

Homing in the Field Cricket, *Gryllus campestris*

Guy Beugnon¹ and Raymond Campan¹

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Homing ability of the cricket Gryllus campestris was experimentally studied in the field after passive and active displacements. Whatever the weather conditions and the nature of the displacement, crickets (18/18) home directly when they are located between 5 and 15 cm from their burrow by performing real-time orientation. When moved by the experimenter between 15 and 55 cm away from home, some crickets (26/43) can retrieve their burrow by systematic searching only after winding inward trips but they get lost (0/18) beyond 55 cm. After self-generated movements between 5 and 85 cm away from home, crickets (33/35) return to their burrow under blue sky, but they cannot home as well under overcast sky (22/34 from 5 to 65 cm and 0/5 beyond). The volatile-memory orientation system allowing path integration is based on the polarized skylight of the sun.

KEY WORDS: *Gryllus campestris*; homing; field cricket; spatial memories; active and passive displacement; polarized skylight.

INTRODUCTION

Homing in animals has been extensively analyzed (see reviews by Schmidt-Koenig, 1975; Schmidt-Koenig and Keeton, 1978; Able, 1980). When they do not perform random or systematic searching or when they do not only refer to idiothetic (internal) information, some vertebrates and invertebrates use spatial cues provided by their environment. If the goal is directly perceived by the sense organs, homing is quite simple and has been described as direct or proximate orientation (Schöne, 1984). Sometimes, the animal can retrace its outward trip by following a trail leading to home. Such a route reversal occurs in

¹Centre de Recherche en Biologie du Comportement, Université Paul Sabatier, U.R.A. CNRS No. 664, 118 Route de Narbonne, 31062 Toulouse cédex, France.

ants with chemical trails or whenever an animal follows a conspicuous trail as a guide line (forest edge, fences). In all these homing situations there is no need for memorization of spatially defined cues, and thus spatial information processing is realized in a short integration time; consequently homing is performed during what can be called *real-time orientation* (Beugnon, 1986a).

A second type of homing appears when the animal knows the spatial organization of its home area and accordingly uses familiar landmarks to guide its action within it. During its ontogenetic development, an individual can learn the spatial relationships between some features of the environment and the exact location of its home in order to identify and localize them accurately when moving back home. This *constant-memory orientation* (Beugnon, 1986a) is functionally based on two different kinds of mechanisms according to the specification of the animal's sensorimotor equipment. On one hand, some vertebrates could use a cognitive map representing the spatial organization of their environment. Whatever its current location, the individual would be straight-away aware of its position relative to its home and to any other point of its living area. Even after being passively displaced to an unknown place located within its home area, the animal would be able to return successfully to its home. On the other hand, it is generally assumed that invertebrates have a narrower knowledge of spatial layout (Wehner, 1983). The route-based information used by insects would rather be a sequence of snapshot images stored during previous trips. During its displacement, the individual would try to match the current retinal image of the external world with the memory picture previously stored (Wehner, 1981; Cartwright and Collett, 1983). Recent works on bees (Gould, 1986; Cartwright and Collett, 1987) indicate that their representation of the external world is rather a *random-access file orientation* system (Beugnon, 1986a) more comparable to cognitive maps. However, the *sequential-file orientation* system would be sufficient to explain homing in walking insects as proposed in ants which repeatedly move along familiar routes (Rosen- gen and Fortelius, 1986).

In contrast, a third hypothesis, also involving the process of memorization, concerns the ability of animals to integrate over the different legs of their outward trip. The individual is permanently aware of its current position relative to home, and even very winding outward trips are followed by beeline inward trips (Frantsevitch *et al.*, 1977; Wehner, 1981; Etienne *et al.*, 1986). This path integration is based on spatial information given by internal (idiothetic) and/or external (allothetic) cues (Mittelstaedt and Mittelstaedt, 1982). Magnetic and celestial cues are used mainly as external references; many insect species also use the patterns of the polarized skylight to perform vector orientation (Fent and Wehner, 1985). The spatial information gathered during active and sometimes during passive displacements (Mittelstaedt, 1985; Ugolini, 1986) is used only for the return trip from the current displacement. As the animal has to

reload its memory during the next outward excursion (Görner and Claas, 1985), this kind of homing can be described as a *volatile-memory orientation* system which is reset to zero when the individual has returned to home (Beugnon, 1986a).

