

Tracking butterfly flight paths across the landscape with harmonic radar

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For the first time, the flight paths of five butterfly species were successfully tracked using harmonic radar within an agricultural landscape. Until now, butterfly mobility has been predominantly studied using visual observations and mark–recapture experiments. Attachment of a light-weight radar transponder to the butterfly's thorax did not significantly affect behaviour or mobility. Tracks were analysed for straightness, duration, displacement, ground speed, foraging and the influence of linear landscape features on flight direction. Two main styles of track were identified: (A) fast linear flight and (B) slower nonlinear flights involving a period of foraging and/or looped sections of flight. These loops potentially perform an orientation function, and were often associated with areas of forage. In the absence of forage, linear features did not provide a guiding effect on flight direction, and only dense treelines were perceived as barriers. The results provide tentative support for non-random dispersal and a perceptual range of 100–200 m for these species. This study has demonstrated a methodology of significant value for future investigation of butterfly mobility and dispersal.

Keywords: butterfly flight; harmonic radar; linear landscape features; Aglais urticae; Inachis io

1. INTRODUCTION

Examining the scale at which butterflies navigate and respond to landscape geometry, while in flight, is fundamental to understanding the role played by landscape in the dispersal and survival of populations. For example, isolation of habitat fragments may have detrimental effects on the sustainability of populations within them (Sutcliffe et al. 2003). The size of the effect will depend on the mobility of the species under consideration, the scale at which it perceives the landscape (Taylor 1997; Baudry & Burel 1997; Dover & Fry 2001), and the strategy used to navigate through it. To determine how butterflies respond to the landscape, actual trajectories of flying individuals need to be analysed (Conradt et al. 2000).

To date, most information on butterfly flight paths has been collected indirectly through mark-release-resight experiments (Hill et al. 1996; Brommer & Fred 1999; Haddad 1999a; Schneider 2003; Wang et al. 2004) or by following individuals visually (Shreeve 1995; Conradt et al. 2000, 2001; Dover & Fry 2001) which is difficult for distances greater than 200 m. Recently developed harmonic radar (Riley et al. 1996; Riley & Smith 2002) has the capability to 'extend the range of detection far beyond that of human vision' (Riley & Osborne 2001), and has been used to track individual flying honeybees and bumble-bees over hundreds of metres (Osborne et al. 1999; Capaldi et al. 2000; Riley et al. 2003). The first aim of this study was to assess the potential of this radar for tracking butterfly flight paths and thus for filling the gaps in current knowledge of butterflies' inter-patch movement.

The use of radar technology to observe lepidopteran movement is not novel in itself; the harmonic radar was used to track pheromone-finding flights of Agrotis segetum moths (Riley et al. 1998). Roland et al. (1996) used a portable direction-finding radar device, similar to that used on beetles (Wallin & Ekbom 1988), to relocate Apollo butterflies up to a range of 50 m through triangulation. However, Riley & Smith's device (although static) measures range as well as direction and has a superior detection range of up to 1 km, providing a geometrically accurate map of the insect's trajectory while in flight (Riley & Osborne 2001). One limitation is that it cannot detect insects obscured by vegetation or trees. Aside from areas of woodland, vegetative landscape features in an agricultural terrain are rarely spatially or temporally continuous, and gaps in their structure enable detection of a flight track for several hundred metres.

Having established that harmonic radar could be used to track individual butterflies, the second aim of this study was to contribute to the current understanding of the influence of linear landscape features and forage patches on flight trajectories. Dover & Fry (2001) and Conradt et al. (2000, 2001) visually recorded butterfly flights, and together suggest that butterflies recognize and respond to landscape features, rather than dispersing at random. Dover & Fry (2001) observed the responses of four butterfly species to artificial visual or physical linear features, as guides between areas of suitable habitat. In general, butterflies were found to be more affected by the presence of a physical (3D) than a merely visual (2D) feature in the landscape. Conradt et al. (2000, 2001) gave convincing evidence for the recognition of favourable or familiar habitats by Maniola jurtina and Pyronia tithonus (Nymphalidae) and suggested that these butterflies may have a perceptual range of between 100 and 150 m (approximately twice their usual dispersal distance within a favourable habitat). Within this

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Figure 1. A. urticae with transponder attached, wings open (left) and closed (right).

range, these butterflies have the ability to identify habitat and orient their movement accordingly. Using the radar to track butterfly foraging behaviour extends these previous studies by providing more accurate measurements of butterflies' behavioural responses to landscape geometry over a larger scale, and direct evidence of whether or not linear features act as guides or barriers to movement.

