ORIGINAL PAPER

S. Sommer · R. Wehner

The ant's estimation of distance travelled: experiments with desert ants, *Cataglyphis fortis*

Abstract Foraging desert ants, *Cataglyphis fortis*, monitor their position relative to the nest by path integration. They continually update the direction and distance to the nest by employing a celestial compass and an odometer. In the present account we addressed the question of how the precision of the ant's estimate of its homing distance depends on the distance travelled. We trained ants to forage at different distances in linear channels comprising a nest entrance and a feeder. For testing we caught ants at the feeder and released them in a parallel channel. The results show that ants tend to underestimate their distances travelled. This underestimation is the more pronounced, the larger the foraging distance gets. The quantitative relationship between training distance and the ant's estimate of this distance can be described by a logarithmic and an exponential model. The ant's odometric undershooting could be adaptive during natural foraging trips insofar as it leads the homing ant to concentrate the major part of its nest-search behaviour on the base of its individual foraging sector, i.e. on its familiar landmark corridor.

Keywords Ants · *Cataglyphis* · Odometry · Path integration · Travel distance

Introduction

The question of how social insects, which routinely return to a central place (the colony), gauge their distances travelled has caused a recent upsurge of interest. This interest has focused on the sensory cues providing the

S. Sommer · R. Wehner (✉)
Institute of Zoology,
University of Zürich,
Winterthurerstrasse 190, 8057 Zürich,
Switzerland
E-mail: rwehner@zool.unizh.ch
Tel.: +41-1-6354831
Fax: +41-1-6355716

input signals to the insect's "odometer". Honeybees, which have been studied most intensively in this context, measure distance flown by gauging the extent of image motion experienced as they fly through cluttered environments. In a number of elegantly designed experiments Esch and Burns (1995), Srinivasan et al. (1996, 1997) and Esch et al. (2001) have shown that in bees distance flown is gauged in terms of self-induced image motion in both the ventral and the lateral fields of view (Si et al. 2003). If the bees are deprived of image motion cues, they are unable to record how far they have flown.

In walking insects, visual flow-field cues play a minor role (desert ants: Ronacher and Wehner 1995; Ronacher et al. 2000; honeybees: Schöne 1996; bumblebees: Chittka et al. 1999). When walking these insects seem to rely on proprioceptive cues most probably derived from the movements of the legs. In this context, desert ants, *Cataglyphis fortis*, are able to process not only information gained in the horizontal plane, but also information about the angular upward or downward tilt of inclined planes (Wohlgemuth et al. 2001, 2002). The nature of the proprioceptive cues involved in the ant's odometric mechanisms remains to be elucidated.

In the present account we do not enquire about the sensory system by which *C. fortis* keeps track of how far it has walked, rather we focus on a more central aspect of the ant's odometer, namely on how the distance the ant "thinks" it has walked depends on the distance it has actually walked. We shall show that the larger the distance gets which the ant has travelled from the nest to a feeder, the more the ant will underestimate this distance when later returning home. This leads to a non-linear relationship between the ant's estimate of the distance travelled and the true distance travelled. A similar effect has been observed in honeybees (von Frisch and Kratky 1962). In this case, however, the bees' distance estimates have been derived from the waggle durations of the recruitment dances to a food source rather than from the distances actually flown. These waggle durations are related to the distances flown in a non-linear way. However, as the recruited bees interpret the indicated

distances correctly (von Frisch 1965, pp 94–95; Esch et al. 2001), the non-linearity is likely to result from "dance conventions". In the present account the test parameter is distance travelled rather than some other parameter related to it, so that any resulting non-linearity must be a property of the odometer itself.

Materials and methods

The experiments were performed on foraging desert ants, *C. fortis*, in a salt pan near Maharès, Tunisia (34.58° N, 10.50° E) during the ants' main activity period between late June and early September 2002.