To test whether field crickets *Gryllus campestris* refer to real time, to constant-memory, and/or to volatile-memory orientation during homing to their burrow, several experiments were conducted in the natural habitat of the insect.

METHODS

Experimental Sites

Experiments were performed in natural meadows (Station biologique des Artigues and Plagne, South of France) during spring and early summer from 1983 to 1987.

Experimental Designs

Two kinds of experimental procedures were applied alternatively with the same individual (starting with procedure 1 or procedure 2), or only one procedure was applied by individual.

Active Displacements. Male crickets *G. campestris* were gently pushed out of their burrow and forced to walk for some centimeters until they stopped their run before returning.

In most of the cases, the tracks of the returns trips are plotted on a paper by direct observation and durations of returns are recorded. To make the analysis of the data easier, distances are regrouped in classes of 10 cm. For instance, all crickets returning from distances ranging between 35 and 45 cm are found in the 40-cm class. The straightness index ($0 \leq S \leq 1$) corresponds to the ratio between the beeline distance to the burrow on the total length covered during the inward trip (Batschelet, 1981).

Passive Displacements. Crickets caught at their burrow entrance are immediately passively displaced in the hand of the experimenter and released close to the burrow (10 to 80 cm). Durations and tracks of returns are also recorded.

To test for the overall influence of weather conditions and for any role of celestial cues during the orientation of the insects, both active and passive displacements were observed under blue sky and totally overcast conditions. As field crickets are more active in sunny weather, it was more difficult to localize them and to force them out of their burrow under total overcast. This explains the low sample size of experiments conducted under cloudy cover.

In a second series of experiments, we tested the role of polarization patterns of the blue sky with a polarization filter placed above the walking crickets;

Polaroid filter HN38, 48.2×63.5 cm, polarization degree of 99.7%, and transmission of UV light $>20\%$ at 375 nm.

RESULTS

Active and Passive Displacements Under Different Weather Conditions

Preliminary Observation of a Spontaneous Foraging Excursion. A male cricket was observed when spontaneously foraging under blue sky from the start to the return at its burrow. The total excursion lasted 17 min 35 s and the total distance traveled was 8.50 metres (Fig. 1).

When passively displaced 50 cm southwest of its burrow at a place already visited 2 min before, the cricket failed in reaching its home and wandered before escaping in a crack located 12.5 m from the burrow.

Active Outward Displacements. When crickets are forced to walk out of their burrow under blue sky, about 94% of the return trips are directly performed back to home (33/35). However, the insects do not follow back their steps of the outward trip (Figs. 2a and b). The inward paths are rather direct (median value of the straightness index is $S = 0.81$) and fast (median value of the duration is $T = 21$ s) even if the straightness values decrease and the durations values increase along with the distance covered (see Table I).

Under total cloud cover, crickets are still able to home, but homing success is reduced to 65% (22/34). Beyond 10–20 cm from the burrow (see Table I), the inward trips of the returning crickets are more winding than under blue sky (Mann-Whitney two-tailed test, $P = 0.089$ at 30 cm and $P = 0.016$ at 40 cm) and the durations of returns are also significantly increased (Mann-Whitney

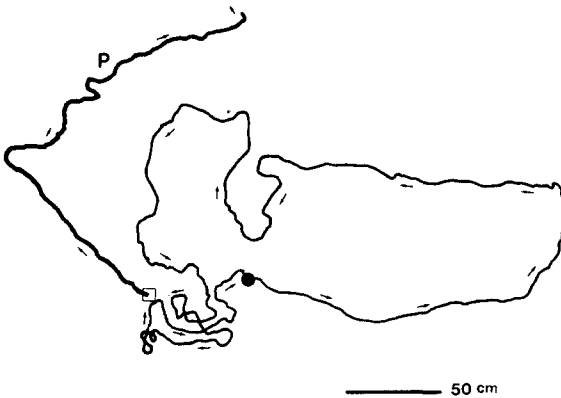


Fig. 1. Path of a male *Gryllus campestris* observed while spontaneously foraging. The thick line indicates the path of the same cricket when passively (P) displaced 50 cm SW of its burrow (filled circle).

