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Long-distance Homing Ability in *Dasypoda alternator* (Hymenoptera, Melittidae)

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Abstract

Homing rates and initial orientations after release from different directions were investigated in the solitary bee *Dasypoda alternator*. Homing rates and the proportion of individuals returning on the day of release declined with distance, implying that homing from greater distances is not based solely on the use of landmarks. A long duration of return (often not on the same day) and high efficiency of homing (four bees out of 10 returned from a 4 km distance over the lake), as well as an increase in average return speed ≈ 10 m/min) with distance of bees homing on the same day suggest that homing is also not based upon radial scatter as the sole tactic. This is supported by the observation that the initial orientations of the bees were not equally probable. Departures towards the sun greatly exceeded those away from the sun and the bees also tended to depart in cardinal geographical (or geomagnetic) directions, preferring meridional directions (especially southward) to parallel ones (of which east was preferred). Departure directions did not depend on wind direction but did depend, to some extent, on the landscape features of release sites. However, bees neither tended to depart in the direction of the nest, nor did homing success correlate with the direction of departure in relation to that of the nest.

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Introduction

Aculeate Hymenoptera are ‘philopatric’, showing behavioural attachment to specific sites. The homing ability of such animals has been studied by various methods for over a century. For example, Jean-Henri Fabre investigated the long-distance homing faculty of insects by displacing individuals in darkened containers beyond their familiar area (cf. Wehner 1981; Schöne 1984). Homing success revealed by such experiments declined markedly with increasing release distance in a range of species including solitary sphecoid wasps, *Cerceris tuberculata* Vill. (see Fabre 1879, 1882) and *Cerceris hortivaga* Kohl (see Tsuneki 1965), as well as social wasps, *Polistes gallicus* L. (see Ugolini 1986) and *Vespa orientalis* L. (see Ugolini et al. 1987).

Different insect species home at different rates. Among homing honeybees, *Apis mellifica*, those which returned on the same day took longer than 135 s to return 500 m (an average velocity of ≤ 3.7 m/s; Uchida & Kuwabara 1951), a rate similar to the fastest individuals of gregarious bees *Chalicodoma muraria* F. which covered 3 km in 15 min (an average of 3.3 m/s; see Fabre 1879, pp. 275–292). These individuals appear to have flown directly towards the hive. Other individual *Chalicodoma* and other aculeate insect species including the solitary digger wasp bee-wolf, *Philanthus triangulum* F. (Tinbergen & van der Linde 1938) took much longer than if they had flown directly to the nest. Slow return may occur for various reasons. Fabre (1882), for example, noticed that some of his *Chalicodoma* returned with pollen.

We undertook this study to investigate whether the homing of solitary bees from an unknown area was more like that of honeybees or of social or solitary wasps.

Materials and Methods

The experiments were carried out in 1993 and 1994 on a large (*c.* 400 nests) colony of *Dasypoda alternator* (Harris 1780), widely known under other names such as *D. plumipes* (Panz.) or *D. hirtipes* (Fabr.) (see Radchenko & Pesenko 1989). The colony, found by Krzysztofiak (1993, 1994), covered an area of about 0.5 ha on the outskirts of the Wigry National Park (9 km from Wigry) in north-east Poland, on the southern slope of a hill near Magdalenowo village (Fig. 1).

Fifteen (or, sometimes, 10) *Dasypoda* were caught in their nests, individually marked with a set of colour dots on their notum, and transported singly in glass tubes within a dark container to a release point. Each bee was tested only once. Releases took place between 10 and 14 h summer Central European Time (30 min earlier than local time) during July and the beginning of August. Release points were between 0.3 km and 4 km from the nests and were situated either on land or on Wigry Lake, so that the bee-line home sometimes passed over water. We normally released the bees on flowers (to enable them to feed after being held for up to 1 h), except for releases over the lake that took place from a stationary boat.

Bees were released individually. Three experimenters observed the vanishing point, from which the orientation of the bee was determined to the nearest point (i.e. 11.25°) using a compass. The bees usually flew off less than 2 m above the ground or water surface, but many immediately visited flowers, flying from one to another, so that the vanishing point could not be determined. Other members of the team searched the nesting area for returning insects from the time of release for up to 16–17 h (exceptionally 18–19 h). They were also sought during subsequent days for up to 5 days after the last release.