Experimental procedures

Ants were trained to forage in linear channels at seven distances ranging over two orders of magnitude from 0.5 m to 50 m. The training channels extended from the nest entrance hole of a colony to a feeder (Fig. 1a). They were aligned in a north-south direction with the feeder to the north and the nest entrance at 4 m from the southern end of the channel. The walls of the channels consisted of wooden plates, which were 1.5 m long and joined, as well as anchored to the salt-pan floor, by 3-cm-wide connecting pieces. The latter virtually blended with the plates. Preliminary tests showed that they had no influence at all on the ants' estimation of distance. As both the width and the height of the channel measured 10 cm, the ants running on the natural desert surface in the centre of the channel (Heusser and Wehner 2002) experienced a 53° wide strip-like skylight window providing them with compass information. After at least 1 day of training, individual ants marked every day by a particular colour code were taken from the feeder and released in a test channel (Fig. 1b). The test channel was aligned parallel to the training channel and identical to the latter except for its considerably increased length (up to 80 m in the case of the 50-m training distance). Only those ants were tested on their homebound runs that were still carrying their booty, a biscuit crumb, which they had grasped shortly before the test run started. Upon release, the ants tested one by one immediately headed for home by performing their straight homebound paths within the test channel. Starting with the onset of the ant's nest-searching behaviour as indicated by the ant's first 180° turn (Wehner and Srinivasan 1981), we recorded the positions of all consecutive U-turns to the nearest
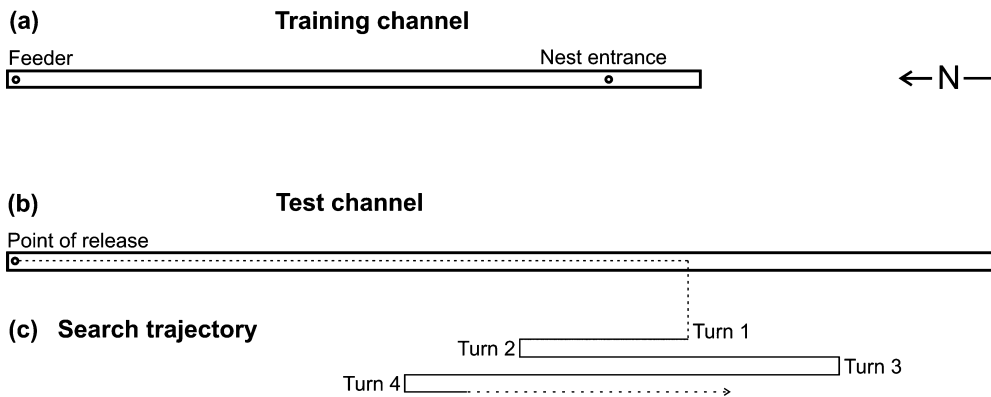
0.1 m for a test period of 5 min (Fig. 1c). Abortive runs, i.e. runs in which the ants headed in the opposite direction or tried to leave the test channel prematurely, were not recorded. Each ant was tested only once.

Data analyses

The objective of this study was to examine how accurately the ants gauge their distances travelled. Two criteria were used as measures of the ant's distance estimate: (1) the position of the ants' first 180° turn, and (2) the centre of the ants' subsequent linear search path. The latter was computed as the mean of the positions of all U-turns performed by each ant during the 5-min test period.

Four statistical models, each representing a specific hypothesis about the ant's assessment of its homing distance, were fitted to the data by calculating non-linear regressions using the Gauss-Newton method of PROC NLIN in SAS (SAS OnlineDoc, v. 8, 1999; SAS Institute, Cary, N.C., USA). This method iteratively adjusts the model parameters to minimize the residual sum of squares (*RSS*). We used the adjusted coefficients of multiple determination (R^2_{adj}) to assess the goodness-of-fit for each model in an absolute sense (Burnham and Anderson 2001).

The relative fits of the models were compared by using model selection based on information theory (Burnham and Anderson 2002). We chose information-theoretic criteria for model comparison, because the models were not nested in a statistical sense, so that traditional likelihood ratio tests could not be applied (Anderson et al. 2000; Burnham and Anderson 2002). The model selection approach involved the calculation of Akaike's information criterion (AIC). The AIC of a particular model is an estimate for its relative information loss from the original data set. Hence, the lower the AIC of a particular model, the better the fit. The use of AIC instead of other criteria (e.g. AIC_c, QAIC, or $QAIC_c$; Burnham and Anderson 2002) was justified, because the sample size ($n = 175$) was large compared to the number of estimable parameters ($K = 2$–4), and because the variance inflation factor estimated from the χ^2 statistics and its degrees of freedom did not indicate any overdispersion in the data (i.e. $\hat{c} = \chi^2/df < 1$ for all models; Burnham and Anderson 2002). The AIC was calculated as

$$\text{AIC} = n \log_e(\hat{\sigma}^2) + 2K \tag{1}$$

where $\hat{\sigma}^2 = RSS/n$ (Burnham and Anderson 2002, p 63). Models that differed in their AIC values by less than 2 units (i.e. $\Delta_i < 2$) as compared to the selected best model (the model with the lowest AIC) were considered competitive (sensu Burnham and Anderson 2002).