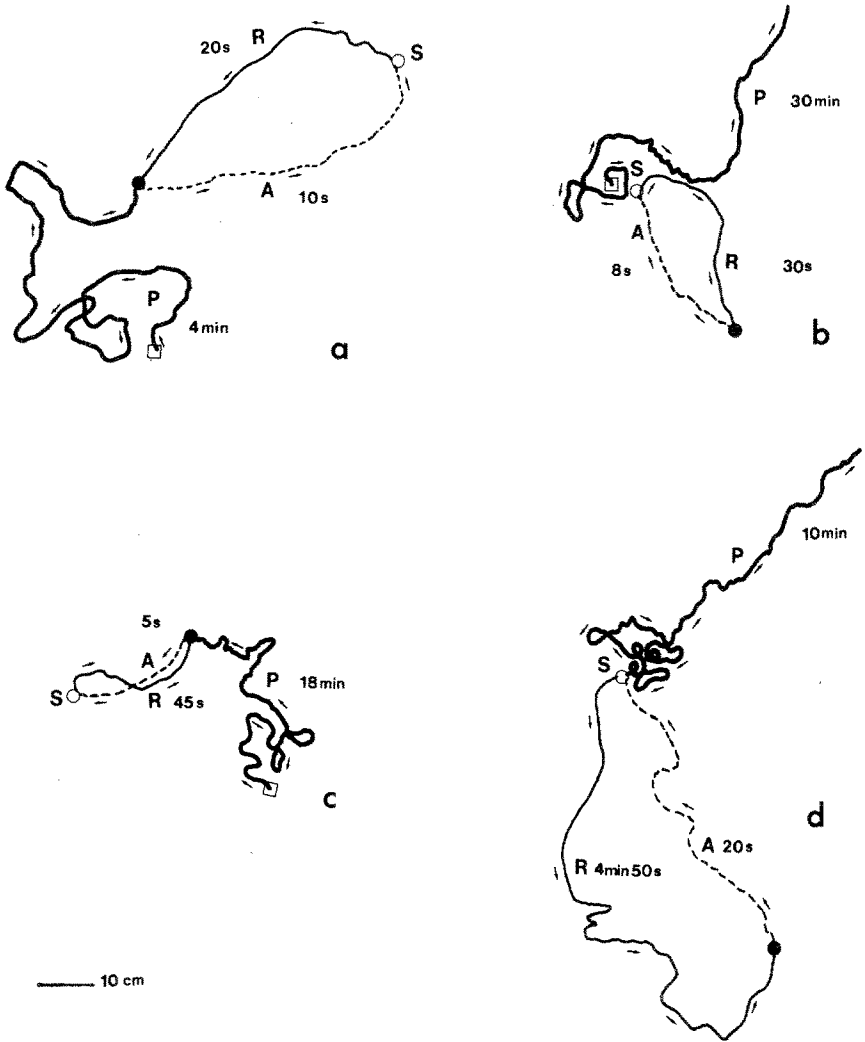


Fig. 2. Paths of field crickets observed under different experimental conditions. A indicates the active outward trip (dashed line), S shows the place (open circle) where the cricket stopped its course before returning, R indicates the following inward trip (thin line), and P shows the trip observed after passive transport (thick line). Durations of returns are also indicated. (a, b) Homing under blue sky. (c, d) Homing under total cloud cover.

two-tailed test, $P = 0.041$ at 30 cm and $P = 0.032$ at 40 cm). Beyond 40 cm, homing success is reduced to 2/10.

As already stated, during experiments conducted under blue sky, crickets do not retrace the outward trip when returning home (Figs. 2c and d).