Aglais urticae (small tortoiseshell) and Inachis io (peacock) butterflies were the major species in this study. Both species are widespread and common within the British Isles, capable of migration between continental Europe and Britain, and daily dispersal and foraging can range over several kilometres (Asher et al. 2001). While both species are relatively ubiquitous, A. urticae is more commonly encountered within open agricultural habitats and I. io in sunny open woodland areas (Asher et al. 2001). Single releases were also made of Vanessa atalanta (red admiral), Polygonia c-album (comma) and Vanessa cardui (painted lady).

2. METHODS

(a) Transponder attachment

To track an insect's movement using harmonic radar, a transponder must be attached to the thorax in an upright position (Riley et al. 1996; figure 1). A transponder consists of a 16 mm half wavelength dipole antenna, made of fine copper-coated steel wire with an inductor and Schottky barrier diode in parallel at the centre of the dipole. One end of the transponder is glued into a narrow plastic tube, and attached to a numbered coloured disk, used for marking bees (Opalith-Plättchen, Thornes, UK). The transponder weighs 12 mg, equivalent to approximately 8% of the body weight of an A. urticae, or 4% of an I. io.

All butterflies were caught within 1 km of the experimental arena and stored in an outdoor $2 \times 3 \times 3$ m³ mesh cage with nectaring plants and shelter materials, for less than 7 days before use. Each butterfly had the scales and hairs removed from the dorsal thorax and was uniquely marked with a combination of coloured paint dots (Liquitex, medium viscosity acrylic) towards the rear of the dorsal thorax. The butterfly was then released within the holding cage until the paint had dried. After a minimum of 30 min, the butterfly was re-caught and the transponder was attached to the insect's thorax using a circle of double-sided sticky foam (W.H. Smiths, UK), to hold the transponder in place.

(b) Preliminary behaviour bioassays

Behavioural bioassays were conducted, in the controlled conditions of the Rothamsted Research flight room (Poppy & Williams 1999), to determine if the presence of a transponder affected the butterflies' behaviour. Bioassays were conducted

between 09:30 and 17:00 h, in the presence of at least two other non-experimental, healthy adult butterflies and a patch of nectaring and larval food plants.

Individual butterflies were observed for two consecutive periods of 30 min: in one period with, and in the other without, a transponder. Treatment order (with/without transponder) was chosen randomly for each butterfly. An individual butterfly was not observed for more than four consecutive 30 min periods, and for no more than six periods in total. Within each 30 min period, duration of walking, flying, and resting, or other activities (components noted) were timed (seconds).

A total of 5.5 h per treatment were conducted. Data were analysed using a log-ratio analysis in which logs of the ratios of times spent walking and flying relative to the time spent doing other activities were calculated and analysed using multivariate analysis of variance in Genstat (v. 6.0; VSN International Ltd, Hemel Hempstead, UK).

(c) Field observations

The field arena was approximately $500 \times 400 \text{ m}^2$ of land on the Rothamsted estate (Harpenden, Hertfordshire, UK), including short pasture, harvested fields and scattered trees. Linear features dissecting and enclosing the arena included hedge and fence-lines, tall treelines (greater than 5 m), field boundaries and tracks (figure 2). Butterfly releases were only made when ambient temperature exceeded 13 °C and over 60% of the sky was clear, or when ambient temperature exceeded 17 °C in any cloud conditions unless it was raining (recognized as suitable conditions for butterfly activity: Haughton et al. 2003). Wind speed (m s⁻¹) and direction were recorded 2.7 m above ground level at 10 s intervals throughout observations. The harmonic radar was located to allow maximum visibility of the arena (figure 2). A butterfly with transponder attached was transported to the release point in a 30×30 cm² mesh-covered release box with a clear sliding lid (Conradt et al. 2001), covered with dark cloth. There were two release points within the arena; each consisting of seven patches of potted nectaring plants (Cirsium arvense and Brassica napus), arranged in a hexagonal shape (~50 m diameter). Artificial linear features (visual guide and wind shelter) connected alternating circumference patches to the central patch. These two experimental arrays were originally designed to investigate the small scale influence of linear features on insect pollinators (E. Cant, unpublished work).