Additional model selection inference was based on the Akaike weights, which were calculated as

$$w_i = \frac{e^{-\frac{1}{2}\Delta_i}}{\sum\limits_{r=1}^{R} e^{-\frac{1}{2}\Delta_r}} \tag{2}$$

Fig. 1 Schematic top views of the channels used for **a** training and **b** testing foraging desert ants, *C. fortis*; not drawn to scale. **c** The ant's linear search pattern illustrated for the first four U-turns was performed inside the test channel as described in Materials and methods

(a) Training channel
Feeder   Nest entrance

← N —

(b) Test channel
Point of release

(c) Search trajectory

Turn 1
Turn 2
Turn 3
Turn 4

and on the evidence ratios (w_i/w_j). i and j refer to single models, and R refers to all models under consideration. w_i gave the relative support for the ith model by the data on a scale from 0 (no support) to 1 (maximum support). Hence, w_i/w_j estimated the strength of evidence in favour of the ith model compared to the jth model (Burnham and Anderson 2002, pp 75–79).

Results

As shown in Fig. 2, which presents the main results of this study, the ants tend to underestimate their homing distances. From 25 m onwards, the tendency to undershoot gradually increases with homing distance, and does so for either criterion used in determining the ant's estimate of distance travelled (the ant's first 180° turn and the centre of the ant's search pattern). Hence, there is no linear relationship between the ant's estimate of the distance travelled, as revealed in the test, and the real distance travelled during training. How then are the two parameters related? Here we conceive three alternative hypotheses to the linear model (model 1 in Table 1).

The first hypothesis is based on the assumption that equal relative increases in the distance travelled by the ant (ant-nest distance) cause equal relative increases in the reading of the ant's odometer. This hypothesis corresponds to the psychophysical law for sensory coding as proposed by Stevens (1957). It implies that the ant's distance estimate grows as a power function of the real homing distance (model 2 in Table 1). The exponent β
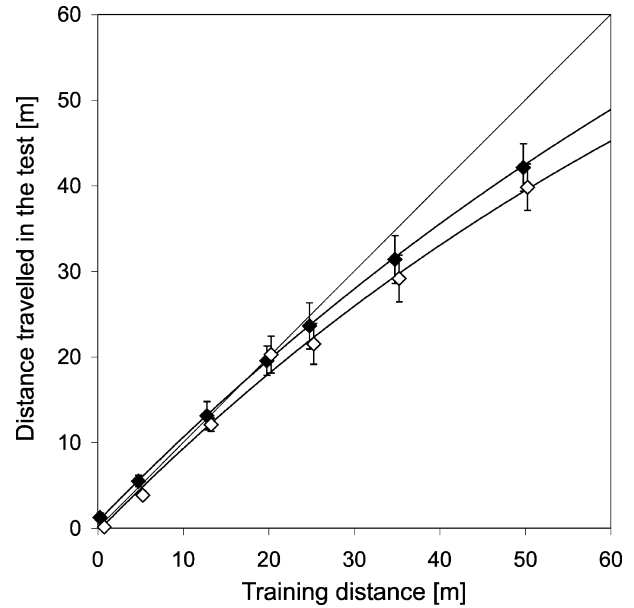

Fig. 2 The ants' estimates of homing distance as a function of training distance. Symbols represent the means (*filled diamonds* first turn, *open diamonds* centre of search), and bars denote the 99% confidence intervals. The zero point on the y-axis corresponds to the point of release. The straight line ($y = x$) indicates the position of the fictive nest entrance in the test channel. Sample size $n = 25$ for each training distance. Curves (*upper line*: first turn, *lower line*: centre of search) are calculated from the exponential model (see Table 1). Within the range of the experimental training distances the predicted y-values of the logarithmic model (curves not shown) differ by ≤ 0.05 m (first turn) and ≤ 0.12 m (centre of search) from the exponential model

Table 1 Summary of model selection statistics for the analyses of the relationship between training distance (x) and estimated homing distance, measured as the first turn (y_t) and the centre of search (y_c) in desert ants, *C. fortis*

