal visited by the scout significantly more often than the other two goals combined (Fig. 1a, histograms). These results are particularly compelling because, to get to the 'correct' food goal, recruits usually had to pass by one or two goals containing an equal number of identically sized pieces cut from the same sweet potato as that retrieved by the scout. Because our experimental design precluded the possibility that the scout was physically leading recruits back to the correct food goal, the preferences that we observed imply that recruits used locational information.

EXPERIMENT 2: THE MECHANISM OF RECRUITMENT

We designed a follow-up experiment to determine how naked mole-rat recruits obtain information about the location of new food sources. Two possibilities were tested, namely that (1) the initial forager indicates 'map' directions behaviourally, or (2) recruits follow the scout's odour to the food.

Methods

Subjects and procedures

Study colonies, housing and husbandry procedures were the same as in Experiment 1. We modified the test ring by removing the two side goal tubes, leaving only the goal opposite to where the ring was attached to the colony (Fig. 1b–d, left). After the mole-rats had fasted for 18–22 h, we placed 16–20 pea-sized pieces of sweet potato in the remaining goal. We opened the main shutter blocking access to the food ring just long enough for one animal to enter and then closed it again. This initial forager was forced to turn either left or right (determined by a coin flip) at the first T-junction, and to return along the same path, by closing off one side or the other of the ring using shutters placed next to the entrance and the food goal.

Once the scout had traversed the designated half of the ring, found the food, and exited with a piece, we briefly closed the main shutter and conducted one of three types of trials (below). In every trial, we allowed one mole-rat to enter the apparatus at a time and recorded the identity of each and the path it used to get to the food goal. We counted each recruit only once per trial. After each trial ended, we scrubbed the entire ring with soap and hot water.

Directional test

To confirm that recruits possessed locational information, we removed all shutters immediately after the initial forager left the food ring (Fig. 1b, centre) and allowed other colony members to enter the ring one at a time. Then we recorded whether each individual turned left or right at the first T-junction. We conducted 21 directional trials on colony K and 22 on colony TT.

Switch test

To separate directional signalling from odour trails as possible recruitment mechanisms, we switched the two sides of the food ring immediately after the initial forager left. This manipulation placed the tunnels through which the initial forager had passed on the opposite side of the T-junction from their original position (Fig. 1c, centre). If the mole-rats used directional cues, they should have turned preferentially the same way as had the initial forager (i.e. into the 'clean' tunnels). If they followed a trail, however, they should have turned preferentially in the opposite direction from that taken by the scout (i.e. into the 'used' tunnels). We conducted 16 switch trials on colony TT; we did not test colony K because, by the time we started this experiment, there were few enough regular foragers that pseudoreplication was unavoidable.

Control tests

We conducted three kinds of control tests, as follows.

(1) To see what recruits do when offered a choice between two unused tunnels, we replaced the tubes and junctions the initial forager had traversed with clean substitutes immediately after it left the ring (Fig. 1d, centre). Thus, no physical traces of the scout were available to recruits arriving at the first T-junction. If the mole-rats used directional cues, they should have turned preferentially the same way as had the scout, but if they followed the scout's odour trail they should have been confused. We conducted 12 of these control trials on colony TT; we did not test colony K.

(2) To see what recruits do when offered a choice between a clean tunnel and a tunnel recently used by a colony mate other than the initial forager, we turned the ring into a Y-maze by removing the food goal and the short tunnels leading to it (Fig. 1e, left). We baited the distal end of both remaining long tunnels with pea-sized pieces cut from one sweet potato, capped them, and admitted one mole-rat to the apparatus. We forced this individual to turn either right or left (determined by a coin flip) with a shutter. We allowed it to find the food and carry a piece back to the main access shutter, then swiftly removed the individual before it could communicate its find to colony mates. We then allowed another mole-rat into the apparatus, and forced it to turn in the

opposite direction from the first; if no other individual entered the maze within 10 min, we started the trial over. We permitted the second animal to find the food, carry a piece out of the apparatus, and give recruitment calls (i.e. to behave as the 'initial forager'). We closed the main shutter and immediately replaced the tunnels used by the second animal (but not the first) with clean, baited substitutes (Fig. 1e, centre). Then we allowed mole-rats to enter the Y-maze one at a time and recorded their behaviour. If recruits simply followed odours of any colony mate, they should have preferred the 'dirty' over the 'clean' tunnel, but if they were specifically following the initial forager they should have been confused by the absence of any trace of that individual. We conducted 13 of these control trials on colony K and 14 on colony TT.