Where appropriate, circular statistics (Batchelet 1981) have been used in the analysis.

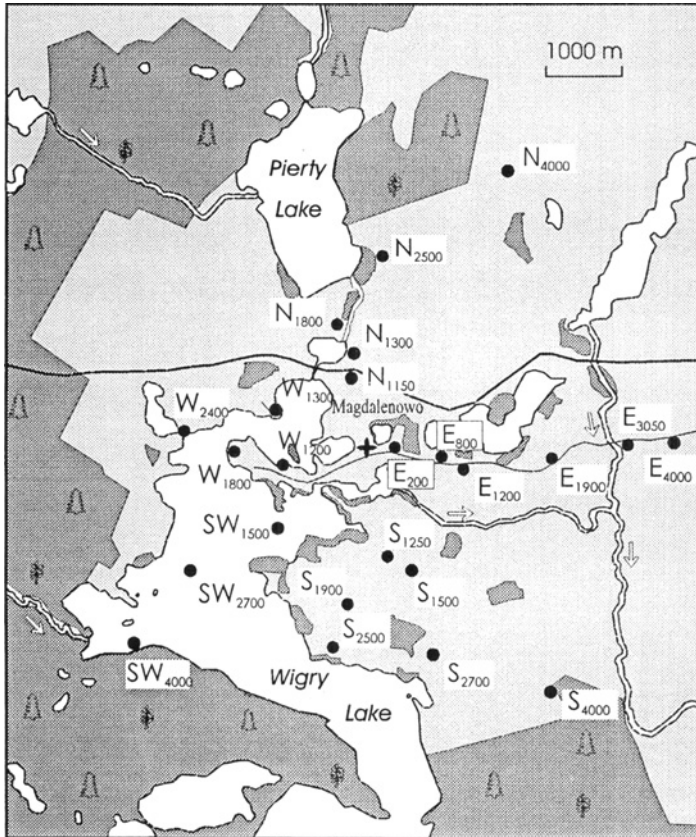


Fig. 1: Area surrounding the nesting colony of *Dasypoda altercator* (+) with release points used during displacement experiments (full circles). Woods are marked in dark grey, open areas (fields and meadows) in light grey, rivers and lakes are unshaded

Results

Homing Success in Relation to Distance of Release and Site Characteristics

The proportion of individuals returning successfully declined with increasing distance of release (Fig. 2; Spearman rank correlation $r_s = -0.674$, $N = 30$, $p < 0.001$).

Slight differences in homing success in relation to the direction of displacement (north or south over open land, or to the east behind woods) were not significant. Similarly, homing success did not differ between release sites on land or over water (Fisher exact probability tests for five matched pairs of release sites at the same distance from south (overland) and south-west or west (over lake) were all non-significant). Thus, even gross landscape differences did not influence the homing success.

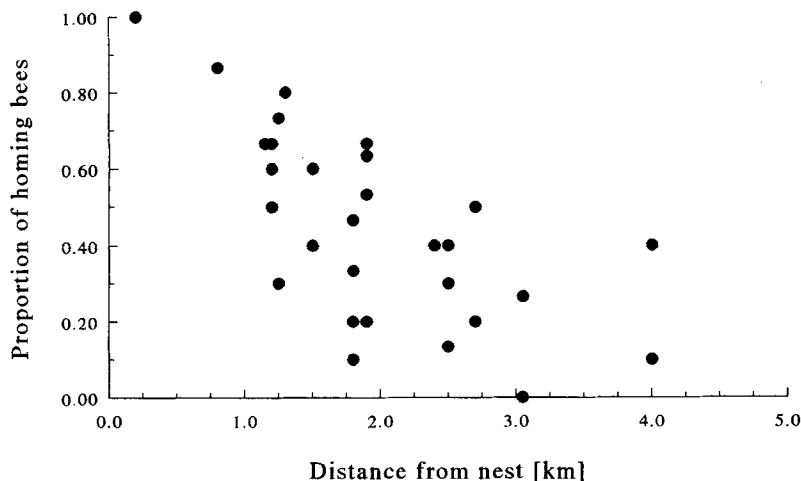


Fig. 2: The relation between the proportion of successfully returning insects and the distance of release