Table I. Number of Male *Gryllus campestris* Returning to Their Burrow (H = Rate of Homing Success) from Distances [D (cm)] Ranging Between 10 and 80 cm After *Active* Outward Trips Conducted Under Blue Sky and Total Cloud Cover; Durations (T , Expressed as Seconds) and Straightness Index ($0 \leq S \leq 1$) of the Inward Trip are Median Values

D (cm)	Blue sky			Cloud cover		
	H	S	T	H	S	T
10	5/5	0.86	4	5/5	0.85	4
20	7/7	0.82	10	6/7	0.81	120
30	6/7	0.79	90	5/7	0.47	660
40	5/5	0.81	50	4/5	0.67	135
50	5/5	0.81	45	1/3	0.63	120
60	3/4	0.72	90	1/2	0.53	300
70	—	—	—	0/3	—	—
80	2/2	0.62	420	0/2	—	—
Total	33/35 (94%)			22/34 (65%)		

Passive Outward Displacements. Most of the crickets do not home (56%, 19/34) when passively displaced from their burrow under blue sky. When 6/7 crickets find their burrow when released between 10 and 20 cm from it, only 9/17 home between 30 and 50 cm and none beyond 50 cm (0/10). In fact, returns after passive or active displacement below 20 cm (see Tables I and II) are always (18/18) direct and fast, independent of the weather conditions (Kruskal-Wallis ANOVA, $H = 0.627$ for the straightness values and $H = 1.664$ for the duration values, 3 df, $P_{0.05} = 7.82$).

Table II. Number of Male *Gryllus campestris* Returning to their Burrow (H = Rate of Homing Success) from Distances [D (cm)] Ranging Between 10 and 80 cm After *Passive* Outward Trips Conducted Under Blue Sky and Total Cloud Cover; Durations (T , Expressed as Seconds) and Straightness Index ($0 \leq S \leq 1$) of the Inward Trip Are Median Values

D (cm)	Blue sky			Cloud cover		
	H	S	T	H	S	T
10	4/4	.87	5	4/4	.84	4
20	2/3	.85	7	1/3	.82	20
30	5/7	.17	360	3/5	.30	720
40	3/6	.24	630	2/4	.20	480
50	1/4	.24	1260	1/3	.18	900
60	0/4	—	—	0/3	—	—
70	0/2	—	—	0/2	—	—
80	0/4	—	—	0/3	—	—
Total	15/34 (44%)			11/27 (41%)		

Releases conducted under cloud cover show that weather conditions do not affect the rate of homing success after passive displacement: 16/27 crickets (59%) failed to return home. The straightness index (median value $S = 0.32$) and the duration of returns (median value $T = 210$ s) of the homing crickets are not statistically different from those observed under blue sky after passive transport (Mann-Whitney two-tailed test, $P = 0.589$ for the straightness index and $P = 0.896$ for the duration values). These values are also not significantly different from those recorded during cloud cover after active transport (Mann-Whitney two-tailed test, $P = 0.285$ for the straightness index and $P = 0.818$ for the duration values).

Role of Patterns of Polarization During Homing

We recorded the outward and inward trips of crickets walking under a polarizing filter. Two series of experiments were conducted under total cloud cover.

Experimental Series. In order to shift the direction of the axis of polarization at right angle of the direction of the outward trip, the filter was rotated by 90° before the return trip, that is, while the cricket stopped its run.

In this situation, only 2/11 crickets return to their burrow. One returned directly ($D = 20$ cm, $r = 0.9$, $T = 2$ min 30 s) and the other after a very sinuous path ($D = 40$ cm, $r = 0.15$, $T = 3$ min 20 s; Fig. 3d). The other crickets departed at $\pm 90^\circ$ of the direction of the burrow and *did not* return (as in Figs. 3b and c).

Control Series. The filter was rotated by 180° before the return trip in order to keep the axis of polarization in the same direction as during the outward trip but by inducing the same mechanical disturbances, *i.e.*, movement of the filter above the cricket.

In this situation, 8/9 crickets return directly to their burrow and the median value of the straightness index is $S = 0.77$ (Fig. 3a).