(3) To see what recruits do when offered a choice between a tunnel used by the initial forager and a tunnel used by another colony mate, we followed the same procedures as in control 2, except that after the second animal (the 'initial forager') left the Y-maze we did not replace any tunnels (Fig. 1f, centre). We simply removed all shutters, allowed mole-rats to enter the apparatus one at a time, and recorded their behaviour patterns. If recruits followed odours of any colony mate, they should have chosen the left and right maze arm equally often, because both had recently been traversed by an individual carrying a piece of the same sweet potato. If they were specifically following the odour of the initial forager, however, their choices should have been biased in favour of the tunnel it had traversed. We conducted 14 of these control trials on colony K and 9 on colony TT.

Data analyses

We analysed data as in experiment 1, except that the null (random) binomial probability was 0.500 because recruits had only two choices (i.e. turn left or right) when they entered the food ring or the Y-maze.

Results

Directional test

In both colonies, recruits arriving at the first T-junction in the food ring preferred to enter the tunnel used by the initial forager over the clean

alternative (Fig. 1b, histograms). Choice for the previously used pathway was significant in colony TT ($N=40$ observations on 17 different recruits, $P=0.020$); in colony K a non-significant bias was evident ($N=36$ observations on 11 recruits, $P=0.068$). We combined data from the two colonies because the proportion of 'correct' choices (i.e. turning into the previously used tunnel) did not differ between them ($P=0.510$). The generalized linear model analysis revealed that the 99% confidence interval for the proportion of correct choices was 0.563–0.788; this interval does not include (i.e. is above) the binomial null probability. Counting each individual mole-rat only once in the experiment (i.e. only the first time it recruited), in colony K, seven recruits chose the previously used tunnels and five chose the clean alternatives ($P=0.558$); in colony TT, 11 recruits chose the previously used tunnels and five chose the clean alternatives ($P=0.105$); for the two colonies combined, $P=0.115$.

Switch test

When we switched the two sides of the food ring in colony TT, recruits arriving at the first T-junction favoured the tunnel used by the initial forager over the clean alternative by nearly a 3:1 ratio (Fig. 1c, histogram), even though their choice took them in the opposite direction from that of the initial forager ($N=41$ observations on 15 different recruits, $P=0.002$). Using the generalized linear model approach, the 99% confidence interval for the proportion of 'correct' choices (i.e. turning the same way the initial forager had turned) was 0.595–0.846; this interval does not include (i.e. is well above) the binomial null probability. Counting only the first choice of each mole-rat, 14 recruits chose the previously used tunnels and three chose the unused tunnels ($P=0.001$).

Control tests

(1) When recruits in colony TT could choose between two clean tunnels, they behaved much like the initial forager: hesitating, sniffing, crouching and backing up frequently before proceeding slowly in one direction or the other. They showed no preference for turning right or left ($N=30$ observations on 10 different recruits, $P=1.000$; Fig. 1d, histogram). Using the generalized linear

model approach, the 99% confidence interval for the proportion of 'correct' choices was 0.309–0.659; this interval includes (indeed, it is nearly centred on) the binomial null probability. Counting only the first choice of each mole-rat, six recruits chose the previously used pathway and five chose the unused pathway ($P=0.736$).

(2) When recruits could choose between a clean tunnel and one used recently by a colony mate other than the scout, both containing food, they showed a slight but non-significant preference for the 'dirty' tunnel ($N=31$ observations on 13 different foragers in Colony K, $P=0.300$; $N=22$ observations on 10 different foragers in Colony TT, $P=0.500$; Fig. 1e, histogram). We combined data from the two colonies because the proportion of 'correct' choices did not differ between them ($P=0.570$). The generalized linear model analysis indicated that the 99% confidence interval for the proportion of 'correct' choices was 0.434–0.660; this interval includes (indeed, it is nearly centred on) the binomial null probability. Counting only the first choice of each mole-rat, in colony K, seven recruits chose the previously used tunnels and six chose the clean alternatives ($P=0.500$); in colony TT, four recruits chose the previously used pathway and six chose the unused pathway ($P=0.518$); for the two colonies combined, $P=0.835$.

(3) When recruits could choose between tunnels used by the scout and tunnels used by another colony mate, they preferred the former in both colonies ($N=26$ observations on 12 different foragers in Colony K, $P=0.060$; $N=23$ observations on 11 different foragers in Colony TT, $P=0.144$; Fig. 1f, histogram). We combined data from the two colonies because the proportion of 'correct' choices did not differ between them ($P=0.765$). The generalized linear model analysis revealed that the 99% confidence interval for the proportion of 'correct' choices was 0.560–0.775; this interval does not include (i.e. is above) the binomial null probability. Counting only the first choice of each mole-rat, in colony K, eight recruits chose the tunnels used by the initial forager and three chose the alternative tunnels ($P=0.091$); in colony TT, eight recruits chose the tunnels used by the initial forager and four chose the tunnels used by another colony mate ($P=0.221$); for the two colonies combined, $P=0.041$.