Departure Directions

Although *Dasypoda* rarely circle after release, departure direction sometimes could not be determined because they either flew from flower to flower or flew away too quickly. We succeeded, however, in recording 286 individual departure directions from 425 releases. Bees did not depart with equal frequencies in all 16 directions (Fig. 3(a); $\chi^2 = 215.2$, $df = 15$, $p < 0.001$), but tended to depart in cardinal geographical (or geomagnetic) directions, particularly towards the south and east. Homing success did not depend on the compass direction of departure (contingency test comparing number of bees returning and not returning when departing in various directions (adjacent directions in Fig. 3a pooled): $\chi^2 = 12.55$, $df = 7$, $p > 0.05$).

Bees did not tend towards their home direction, even when released from only 200 m away. It can be seen in Fig. 3a from significant difference between the observed departure directions, and the actual distribution of home compass directions — dashed line ($\chi^2 = 598.9$, $df = 15$, $p < 0.001$). It is more clear from Fig. 3b where the same data are oriented with relation to the home direction; there is no difference between the number of departures in the semi-circles towards home ($n = 126$) and that away from it ($n = 111$, $\chi^2 = 0.95$, $df = 1$, $p > 0.30$), departures 90° to the home direction were excluded). The proportion of bees homing successfully did not depend on whether they departed towards (38 % homed successfully) or away from home (50 %, $\chi^2 = 3.17$, $df = 1$, $p > 0.05$; Fig. 3b).

On days with breeze (strong winds precluded experimentation) more bees departed downwind ($n = 145$) than upwind ($n = 100$, $\chi^2 = 8.27$, $df = 1$, $p < 0.02$. Bees departing in the two crosswind direction categories were excluded).

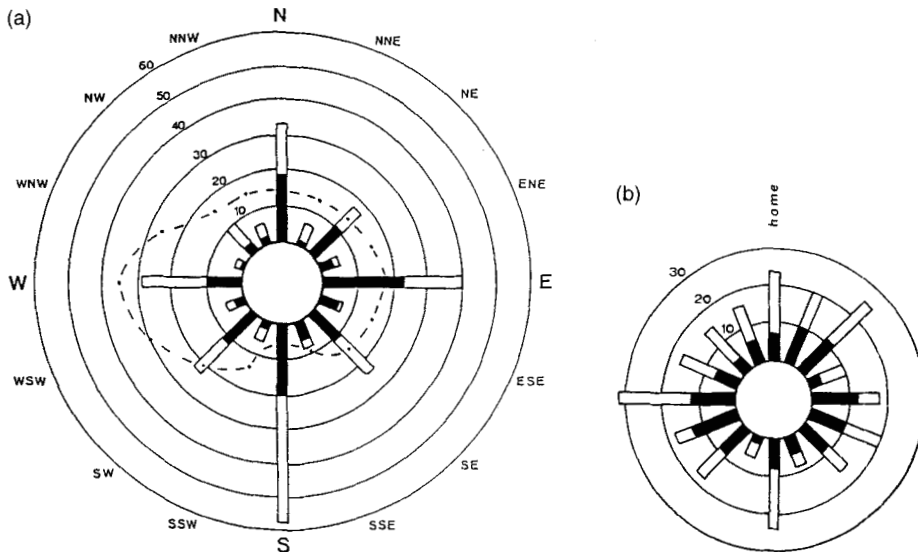


Fig. 3: Departure directions of *Dasypoda alternator* released at 30 spots outside the nesting area ($n = 286$) (a) in relation to magnetic directions, and (b) in relation to homeward direction. Black sections of the bars indicate insects that successfully homed. In (a) the dashed line shows the distribution of the direction of the nesting area from the release point for the bees released

Although some bees departed in all directions with respect to the azimuth of the sun, departures were not random with respect to the azimuth of the sun ($\chi^2 = 26.3$, $df = 15$, $p < 0.01$). In particular, departures in the semi-circle from the release site towards the sun greatly exceeded ($n = 152$) those away from the sun ($n = 95$, $\chi^2 = 3.15$, $df = 1$, $p < 0.001$). Bees departing under azimuth 90° and 270° were excluded).