Model	RSS	K	AIC	Δ_i	w_i	α_i	β_i	δ_i
First turn								
(1) $y_t = \alpha_1 \cdot x + \delta_1$	2772.85	3	489.50	6.79	0.012	0.8295 (0.0189)	-	1.9 (0.5)
(2) $y_t = \alpha_2 \cdot x^{\beta_2} + \delta_2$	2649.70	4	483.55	0.84	0.245	1.4581 (0.2830)	0.8603 (0.0476)	0.2 (0.8)
(3) $y_t = \alpha_3 \cdot \log_e\left(\frac{x+\beta_3}{\beta_3}\right) + \delta_3$	2637.33	4	482.73	0.02	0.370	96.7017 (32.9580)	93.2296 (38.9988)	0.6 (0.7)
(4) $y_t = \alpha_4 \cdot \left(1 - e^{-\beta_4 \cdot x}\right) + \delta_4$	2637.09	4	482.71	0	0.373	118.5000 (32.3498)	0.0086 (0.0029)	0.7 (0.7)
Centre of search								
(1) $y_c = \alpha_1 \cdot x$	2816.77	2	490.25	18.50	< 0.001	0.8363 (0.0114)	-	-
(2) $y_c = \alpha_2 \cdot x^{\beta_2}$	2549.70	3	474.82	3.07	0.098	1.3437 (0.1467)	0.8681 (0.0305)	-
(3) $y_c = \alpha_3 \cdot \log_e\left(\frac{x+\beta_3}{\beta_3}\right)$	2505.42	3	471.75	0	0.453	78.2532 (18.4169)	75.7423 (21.5284)	-
(4) $y_c = \alpha_4 \cdot \left(1 - e^{-\beta_4 \cdot x}\right)$	2505.63	3	471.76	0.01	0.449	98.2666 (18.2289)	0.0103 (0.0023)	-

The model functions are: (1) linear, (2) power, (3) logarithmic and (4) exponential

Standard errors of regression parameters α_i, β_i and δ_i are given in parentheses

Goodness-of-fit: $0.911 < R^2_{adj} < 0.921$ for all models; sample size $n = 175$

The intercept δ_i in the models for the ant's first turn is derived from the assumption that this criterion includes an overshoot relative to the ant's expectation of the position of the nest entrance

(i.e. $y_t(0) > 0$; Wehner 1992). For the models of the centre-of-search criterion we specify no intercept because we assume no overshoot (i.e. $y_c(0) = 0$; Wehner and Srinivasan 1981)

RSS residual sum of squares; *K* refers to the number of regression parameters plus 1 for $\hat{\sigma}^2$; AIC, Akaike's information criterion (the lower the AIC, the better the fit); Δ_i is the difference in AIC of a particular model to the model with the lowest AIC; w_i denotes the Akaike weight. The w_i values sum to 1 and estimate the relative support for each model by the data (Burnham and Anderson 2002)

represents the rate of that growth, and the parameter α is a scaling factor.

Next we tested whether each input to the odometer resulting from a unit increase in the ant's distance travelled is scaled down proportionally to the distance already travelled by the ant. This hypothesis, which is similar to the one proposed for how the ants use information about directions in their path-integration process (distance-weighted mean-direction hypothesis; Müller and Wehner 1988), implies a logarithmic relationship between estimated and real homing distance (model 3 in Table 1). This is what the Weber-Fechner law of psychophysics implies (Fechner 1860). The model parameter α is a scaling factor, while β denotes a shape parameter necessary to obtain a biologically reasonable result for all travel distances (i.e. $y_t(x)$ and $y_c(x) \geq 0$ if $\beta > 0$ and $x \geq 0$).

Our final assumption is based on the idea that the ants might gradually "forget" parts of their distance travelled. This hypothesis was proposed by von Frisch and Kratky (1962) for honeybees performing their recruitment waggle dances. It implies that the ant's odometer is leaky. The mathematical characteristics of a leaky integrator are described by an asymptotic exponential function with an asymptote α and a leak rate β (model 4 in Table 1).

