The random elements in the systematic search behavior of the desert isopod Hemilepistus reaumuri

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Summary. Most of the year the isopod crustacean Hemilepistus reaumuri depends for survival on the protection of a permanent shelter (i.e., the burrow occupied by its family), despite its remarkable physiological adaptations to its desert habitat. If an isopod gets lost after an excursion from the burrow, it has to find it as quickly as possible.

Displacement experiments show that H. reaumuri is indeed successful in homing. Even if a desert isopod is displaced in an arbitrary direction over a distance (starting distance \( r_0 \)) from the burrow that exceeds 15 times the distance from which it can detect the entrance, it returns on average in less than 400 s.

The homing behavior of H. reaumuri is successful not because of the isopod’s ability to navigate to its burrow by using external orientation stimuli but because of the intrinsic structure of its search pattern. An isopod that is displaced from its burrow first searches approximately in the form of a spiral, then it moves through increasing loops on which meanders are superimposed. It concentrates these subunits of its search around the starting point by occasionally returning there. The time course of the azimuthal direction component of its position is not clearly regular. The surroundings of the starting point are searched evenly in every direction.

The search behavior of H. reaumuri is composed of systematic subunits together with many random elements. The form of discrete brownian (random) search without directional correlations between its steps that best describes the observed behavior of H. reaumuri for search-path segments with a length between 1 and 7 m has an average step length of 33 cm. For segments with a search-path length below 1 m the agreement between theory and observations is better if one starts from a discrete brownian search with a much smaller step length (one body length), but in which the direction of the steps is strongly correlated.

Despite these geometrical similarities to a brownian search the search behavior of H. reaumuri is distinctively more successful because of the combination of two characteristics. H. reaumuri avoids the disadvantage of the most successful form of a brownian search (i.e., the frequent passage through a region in which it has searched just before) by moving in straighter lines. A brownian search with the same directional constancy shown by H. reaumuri would be inefficient because the thoroughness with which a given region is searched would be too low. H. reaumuri avoids this problem and concentrates its search around the starting point by sometimes returning to that place.

Introduction
The isopod crustacean Hemilepistus reaumuri exhibits a resistance to heat and dehydration comparable to that of many insects living in the same habitats, the semideserts and true deserts of North Africa and the Near East (Edney 1968; Linsenmair 1975; Pretzl 1976). Nevertheless, it must have access to a permanent shelter that offers a more favorable microclimate. This is provided by its burrow, which is about 0.4–0.9 m deep and 1–2 m long in summer. At the height of summer it can survive outside the burrow no longer than a day.

Monogamous pairs and closed family groups with a division of labor within the group inhabit a common burrow and defend it against strange conspecifics and other intruders (Linsenmair and Linsenmair 1971; Linsenmair 1979). Individual-, family-, sex- and situation-specific pheromones
assist the intraspecific and intrafamilial communication required (Linsenmair 1972 and unpublished data).

Frequently the woodlice must leave their shelter to forage for food, to dispose of fecal pellets during cleaning, and to remove soil when enlarging the burrow. A precise orientation capacity enables them to find their way back to the burrow. Even after moving over a tortuous path 20 m long (about 900 body lengths) which leaves it 6 m from the burrow, a woodlouse moves in a straight line back to the immediate vicinity of the burrow (Hoffman 1978, 1983a; Linsenmair 1979).

If an isopod makes a small orientational error on its return to the burrow and thus misses the edge of the entrance by a few millimeters only, it does not detect it. This is probably because H. reaumuri detects the entrance to its burrow mainly by contact chemoreceptors on the terminal segment of the second antennae (Linsenmair 1972; Seelinger 1977). Therefore woodlice can often be seen searching for the burrow entrance in a peculiar way and finding it only after some time.

