up to 150 eggs (average batch size 20–40), the importance of an avoidance mechanism seems obvious. For *P. rapae*, which lays eggs singly and whose larvae remain considerably smaller than those of *P. brassicae*, the need to avoid conspecifics may be less important. On the other hand *P. rapae* may benefit considerably from the capacity to perceive *P. brassicae* egg clutches. The ability of *P. brassicae* to detect the presence of *P. rapae* eggs may appear less functional, but it should be realized that the described responses were obtained with washes from large numbers of *P. rapae* eggs. Moreover, *P. rapae* larvae have been observed to attack and feed upon *P. brassicae* larvae in the presence of their normal food [14]. The observation that *P. rapae* butterflies originating from the USA produce the same amount of ODP as females from European stock [6], in spite of the fact that the American population has existed for more than 100 years in the absence of *P. brassicae* [15], suggests that the ODP serves primarily to deter conspecific females from oviposition close to eggs deposited earlier.

The heterospecific effects of the ODPs of the two pierids is, to our knowledge, the first case described in Lepidoptera. These substances seem to serve not only their primary function of promoting an even distribution of conspecifics over available host plants, but also the secondary function of promoting an even distribution of larvae across species. Since the ODP of *P. brassicae* also acts as a kairomone to a parasite [16], this semiochemical plays a role in an ecological web, involving at least three insect species at two trophic levels.

Acknowledgments. We thank Ms B. Nübel for technical assistance and Dr D. N. Karowe for helpful discussions and linguistic advice.

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0014-4754/90/050526-03$1.50 + 0.20/0
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Magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (Bathyergidae)

H. Burda, S. Marhold, T. Westenberger, R. Wiltschko and W. Wiltschko

Fachbereich Biologie der Universität, Zoologie, Siesmayerstraße 70, D-6000 Frankfurt a.M. (Federal Republic of Germany)
Received 15 November 1989; accepted 18 December 1989

Summary. To test whether mole-rats *Cryptomys hottentotus* were able to use the magnetic field for orientation, laboratory experiments were conducted which were based on the animals' spontaneous tendency to build their nests at the same position in a circular arena. In the local geomagnetic field, the animals preferred the SE-sector. When magnetic north was turned by 120° or by 180°, the mole-rats changed their nest position accordingly. This clearly shows that they can use the magnetic field for direction finding.
Key words. Magnetic compass orientation; mole-rat; *Cryptomys*; subterranean rodents.

The African mole-rat, *Cryptomys hottentotus* (Bathyergidae), a subterranean rodent, digs the longest, permanent underground systems produced by any animal studied so far [1,2]. In contrast to the radially arranged burrows of many other subterranean mammals, the burrow systems of *C. hottentotus* tend to be linearly arranged, with the nest at one end and a single, long main tunnel, 200 m or more, which forms the major axis [1]. In most of the burrows analyzed so far the main tunnel extended roughly southward [3,4] (and own observations). Each system is constructed, occupied, extended, and maintained over many years by a eusocially living family group of up to 25 members [5].

The remarkable ability of *C. hottentotus* to maintain its course while digging long, straight tunnels [3] gave rise to speculations on possible orientation cues. Air currents [6–8] and acoustic cues [3,9,10] have been discussed; internal mechanisms, like kinesthetic sense and/or vestibular cues [11,12] may also be considered, yet neither of these mechanisms seems to be able to provide a satisfactory explanation for the highly efficient directional orientation observed in *C. hottentotus*[8-11]. Thus, it seemed promising to check whether magnetic information might be involved.

The mole-rats used in our study were caught near Lusaka, Zambia. They are kept and bred at the Zoological Institute of the University in Frankfurt (for details, see Burda[5]), where the experiments were conducted. We used family groups consisting of parents and three adult offspring.

When provided with nest material, *C. hottentotus* builds a nest which is usually adjacent to the wall of the cage. This tendency was taken into consideration in our experiments. A family group was placed in a circular arena (82 cm diameter, 30 cm high) made of vinidur plastic impervious to light. The arena was filled with a layer of horticultural peat, over which slips of toilet paper and paper tissues were uniformly scattered. Food was offered in the center of the arena. The floor and the walls of the arena were washed and the peat litter was stirred (or even changed in many cases) prior to each trial. A nest was considered completed when almost all the available material had been gathered and piled up and the mole-rats slept in it. Only nests built at a wall of the arena were considered.

The test arrangement was placed in a simply-built wooden shed; i.e., with respect to the magnetic field, practically under outdoor conditions. The arena was placed on a wooden table, 60 cm high, in the center of a pair of Helmholtz coils (2 m diameter, 1 m clearance) which were used for altering the magnetic field. The same arena in the same position was used for all tests. Experiments were performed under three test conditions:

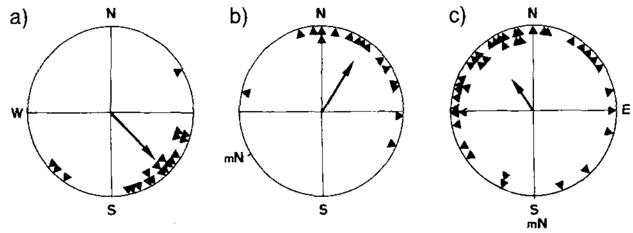
1) Control tests in the local geomagnetic field (mN = 360°, 46 000 nT, 66° inclination).

2) Tests in an experimental magnetic field the north of which was turned 120° counterclockwise to geographic WSW, while total intensity and inclination remained unchanged.

3) Tests in an experimental magnetic field, the horizontal component of which was reversed, pointing toward geographic south. Total intensity and inclination remained unchanged.