The use of the AIC criterion (see Materials and methods) for evaluating the various models results in the logarithmic model (model 3) and the exponential model (model 4) being equally good in fitting the data, irrespective of whether one uses the ants' first turns or the centres of the ants' search patterns as the experimental measure (Table 1). The power model (model 2) is competitive to the above models if the first-turn criterion is used ($\Delta_2 = 0.84$), but not if one refers to the centre-of-search criterion ($\Delta_2 = 3.07$). Accordingly, the evidence in favour of the logarithmic model and the exponential model as compared to the power model is low for the first criterion (w_3/w_2 and $w_4/w_2 = 1.5$), but substantial for the second one (w_3/w_2 and $w_4/w_2 = 4.6$). Taken together, the power model has considerably less support by the data than both the logarithmic and the exponential model. On the other hand, the linear model (model 1) has no support irrespective of the criterion used for determining the ant's estimate of homing distance ($w_1 \approx 0$; Table 1).

The variance of the ants' distance estimates (interindividual variance) increases with the distances travelled, but tends to level off at the largest training distance (Fig. 3). Hence, as the variances do not increase linearly with the distances travelled, the ant's odometer does not seem to simply sum up errors made at successive unit steps. This is additional evidence in favour of an odometer with non-linear properties. Likewise, the variance of the nest-search position, i.e. the variance of all U-turns performed by each ant during the 5-min test period (intra-individual variance in Fig. 3), increases with training distance and tends to level off at distances > 20 m. This increase results from broader search ranges at larger
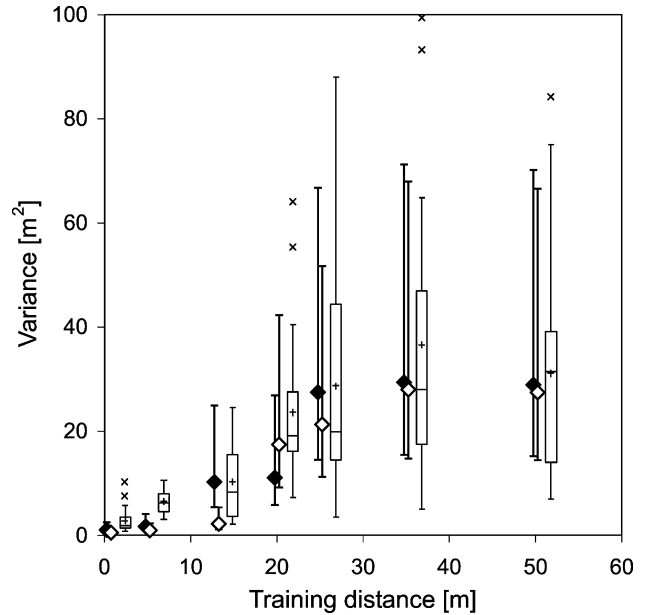

Fig. 3 Variance of the ants' estimates of homing distance (inter-individual variance: *filled diamonds* first turn, *open diamonds* centre of search) and variance of the nest-search position (intra-individual variance: *boxplots*) in relation to the training distance. The 99% confidence intervals (*bars*) for the inter-individual variances were computed following Sokal and Rohlf (1998, pp 154–157). The intra-individual variances were calculated from all U-turns performed by an individual ant during the 5-min test period. *Lower and upper borders* of the boxes are the first and the third quartiles, respectively. The *lines* inside the boxes are the medians. The means are depicted as '+', outliers as '×'. Sample size $n = 25$ for all boxplots

distances in combination with fewer turns made by the ants within the 5-min test period. The broader search ranges at larger foraging distances likely reflect an increase in the ant's uncertainty ("blur circle"; see Discussion) about the pin-point position of the nest entrance.

Discussion

The farther the ants travel, the more do they underestimate the distance they have travelled. How does this underestimation of distance exhibited by the ants in our experiments scale with the distances travelled by the ants during their normal foraging journeys? In the vast salt pans of the Sahara desert such as the Chott el Djerid *C. fortis* may leave its nest for distances of more than 200 m, and usually travels for 80–100 m (Wehner 1987), but in the nutritionally richer coastal inundation plains, in which our experiments have been performed, the foraging distances are much smaller (in the range of about 30–60 m). Hence, for the larger foraging journeys the ant's underestimates of distances travelled become significant. However, it would be interesting to know whether the shape of the distance-estimation function obtained at our study site and presented in Fig. 2 would also apply to the populations of *C. fortis* inhabiting, say,

the Chott el Djerid, in which conspecific ants forage over much larger distances.