Discussion

Naked mole-rats apparently recruit to a new food source by following the pathway of the colony mate who found it. Significantly more recruits followed the pathway taken by the initial forager, regardless of whether they had to turn in the same (Fig. 1b) or the opposite direction (Fig. 1c) to do so. Moreover, recruits preferred to enter tunnels used recently by the scout over tunnels used recently by another food-carrying colony mate (Fig. 1f), but they appeared confused and showed no pathway preferences when the tunnels used by the scout were replaced with clean substitutes (Fig. 1d) or with tunnels used recently by another food-carrying colony mate (Fig. 1e). The scout did not indicate directions behaviourally (e.g. by 'dancing'), nor did it physically lead colony mates to food (e.g. by 'tandem running': Wilson 1959; Möglich 1978).

Results of the directional and switch tests prove that the mole-rats preferred a recently used tunnel over a clean alternative, but do not prove that recruits oriented to the initial forager's trail. This is because each recruit that entered the 'dirty' tunnel might have added something odoriferous to it, thereby further emphasizing it. If the mole-rats were simply following the pathway taken by the majority of previous foragers, however, then some directional bias should have been evident in controls 1 and 2, because once the initial recruit in each trial had visited the food, subsequent recruits should have preferred the used pathway over the less well-travelled alternative. The apparent confusion of recruits at the first T-junction throughout the first two control experiments and their lack of pathway preferences (Fig. 1d, e, histograms) suggest that recruits were indeed searching for the tunnel used by the initial forager, and not just for a recently used tunnel. Results of the third control experiment (Fig. 1f, histogram) confirm that recruits distinguished between tunnels through which the scout had recently carried food and tunnels through which another colony mate had recently carried the same type of food. The latter experiment probably comes closest to duplicating choices the mole-rats make in nature, and the outcome is therefore particularly noteworthy.

Although we did not investigate the chemical nature of the trail recruits followed, it apparently emanated from the initial forager and not (just) from the food it was carrying. In Experiment 1,

recruits preferred to forage in the side tunnel (food goal) the initial forager had entered (Fig. 1a, histogram), even though to get there they usually had to pass by side tunnels containing pieces cut from the same sweet potato as that taken by the initial forager. If the smell of the food were the primary cue, then presumably recruits should have entered the first side tunnel they encountered which contained that food. In Experiment 2, control 2, recruits showed no preferences, even though one of the Y-maze arms had recently been traversed by a colony mate other than the scout who was carrying a piece of sweet potato (Fig. 1e, histogram). If the smell of the food were the primary cue, recruits should have preferred the tunnel through which it had just been carried. Finally, in Experiment 2, control 3, recruits distinguished between tunnels through which the scout had recently carried a piece of sweet potato and tunnels through which a different colony mate had recently carried another piece of the same potato (Fig. 1f, histograms). This discrimination is not predicted under the hypothesis that the smell of food was the primary recruitment cue.

We did not observe any special scent-marking behaviours by initial foragers as they returned to the nest. A mole-rat may leave a distinctive chemical trace, however, by simply walking through a tunnel. After urinating, the animals often scratch their head, shoulders or cheeks with their hind feet (Lacey et al. 1991). As they proceed through their tunnels, they constantly brush the walls, potentially smearing such odours along them; moreover, there is minimal air movement to dissipate odours in the mole-rats' closed tunnel systems. Unfortunately we do not know whether odours adhere better or worse to Plexiglas than to the hard-packed dirt walls of tunnels in the field and thus whether recruitment is enhanced or reduced in nature.

GENERAL DISCUSSION

There are several intriguing parallels between the foraging recruitment system of naked mole-rats and those of various social insects and vertebrates that also forage on patchy, unpredictably distributed food resources which are hard to locate but abundant when found. These similarities add another dimension to the multiple behavioural convergences between eusocial insects and

cooperatively breeding vertebrates (see Sherman et al. 1995). For example:

(1) In some species of stingless bees (e.g. *Trigona* and *Melipona*: Lindauer 1961; Michener 1974; Gould et al. 1985) and ants (*Camponotus* and *Atta*: Hölldobler 1971b, 1995) when successful foragers return to their nest, they buzz or stridulate loudly, and the sound/vibration attracts recruits to the forager. Likewise when a hungry mole-rat found a new food source, it gave a special call (Fig. 2) on its way back to the nest.

(2) In several species of honey bees, stingless bees and ants, successful foragers offer a sample of food to potential recruits during waggle dances or other displays (Lindauer 1967; von Frisch 1967; Michener 1974; Hölldobler 1971b). In the weaver ant, *Oecophylla longinoda*, scouts perform an unusual head-waving behaviour just before offering food to naive colony mates (Hölldobler & Wilson 1978). By learning the taste or smell of food, foragers presumably enhance their likelihood of and expedience in locating it. When a naked mole-rat that discovered a new food source arrived back at the nest, it often waved the food around. One possible function of this behaviour pattern is advertising. Because the behaviour pattern is normally performed in the subterranean darkness, it probably alerts colony mates to the smell of the food.