DISCUSSION

Like numerous other arthropods (Pardi and Papi, 1952; Papi and Tongiorgi, 1953; Scapini, 1986), crickets perform spatial orientation mainly by using visual cues (Campan and Gautier, 1975; Beugnon, 1983). When the insects live along a one-dimensional strip of habitat either along a forest edge, as the wood-crickets *Nemobius sylvestris* (Morvan *et al.*, 1977, 1978; Beugnon, 1980), or along lake shores, as the riverine crickets *Pteronemobius* (Beugnon, 1985, 1986b), they perform *Y*-axis orientation (Ferguson, 1967). Namely, after passive or active movements outside the forest or on the water surface, they return by the shortest way to the nearest part of their habitat; this involves

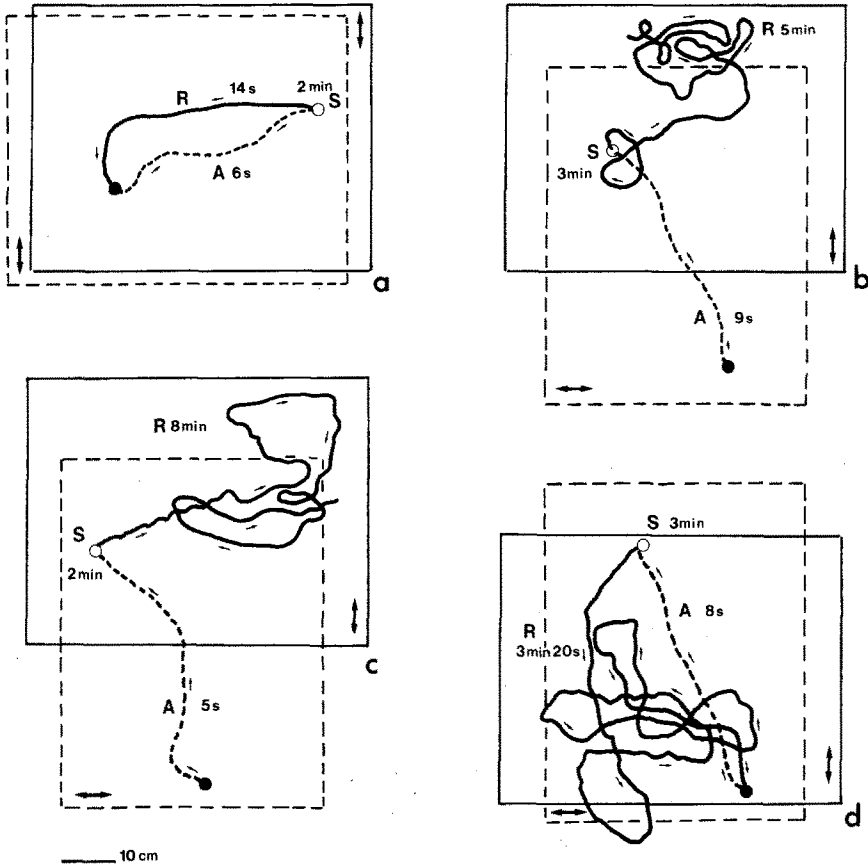


Fig. 3. Paths of field crickets walking under a polarizing filter. The position of the filter during the outward active trip (A and dashed line) is indicated by a dashed rectangle. Its position during the following return trip (R) is indicated by the solid line. The arrows indicate the axis of polarization.

moving perpendicularly to the habitat edge. The directional information is extracted from terrestrial and celestial cues used by the individual either during real-time orientation or after learning during its ontogenetic development by building a constant-memory orientation system (Beugnon, 1986a; Campan *et al.*, 1987).

On the other hand, field crickets *Gryllus campestris* dig burrows in the ground. Their home is not a one axis strip but rather a pinpoint location with spatially defined coordinates, as in any central place foragers. Beetles (Fransevitch *et al.*, 1977) and ants (Wehner and Wehner, 1986) usually perform

path integration to home in such conditions by use of spatial information acquired en route. To explain the homing ability of the field crickets we can propose several hypotheses according to the environmental conditions prevailing during the experiments.

We can exclude simple route reversal as a means of homing since inward and outward trips do not follow the same trail.