The integrative properties of the ant's odometer imply that the errors in the ant's distance estimate accumulate with the distance travelled (Wehner 1992). This is supported by the increase of the variance of the ants' distance estimates with training distance (inter-individual in Fig. 3). A similar effect has been demonstrated for honeybees that were trained to forage down a tunnel. In tests with the feeder absent, the odometric error increased linearly with feeder distance (Srinivasan et al. 1997; Cheng et al. 1999). The reason why the odometric error in bees did not level off with travel distance as it did in the ants studied here (Fig. 3) might be explained by the fact that the short distances flown by the bees through the experimental tunnels (Srinivasan et al. 1997; Cheng et al. 1999) corresponded to an outdoor flight distance of only a few hundred metres (see Srinivasan et al. 2000; Esch et al. 2001). This is a relatively short distance as compared to the normal foraging ranges which in honeybees reach distances of several kilometres from the hive (von Frisch 1965, p 89f; Visscher and Seely 1982). On the other hand, the ants of our study were trained to forage for relatively large distances as compared to their natural foraging trips (see above). Hence, the question remains of whether the distance-error function of bees would also level off for larger (several kilometres) training distances.

In any way, the ant's uncertainty about the pin-point position of the nest entrance (the ant's "blur circle", see below) is expected to increase with increasing foraging distance. This is in accord (1) with former open-field experiments, which showed that the search density profiles of homing ants widened and became less peaked as foraging distance increased (Wehner 1992), and (2) with the result of our present channel experiments that the ants' search ranges increase with increasing training distance (as documented by the intra-individual variances in Fig. 3). Furthermore, as the odometric error levels off at the largest training distances, so does the increase in the ant's uncertainty.

The data of Fig. 2 can be described best by assuming that the ant's distance estimate grows logarithmically or exponentially with the distance travelled. Both assumptions fit the data equally well. Hence, in mechanistic terms, the ant's odometer could be described as some kind of leaky integrator (or as a mechanism conforming with Weber-Fechner's law; see Results). Assuming that the ant's integrator steps up by one unit with each step taken by the ant and decays exponentially between steps (cf. model 4 in Table 1), the maximum value of the ant's integrator and its time constant can be calculated. Based on the locomotory pattern and the walking kinematics of *C. fortis* (see Zollikofer 1988; Wohlgemuth et al. 2002) our data predict that the integrator saturates at about 12,000 steps (approximately 120 m; cf. α_4 in Table 1), with a basic integration time constant of roughly 600 s. However, rather than considering this leakiness of the odometer an imperfection or a deficiency,

in functional terms it could be of adaptive value for the following reason.

During the course of their foraging lives *C. bicolor* (Wehner 1987) and *C. fortis* (Wehner 2003, and unpublished data) develop strong direction fidelities by remaining increasingly faithful to a particular foraging sector. Furthermore, within this sector the ants steadily increase their foraging distance. This sector fidelity implies that even in only slightly cluttered environments the returning ants are able to zoom in on familiar landmark corridors, whenever they approach their final destination, the nest (Wehner et al. 1996). Hence, such route memories back up the ant's error-prone path-integration system (Mittelstaedt 1983). They become more important the larger the distance from which an experienced forager returns, because the accuracy of the ant's path integrator decreases with increasing foraging distance (see above). When relying exclusively on path integration the returning ant, having run off its home vector, would end up within an uncertainty range—a "blur circle"—centred about the goal (nest). Without the aid of landmarks, the ant having arrived within that "blur circle" would then have to switch on its hidden-spiral search programme (Müller and Wehner 1994) to finally pinpoint its goal. However, if the ant routinely returned along a familiar route, the "blur circle" would overlap with the familiar route more extensively, if the read-out of the path integrator undershot the true home distance than if it pointed precisely at the goal (for a similar argument see Hartmann and Wehner 1995). This effect is the more pronounced, the farther the ant has originally ventured out from the nest, i.e. the longer the home vector has become. Seen in this light, the ant's distance-estimation function described in the present account might reflect a means of adapting the path-integration system with its intrinsic noise to the ant's landmark-based back-up system.