Control trials and experimental trials alternated in an irregular fashion. In all experiments, the animals were confined in a pail in the center of the arena for 30 min before being released. The directions from the center of the arena to the center of the nest were measured, and from the data obtained in each condition, a mean vector was calculated by vector addition and tested for significance[13]. The data of the various test conditions were compared using standard methods of circular statistics[13].

The figure gives the distribution of the nest sites. In the local geomagnetic field of Frankfurt, the mole-rats build their nests preferably in the SE-sector of the arena. This tendency represents a spontaneous preference; it does not correspond to the 'home' direction – that of the animal house from which the animals were always brought to the experimental site. In both experimental magnetic fields the mole-rats changed their nest sites according to the shift in magnetic north; they continued to build their nests in the magnetic SE sector, which was now geographic NNE or NW. These two sets of distributions also show highly significant directional preferences and are significantly different from the distributions in the geomagnetic field ($p < 0.001$, Watson Williams test and Mardia Watson Wheeler test), indicating that *C. hottentotus* can use the magnetic field for localizing directions.



Positions of nests (a) in the local geomagnetic field: $n = 21$, $\alpha = 143°$, $r = 0.79$, $p < 0.001$, (b) with magnetic north turned to geographic WSW: $n = 16$, $\alpha = 32°$, $r = 0.74$, $p < 0.001$, and (c) with magnetic north turned to geographic S: $n = 40$, $\alpha = 325°$, $r = 0.46$, $p < 0.001$. The arrows represent the respective mean vectors.

In the experimental field with magnetic north turned to geographic south, a significant increase of scatter is observed ($p < 0.01$, Mann Whitney test). The reasons for this are unknown. It cannot be attributed to irregularities or inhomogeneities in the experimental field since it is not observed under the other test condition (scatter compared to controls: $p > 0.05$).

Up to now, the experimental evidence available on magnetic orientation in small mammals has resulted in an inconsistent picture. First indications for a magnetic orientation in rodents were reported from displacement experiments by Mather and Baker[14]. Their work, however, met with great scepticism, the more so since a first attempt to replicate their results had failed[15]. Only very recently were their findings successfully repeated[16]. Attempts to train Djungarian hamsters and bush opossums to search for food in a given magnetic direction, however, gave negative results and caused Madden and Phillips[17] to question generally a mammalian ability to orient according to the geomagnetic field.

In all these experiments, the set direction for magnetic orientation was induced by the experimenters, either by displacement or by conditioning. Successful demonstrations of magnetic compass orientation in several species of birds, on the other hand, made use of the spontaneous directional tendencies associated with migration[18]. Our experimental animal, the mole-rat, likewise offered a suitable spontaneous reaction associated with a natural motivational context. Maybe this is the reason that we obtained a comparatively clear response to the shift in the magnetic field in the laboratory.

Several questions, however, remain open. It will be interesting to learn whether the magnetic compass of *C. hottentotus* is an inclination compass as reported for birds[18], and whether the mole-rats, which are virtually blind and have to orient in absolute darkness underground, can also use the magnetic field in total darkness. The latter will be very important for all considerations on magnetic perception[19-21].

Acknowledgment. This work was supported by the Deutsche Forschungsgemeinschaft in the program SFB 45. H.B. received a A.v.Humboldt Research Fellowship. The computer work was carried out by the Hochschulrechenzentrum of the Universität Frankfurt a.M.

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0014-4754/90/050528-03$1.50 + 0.20/0
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Heritability of locomotor performance and its correlates in a natural population

T. Garland Jr*,[a], A. F. Bennett[b] and C. B. Daniels[c]

[a]Dept of Zoology, University of Wisconsin, Madison (Wisconsin 53706, USA), [b]Dept of Ecology and Evolutionary Biology, University of California, Irvine (California 92717, USA), and [c]Dept of Physiology, School of Medicine, Flinders University, Bedford Park, S.A. 5042 (Australia)
Received 16 August 1989; accepted 27 October 1989

Summary. Locomotor capacities and their physiological bases are thought to be of considerable selective importance in natural populations. Within this functional complex, organismal performance traits (e.g., speed, stamina) are expected to be of more direct selective importance than their suborganismal determinants (e.g., heart size). Quantitative genetics theory predicts that traits of greater selective importance should generally have lower heritabilities at equilibrium. Contrary to these expectations, we report that organismal performance traits had the highest heritabilities in a natural population of garter snakes.
Key words. Evolution; genetics; heritability; locomotion; physiology.

Locomotor abilities set ultimate limits within which normal behavior must be accomplished; in turn, locomotor abilities depend on a large number of underlying physiological, morphological, and biochemical traits. The hierarchical nature of these relationships suggests that some components of activity metabolism will be of more direct selective importance than others. In particular, such whole-animal performance traits as maximal speed or stamina are presumed to be of greater selective importance than are lower-level traits[1-4].

Only traits with heritabilities greater than zero can evolve genetically in response to selection. Heritability (h^2 = ratio of additive genetic variance to total phenotypic variance[5]) is often seen as representing a balance between the rate of polygenic mutation, adding new genetic variance to a population each generation, and the strength of selection, tending to reduce genetic variance[6]. Theory indicates that, at equilibrium, traits that have been subject to strong selection will exhibit relatively little additive genetic variance and low heritabilities[7,8]. Empirical evidence supports this prediction: major components of fitness (e.g., length of reproductive lifespan, fecundity) generally exhibit lower heritabilities than do morphological traits, with behavioral and physiological traits exhibiting intermediate values[5,9,10,11].

Aside from major components of fitness versus other traits, it is not known whether the inverse correlation between strength of selection and heritability holds for traits within a functional complex. We therefore measured heritabilities of various components of activity metabolism, a functional complex of considerable behavioral and ecological relevance. Because locomotor performance capacities are expected to have more direct effects on fitness than do lower-level traits (e.g., tissue