(3) In many ant and tent caterpillar species and some stingless bees, recruits follow trails laid by previous successful foragers. The glands that are the source of ants' odour trails have been identified (reviewed by Hölldobler & Wilson 1990, pages 227–249; Hölldobler 1995). In eastern tent caterpillars (*Malacosoma americanum*: Fitzgerald 1995) and some ants, special behaviour patterns (e.g. abdomen dragging) are associated with trail laying. In other ants, however, colony mates recruit accurately even though the scout simply walked over the substrate (e.g. in *Amblyopone australis*: Hölldobler & Palmer 1989; *Lasius pallitarsis*: Nonacs 1991). Likewise, naked mole-rats that were the first to find a new food source did not show any special trail-laying or scent-marking behaviours, yet recruits were able to retrace their steps.

(4) Confusion among recruits generally results when odour trails in tent caterpillars (Fitzgerald 1995) and social Hymenoptera are experimentally obliterated (e.g. in *Pogonomyrmex badius*: Hölldobler 1971a; *Tetramorium aculeatum*:

Cammaerts et al. 1994; *Trigona postica*: Lindauer 1967). Naked mole-rat foraging recruits were also confused when tunnels used by the scout were replaced with clean substitutes (Fig. 1d, e, histograms).

(5) In honey bees and some stingless bees, transfer of information about the location of food sources takes place within the confines of the nest, making it unlikely that individuals from other nests (non-relatives) could 'eavesdrop.' Likewise, in naked mole-rats, information transfer about food sources takes place in a closed tunnel system or in the nest. The greater the synonymy of reproductive interests between colony members, the more accurate and efficient intra-group communication systems are predicted to be (Krebs & Dawkins 1984; Harper 1991). Food recruitment in naked mole-rats (and the bees) supports this hypothesis because successful foragers and potential recruits benefit from transferring information that enhances the well-being, survival and reproduction of their colony and its breeders, thereby enhancing their own inclusive fitness.

There are also parallels between the foraging recruitment system of naked mole-rats and those of other group-living vertebrates, including:

(1) Individuals that find new, abundant food sources give special vocalizations that attract conspecifics in some social birds (e.g. ospreys, *Pandion haliaetus*: Greene 1987; cliff swallows: Brown et al. 1991; ravens: Heinrich & Marzluff 1991) and mammals (e.g. toque macaques: Dittus 1984; spider monkeys: Chapman & Lefebvre 1990; and greater spear-nosed bats: Wilkinson & Boughman, in press). Similarly, naked mole-rat scouts that found a new food source usually gave a unique vocalization while returning to the colony's nest (Fig. 2).

(2) Many rodent species have scent glands on their face, chest, flanks and back, and odour is a primary means of individual recognition (e.g. Halpin 1986; Lai & Johnston 1994). For example, scent sources have been identified in 11 places on golden hamsters' bodies (*Mesocricetus auratus*), five of which yielded odours that could be individually discriminated by conspecifics (Johnston et al. 1993). Some rodents also have plantar glands on the pads of their feet (Brown 1985); plantar glands of house mice (*Mus musculus*) produce a secretion that may identify individuals or group members (Ropartz 1977). Galef & Buckley (1996) reported that when domestic rats

discovered preferred food sources they left odour (probably urine) trails that attracted conspecifics. Other rats that followed the scout's trail to the food were directed to specific items by scent marks of predecessors (Galef & Heiber 1976; Laland & Plotkin 1993). Naked mole-rats, like wild *R. norvegicus*, are central-place foragers that live in kin groups. Likewise, the odours of individual naked mole-rats can be discriminated by colony mates (see Experiment 2, Controls 2 and 3). This result is particularly interesting in view of the genetic homogeneity within colonies, which should reduce phenotypic differences (e.g. in odours) between colony mates. Although we do not yet know the source(s) of the trails recruits followed, secretions of plantar glands and/or urine are obvious possibilities.

In some species of primates and birds the rate and/or acoustical properties of recruitment calls vary with food quantity (e.g. in toque macaques: Dittus 1984), quality (chimpanzees: Wrangham 1977; rhesus macaques, *Macaca mulatta*: Hauser & Marler 1993; golden lion tamarins, *Leontopithecus rosalia*: Benz 1993; and red-bellied tamarins, *Saguinus labiatus*: Caine et al. 1995), and divisibility (house sparrows, *Passer domesticus*: Elgar 1986). Because we specifically controlled for potential differences in the mole-rats' responsiveness to different foods by using only pea-sized pieces of sweet potatoes in our experiments, we do not yet know how information transfer and recruitment behaviours in *H. glaber* vary with food quantity, quality and divisibility.

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