References

Anderson DR, Burnham KP, Thompson WL (2000) Null hypothesis testing: problems, prevalence, and an alternative. J Wildl Manage 64:912–923

Burnham KP, Anderson DR (2001) Kullback-Leibler information as a basis for strong inference in ecological studies. Wildl Res 28:111–119

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer, Berlin Heidelberg New York

Cheng K, Srinivasan MV, Zhang SW (1999) Error is proportional to distance measured by honeybees: Weber's law in the odometer. Anim Cogn 2:11–16

Chittka L, Williams NM, Rasmussen H, Thomson JD (1999) Navigation without vision: bumblebee orientation in complete darkness. Proc R Soc Lond Ser B 266:45–50

Esch HE, Burns JE (1995) Honeybees use optic flow to measure the distance of a food source. Naturwissenschaften 82:38–40

Esch HE, Zhang SW, Srinivasan MV, Tautz J (2001) Honeybee dances communicate distances measured by optic flow. Nature 411:581–583

Fechner GT (1860) Elemente der Psychophysik. Breitkopf und Härtel, Leipzig

Frisch K von (1965) Tanzsprache und Orientierung der Bienen. Springer, Berlin Heidelberg New York

Frisch K von, Kratky O (1962) Über die Beziehung zwischen Flugweite und Tanztempo bei der Entfernungsmeldung der Bienen. Naturwissenschaften 49:409–417

Hartmann G, Wehner R (1995) The ant's path integration system: a neural architecture. Biol Cybern 73:483–497

Heusser D, Wehner R (2002) The visual centring response in desert ants, *Cataglyphis fortis*. J Exp Biol 205:585–590

Mittelstaedt H (1983) The role of multimodel convergence in homing by path integration. In: Horn E (ed) Multimodel convergences in sensory systems. Fortschritte der Zoologie, vol 28. Fischer, Stuttgart, pp 197–212

Müller M, Wehner R (1988) Path integration in desert ants, *Cataglyphis fortis*. Proc Natl Acad Sci USA 85:5287–5290

Müller M, Wehner R (1994) The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. J Comp Physiol A 175:525–530

Ronacher B, Wehner R (1995) Desert ants *Cataglyphis fortis* use self-induced optic flow to measure distances travelled. J Comp Physiol A 177:21–27

Ronacher B, Gallizzi K, Wohlgemuth S, Wehner R (2000) Lateral optic flow does not influence distance estimation in the desert ant *Cataglyphis fortis*. J Exp Biol 203:1113–1121

Schöne H (1996) Optokinetic speed control and estimation of travel distance in walking honeybees. J Comp Physiol A 179:587–592

Si A, Srinivasan MV, Zhang SW (2003) Honeybee navigation: properties of the visually driven 'odometer'. J Exp Biol 206:1265–1273

Sokal RR, Rohlf FJ (1998) Biometry, 3rd edn. Freeman, New York

Srinivasan MV, Zhang SW, Lehrer M, Collett TS (1996) Honeybee navigation en route to the goal: visual flight control and odometry. J Exp Biol 199:237–244

Srinivasan MV, Zhang SW, Bidwell NJ (1997) Visually mediated odometry in honeybees. J Exp Biol 200:2513–2522

Srinivasan MV, Zhang SW, Altwein M, Tautz J (2000) Honeybee navigation: nature and calibration of the "odometer". Science 287:851–853

Stevens SS (1957) On the psychophysical law. Psychol Rev 64:153–181

Visscher KP, Seeley TD (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest. Ecology 63:1790–1801

Wehner R (1987) Spatial organization of foraging behavior in individually searching desert ants, *Cataglyphis* (Sahara desert) and *Ocymyrmex* (Namib desert). In: Pasteels JM, Deneubourg J-L (eds) From individual to collective behavior in social insects. Birkhäuser, Basel, pp 15–42

Wehner R (1992) Arthropods. In: Papi F (ed) Animal homing. Chapman and Hall, London, pp 45–144

Wehner R (2003) Desert ant navigation: how miniature brains solve complex tasks. J Comp Physiol A 189:579–588

Wehner R, Srinivasan MV (1981) Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). J Comp Physiol A 142:315–338

Wehner R, Michel B, Antonsen P (1996) Visual navigation in insects: coupling of egocentric and geocentric information. J Exp Biol 199:129–140

Wohlgemuth S, Ronacher B, Wehner R (2001) Ant odometry in the third dimension. Nature 411:795–798

Wohlgemuth S, Ronacher B, Wehner R (2002) Distance estimation in the third dimension in desert ants. J Comp Physiol A 188:273–281

Zollikofer CPE (1988) Vergleichende Untersuchungen zum Laufverhalten von Ameisen (Hymenoptera: Formicidae). PhD thesis, University of Zürich