The release box was placed on the upwind side of the central patch of either release point 1 or 2 (figure 2). The dark cloth over the box was removed, and the butterflies were left to settle for 5 min (minimum). Once radio communication confirmed that radar equipment was operational, the lid to the release box was pulled open with string from 5 m away. The radar dish revolved 20 times per min, emitting a 3.2 cm

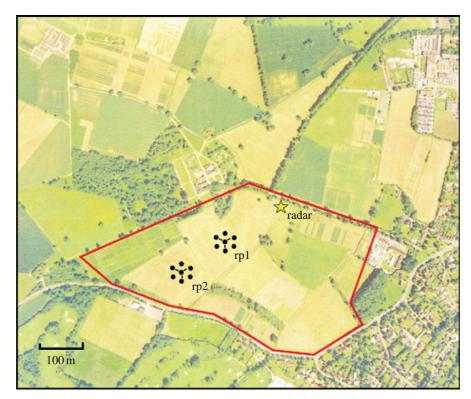


Figure 2. Aerial photograph of arena used for harmonic radar tracking of butterfly flight, (rp=release point). Radar visible arena enclosed in red.

wavelength signal. A harmonic of this signal was reflected back from the transponder attached to the butterfly, allowing movement of the butterfly to be distinguished from the radar clutter signal from all the other objects (ground, vegetation, etc.) in the experimental arena. Where possible, the butterfly was also followed visually from at least 3 m away. This, in combination with radar tracking, allowed nearly continuous recording of behaviour and identification of butterfly movements in the arena, even when a butterfly was invisible to the radar when hidden behind vegetation (e.g. lying low in grass), or sitting at an angle so the transponder was not vertical (e.g. when feeding from a flower). Butterflies were tracked until they were either lost from the arena or were inactive for more than 1 h. In the latter case the inactive butterfly was collected and removed from the experiment.

Between the 21 August and 5 September 2002, a total of 33 releases were made of butterflies with transponders attached, and 30 tracks were successfully recorded by the harmonic radar. The following individuals of Nymphalid species were released: 17 A. urticae (23 tracks), 4 I. io (5 tracks), 1 V. atalanta, 1 P. c-album and 1 V. cardui. These single flights by the last three species (designated style D) were not included in statistical analysis.

The radar tracks were superimposed onto a digitized outline of the fields in the arena using Genstar, and the occurrence, location and size of looped sections of flights were recorded (loops of track less than 10 m radius could not be resolved by the radar). Flights by A. urticae and I. io were categorized into three styles. Style A had no foraging or looping. Style B flights included foraging and/or looping behaviour. The third style (C) included all 'non-eventful' tracks, where the butterfly rarely moved more than 50 m from the release site and spent the majority of the time observed motionless on the grass. Total flight distance (m), average ground speed (m s⁻¹), duration (s) and straightness of route (maximum range/total flight distance) were calculated for each flight, and compared between styles using a one-way analysis of variance (duration and flight distance were transformed: $\log(x+1)$).

Tracks were analysed visually with regards to the potential guiding or barrier effects of the various linear features within the arena. Where a flight path crossed a linear feature, the angle of the flight path (10 m either side of the feature) to the linear feature was measured on both sides of the feature, a difference between opposite angles indicating a response to the presence of the feature. Length and location of flight sections passing parallel to a linear feature, within a 10 m range, were noted.

3. RESULTS

(a) Preliminary bioassays

The behaviour of both A. urticae and I. io butterflies did not appear to be negatively affected by the presence of a transponder during qualitative observations. For I. io there was no significant ($F_{2,9}=2.70$, p>0.05) change to the butterfly's behavioural activities. Five per cent of time was spent flying with the transponder attached compared with 8% without, and respectively, 30% of time was spent walking, compared with 28% without the transponder. In fact the only mating event observed during investigations involved a male with a transponder attached.