In an attempt to illustrate the basic principles of an efficient search, I describe the search task of H. reaumuri and compare theoretical solutions with the method actually used. First, I try to establish to what extent the search behavior of H. reaumuri is systematic and to what extent random. This question arises immediately if one compares the search behavior of different animals under identical conditions. It is obvious that their behavior is not strictly the same. The theory behind the assumption that there are random elements in the search behavior of H. reaumuri, even if it is a systematic search, is twofold. On the one hand, any protracted search, however systematic in intent, orientational errors and other irregularities are fairly sure to impart to the search a random character. On the other hand, for a systematic search there are rules for an active randomization of movements, because in this way the danger of passing over the same path twice in succession is decreased (Koopman 1946).

It will be shown that the search behavior of H. reaumuri is similar to a simple (brownian) search strategy in many respects, although it is more systematic in its entirety. The systematic elements will be analyzed in more detail in a second paper (Hoffmann 1983).

**Materials and methods**

*Hemilepistus reaumuri* Audouin and Savigny (Crustacea, Isopoda, Oniscoidea) were taken from families in which the female was gravid or had already borne young, so that they were firmly settled in a burrow. Animals of both sexes were used and no sex-specific differences in search behavior were observed.

Most field displacement experiments were performed in April and May 1976 near Sidi Abd ar-Rahman (Egypt; 30°58’N, 29°44’E). In the laboratory only animals born in the field were used. These animals were kept in tubes filled with soil into which a small hole had been made, which the woodlice themselves deepened. The animals could move freely over a total area of 6 m². At a temperature of about 20 °C at night and 36 °C at noon, corresponding to the late spring in their habitat, they were active by day only in the morning and evening (light: dark cycle 13:11 h). All experiments were done only in the activity pauses, from about 10 a.m. to 4 p.m., since during this time the tendency to return to the burrow is greatest.

The entrance to a burrow of *H. reaumuri* is always blocked by one member of the family. To elicit the search behavior under controlled conditions this guard was carefully pulled out of the hole with forceps, carried along a straight line to a previously determined starting point, and set down with the long axis of the body perpendicular to the direction between the burrow entrance and the starting point. The direction of displacement was varied in a fixed sequence among the compass directions north, south, east and west with respect to the burrow entrance. For these displacement experiments each animal was used only once. Control experiments have shown that the resulting behavior is indeed a search for the burrow and not, for example, one for food (Hoffmann 1978).

Before each field experiment, the ground within a radius of about 30 cm around the entrance was removed to a depth of approximately 1 cm. This procedure ensured that no familiar chemical landmarks were available to assist the search (unpublished data). For the same reason the animals had no access to the surface over which they would walk prior to an experiment in the laboratory; the plastic disk, 20 cm in diameter, that in this case surrounded the entrance to the burrow was exchanged for another disk cleaned with ethylalcohol for the experiment. All surfaces with which they had contact during the experiments or at other times had been sprayed with the same black paint.

The use of learned visual landmarks was also prevented in the laboratory, since the experiments took place in unfamiliar surroundings. Nor did such clues play a detectable role in the return to the burrow in the field, according to observations. Regardless of whether the displacement distance was 20 cm or 50 cm, the search procedure of a displaced isopod was identical. A comparison between laboratory and field experiments revealed no statistically significant differences in search behavior with respect to the search duration.

Two devices were available in the laboratory for observing and recording the animals' locomotion:

**Locomotion compensator.** The woodlouse was placed on the upper pole of a sphere 60 cm in diameter, where it could move with complete freedom (Fig. 1). It was thus possible, without restraining the animal, to monitor its locomotion precisely for a long period of time. In its basic features the locomotion compensator corresponds to the apparatus developed by Kramer (1976). The chief modifications were to reduce the vibrations of the rotating sphere and to improve the resolution of the distance recording (to about 0.6 mm).

Field experiments were performed to check whether the experimental situation on the locomotion compensator changes the search behavior of *H. reaumuri*. Isopods (*n* = 12) were displaced far from their burrow on a homogeneous sand plane. Their position was measured every 60 s for 1 h. The differences