When they can see the burrow entrance or the little platform built in front of it ($\phi = 5$ cm), field crickets can perform real-time orientation, as indicated by the high straightness indexes and by the quick returns conducted between 5 and 15 cm. Whatever the weather conditions and even after passive displacements, the insects home directly at such short distances.

Returns observed beyond 15 cm after passive transport and under overcast conditions after active transport could be the result of random or systematic searching, as indicated by the circling searches performed by insects compared with the significantly more straight and fast returns realized after active displacements under blue sky. According to these very sinuous and circling paths, we can assume that some kind of systematic search (Hoffmann, 1984, 1985) is performed. In most cases (Figs. 2a and c) crickets start their circling search when passively displaced from the burrow entrance to the release point as described in ants (Wehner and Wehner, 1986), but they can walk in a rather straight line before circling.

Beyond 50 cm from their burrow crickets cannot home after passive displacements and thus do not use site information given by familiar learned cues. At shorter distances some crickets are still able to home but the duration of returns is significantly increased and the straightness index is significantly decreased. Furthermore, mowing the grass around the burrow ($\phi = 60$ cm) does not affect the rates of homing success (personal observations). Thus constant-memory orientation, based on conspicuous proximate visual cues, does not appear necessary to explain homing in field crickets. Of course this does not mean that some distant terrestrial cues as bushes or trees are never used by field crickets during their foraging excursions. So far we have observed individually marked male and female crickets returning to burrows they had previously occupied after having moved from place to place over 20 m per day. When available, conspicuous terrestrial cues are surely used during homing as potential backup cues.

Volatile-memory orientation seems to be the most appropriate theory to describe the strategy used by homing crickets. However, we must note that, after active displacements, returns are not always directed in a straight line toward home. This appears to contradict the prediction of the vector orientation hypothesis since the inward trip is supposed to be the rectilinear resultant vector of the outbound path. So far, ants, beetles, or spiders performing path integra-

tion always home by the shortest way even after detours on the way out (Frantsevitch *et al.*, 1977; Mittelstaedt, 1985; Wehner and Wehner, 1986). The observed winding inward trips (as in Fig. 2d) could result from the insects avoiding obstacles among vegetation; in addition, they may be pausing or hide underneath leaves or grass blades to prevent predation, detouring if these shelters are not located on the straight line leading to home.

Crickets can perform path integration either using idiothetic or allothetic information (as sun, polarized skylight, slope, etc.). For instance, wood-crickets (*Nemobius sylvestris*) were shown to be able to orient by use of geotactic information in order to return toward the forest (Mieulet, 1980; Beugnon *et al.*, 1983). We can also assume that field crickets adopt a kind of compromise course between idiothetic and allothetic information as described in millipedes (Mittelstaedt *et al.*, 1979). Besides this hypothetical slope information, we have experimentally shown the use of celestial cues by field crickets. Returns performed under sunny weather are significantly faster and more direct than under totally overcast conditions. Furthermore, crickets wander at right angle of the home direction when they run under a polarizing filter with an experimentally 90° shifted polarization axis. These field data are in full agreement with laboratory experiments reporting electrophysiological and behavioral evidence of polarization vision in *G. campestris* (Burghause, 1979; Labhardt *et al.*, 1984; Brunner and Labhardt, 1987). Although the use of celestial cues can explain the mean directions of the returns, we do not know how crickets can estimate distances. That they can is indicated by the observation that crickets returning under the polarized filter begin a circling search after a walk approximately equal to the outward excursion (Fig. 3). To tackle this problem, it will be necessary to carry out passive displacement experiments, while the crickets are returning home, in order to see if they kept their course parallel to the former one. As could be expected if the insects perform celestial-compass orientation, they may run a definite distance before starting their circling search. Unfortunately preliminary experiments were inconclusive because the insects that were already forced to leave their burrow a few seconds before the return trip escaped into cracks or get lost rather than returning to their burrow.

Further laboratory and field investigations by use of video recordings and totally automatized trajectometry will help us to study some of the remaining unsolved problems of homing in *G. campestris*.

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