Departure directions of bees were, to some extent, affected by landscape features at the release site. For example, when the data for four release sites on the shores of lakes are combined, 35 bees flew off overland and 15 over the lake ($\chi^2 = 8.00$, $df = 1$, $p < 0.01$; 23 departures parallel to the lake shore excluded). Similarly, combining data for eight release sites by the side of a road crossing a meadow, 50 bees flew off into the meadow on the same side of the road, and only 29 crossed the road ($\chi^2 = 5.58$, $df = 1$, $p < 0.02$; 23 departures parallel to the road were excluded). However, when bees were released at seven sites on the meadow side of a road separating the meadow from woodland, 31 bees crossed the road into the wood and 33 flew off into the meadow ($\chi^2 = 0.06$, $df = 1$, $p > 0.8$; eight departures parallel to the road excluded). In contrast, the number of bees departing to the left or right in the sectors parallel with landscape boundaries did not differ (lake edge, 12 vs 11: $\chi^2 = 0.04$, $df = 1$, $p > 0.8$; roadside, 16 vs. 15; $\chi^2 = 0.03$, $df = 1$, $p > 0.8$).

Return Time

Observations usually ceased at 16.00–17.00 h, so not all returns home on the same day may have been observed. Nevertheless, some minimum return times were determined, so that average return velocity could be calculated.

The proportion of individuals that returned on the same day declined with increasing displacement distance (Table 1; Spearman rank correlation, $r^s = -0.851$, $n = 16$, $p < 0.001$). Both homing time (Table 1; Spearman rank correlation, $r^s = 0.260$, $n = 66$, $p < 0.05$) and return velocity ($r^s = 0.671$, $n = 66$,

Table 1: Observed minimum time of *Dasygoda* homing

Release point	Proportion of bees that returned on same day (no. of bees released)	Same-day return times (min)	Mean of same-day return times (min)	Mean velocity (\bar{v})(m/min)
E ₂₀₀	0.60 (15)	27, 40, 48, 56, 58, 63, 81, 83, 99	61.7 ± 22.7	3.7 ± 1.7
E ₈₀₀	0.47 (15)	150, 161, 177, 180, 186, 200, 216	181.4 ± 22.3	4.5 ± 0.6
N ₁₁₅₀	0.40 (15)	44, 103, 107, 128, 135, 248	127.5 ± 67.2	11.7 ± 7.4
E ₁₂₀₀	0.24 (25)	62, 77, 123, 130, 132, 136	110.0 ± 32.0	12.0 ± 4.4
W ₁₂₀₀	0.53 (15)	116, 168, 173, 184, 197, 220, 234, 271	195.4 ± 47.0	6.5 ± 1.8
S ₁₂₅₀	0.47 (15)	85, 102, 107, 117, 118, 134, 195	122.6 ± 35.4	10.8 ± 2.6
W ₁₃₀₀	0.30 (10)	58, 86, 159	101.0 ± 52.1	15.2 ± 7.1
N ₁₃₀₀	0.40 (10)	165, 191, 195, 273	206.0 ± 46.6	6.6 ± 1.3
S ₁₅₀₀	0.30 (10)	104, 123, 219	148.7 ± 61.6	11.1 ± 3.9
SW ₁₅₀₀	0.10 (10)	47	47	31.9
N ₁₈₀₀	0.07 (15)	194	194	9.3
W ₁₈₀₀	0.33 (15)	157, 166, 200, 237, 279	207.8 ± 50.8	9.1 ± 2.1
E ₁₉₀₀	0.17 (30)	53, 82, 129, 143, 145	110.4 ± 40.9	20.0 ± 9.8
S ₁₉₀₀	0.00 (25)	Next day		
W ₂₄₀₀	0.00 (15)	Next day		
N ₂₅₀₀	0.06 (15)	183	183	13.7
S ₂₅₀₀	0.00 (25)	Next day		
S ₂₇₀₀	0.00 (10)	Two days later		
SW ₂₇₀₀	0.00 (10)	Next day		
E ₃₀₅₀	0.00 (25)	Next day		
E ₄₀₀₀	0.00 (10)	None returned		
N ₄₀₀₀	0.00 (10)	None returned		
S ₄₀₀₀	0.00 (10)	Two days later		
SW ₄₀₀₀	0.00 (10)	Next day		

$p < 0.001$) increased with distance of release. Its mean value was 9.7 ± 6.6 m/min, i.e. about 25 times lower than the usual flight velocity of the honeybee (≈ 4 m/s).

Discussion

Animals without true astronomical navigation (cf. Griffin 1952; Schmidt-Koenig 1965, pp. 218-219) may use landmarks to navigate within their familiar area, and outside this area may perform a random or systematic search for the familiar area. Homing success from outside the familiar area declines dramatically with increasing displacement distance because systematic search gives a decreasing probability of encountering the familiar area before the time at which search ceases, while behaviour such as radial scatter gives a declining probability of finding the familiar area with increasing displacement distance (Griffin 1952; Chmurzyński & Bartoszyński 1995).

In principle, radial scatter (straight flight in a randomly chosen direction from the release site) should lead to return velocities being approximately constant with respect to displacement distance. This is never observed in practice because of foraging by the insect on its way home, or, in the case of females and workers of Apoidea, owing to the collection of pollen or nectar; however, return times should not exceed a few hours. Such short return times have been observed for *Chalicodoma muraria* (Fabre 1879, 1882), *Philanthus triangulum* (Tinbergen & van der Linde 1938), *Argogorytes carbonarius* (Schöne et al. 1993a) and honeybees (Uchida & Kuwabara 1951). In contrast, systematic search (such as spiral or 'molecular' flight) should lead to long homing times (up to several days) and a decrease in mean homing velocity with increasing distance of displacement from the nest (cf. Griffin 1952; Wilkinson 1952). These features are shown in the homing behaviour of solitary Hymenoptera (e.g. *Philanthus triangulum*, Tinbergen & van der Linde 1938; *Argogorytes carbonarius*, Schöne et al. 1993a; *Bembix rostrata*, Tengo et al. 1990; Schöne et al. 1993b), social wasps (e.g. *Polistes gallicus* and the hornet *Vespa orientalis*, Ugolini et al. 1987), and even honey bees (Uchida & Kuwabara 1951). In addition, vanishing points did not usually show any directional bias.

The decline of homing success of *Dasypoda* females with increasing release distance from the nest and the fact that *Dasypoda* do not tend to depart in the nest direction, are consistent with homing being based on search for a familiar area. Conversely, the lack of a strong increase of homing time with increment of homing distance (which should be expected in case of systematic search) suggests that the bees probably use random search (cf. Griffin 1952; Wilkinson 1952).

Three facts suggest that *Dasypoda* do not use radial scatter in its pure form (i.e. straight flight in a randomly chosen direction). First, departure directions were not equally probable, second, homing success was unrelated to departure direction, and third, some long return times were observed (often over one or more days), whereas with radial scatter at the release distances used and a flight velocity of 4 m/s, the insects should have returned in between 1 and 17 min. However, the observed return velocity is low (about 0.2 m/s, see Table 1). It thus seems likely that the experimental females collected pollen or nectar on their return journey,

and used a tactic of random search, which is as effective in speed of homing as radial scatter. It is interesting that *Dasypoda* show the same tendency as swallows *Hirundo rustica* (Wodzicki & Wojtusiak 1934) to home at a faster rate from more distant release sites.

The tendency for *Dasypoda* to depart in cardinal directions is surprising, and initially might appear to be due to observer bias; however, we are convinced that our observations were made carefully. The only similar behaviour known is the avoidance of certain angles in the geomagnetic field by resting blowflies, *Calliphora erythrocephala* Meig. (Becker & Speck 1964) and cockchafers, *Melolontha vulgaris* F. (Schneider 1974). In *Dasypoda* the mechanism and function of the behaviour are obscure.

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