(b) Flight styles

Flight styles A, B and C (table 1) differed significantly for flight distance ($F_{2,24}=8.66$; p=0.001), ground speed $(F_{2,24}=12.97; p<0.001)$ and straightness $(F_{2,24}=10.27;$ p < 0.001). The first style (A) involved approximately linear flights (figure 3a) which typically had a high straightness value (mean=0.65) and the flights were relatively fast (mean ground speed=2.91 m s⁻¹). From both release points, 9 out of 11 of these flights were in a south/southeasterly direction, towards the nearest

Table 1. Summary data for track styles A to D (\pm standard error). (see text for definition of track styles.)

parameter	style A $(n=11)$	style B ($n=10$)	style C $(n=6)$	style D $(n=3)$
mean flight distance (m) mean ground speed (m s ⁻¹) mean straightness	291 (47.5) 2.91 (0.3) 0.65 (0.05)	1210.9 (455.4) 1.59 (0.12) 0.38 (0.06)	150.9 (58.4) 1.25 (0.2) 0.27 (0.10)	310.8 (40.3) 4.79 (0.9) 0.82 (0.06)
mean duration (s)	1451 (559)	2877 (852)	1422 (457)	1597 (714)
number of flights with looped sections	0	7	0	0
number of flights with foraging behaviour	0	7	2	1

(~100 m) hedge or vegetated fence-line to the release points. These linear features may have been recognized as a potentially suitable habitat, and indeed forage (mainly C. arvense) was associated with both features. However, no style A butterflies passing near or over these areas stopped to forage. The second style (B) were the nonlinear, slower flights (mean ground speed=1.59 m s⁻¹), involving foraging activity and/or looped sections of flight. Loop length ranged from 15 to 160 m (mean = 56 m), and width ranged from 10 to 165 m (mean = 40 m). This looping may additionally function in orientation of the butterfly within an area since it frequently occurred in close proximity to the site of release (figure 3b,d). Style B tracks had low straightness values (mean = 0.38), and a long duration within the visible arena. Flights of this style usually involved long flight distances (table 1). Style C flights, in which the butterflies spent the majority of time motionless, had low straightness values (mean = 0.26) and these flights also had the lowest mean ground speed (1.25 m s^{-1}) . Style (D) consists of the three flights performed by V. atalanta, P. c-album, and V. cardui, which were very straight (mean=0.82) and very fast (mean ground speed = 4.79 m s^{-1} ; figure 3c).

(c) Response to linear features

In the absence of nectaring plants along linear features (hedge, fence, field boundary or farm track), there was no difference in approach and leaving angles; all were greater than 30°. This indicates that these linear features did not guide the direction of flight paths, or act as a barrier or deterrent to passage. However, dense trees or tall (greater than 3 m) hedges were generally avoided from a distance of 100–200 m, especially during nonlinear foraging flights (style B) as illustrated by the compilation of three style B flights in figure 3d, where such features appeared to cause a change in the direction of flights and to channel flights over tree-less sections of fence. When butterflies were within a 10 m range of a linear feature, there was no evidence of butterflies searching along the features for forage, mates, oviposition or hibernation sites.

(d) Foraging behaviour

There were five patches of forage within the visible arena that consisted of greater than 1 m^2 nectaring plants (including the two release points). Ten of the 31 tracks involved a period of foraging; six included foraging at more than one location. Tracked butterflies that foraged in these patches were often observed to fly straight and direct towards the forage from up to 100 m away. The majority of

flight loops (13 of 16 loops) that occurred resulted in the return of butterflies to an area of forage (e.g. figure 3b), though repeated foraging did not always occur on return to the previously visited area.

(e) Response to wind

Average windspeed during the observation period was 1.8 m s^{-1} (range 0.38–3.19). Only 7 of 30 flights flew in a down-wind direction, suggesting that flight directions were not affected by predominant wind direction. Butterflies were capable of similar levels of straightness during flight, regardless of prevailing wind direction.

4. DISCUSSION

This study has demonstrated the value of harmonic radar for providing novel data about butterfly flight behaviour at the landscape scale. Unavoidably, in any vegetationally cluttered landscape, parts of tracks will be obscured from the radar's field of view, but the ability to pinpoint the location of an individual at a range of up to approximately 1 km far exceeds the capabilities of even the most diligent fieldworker. Harmonic radar is most suitable for studies of medium ranging flights (hundreds of metres): at a smaller scale (several metres), the current technology cannot provide a level of accuracy above that of visual observation. Studies of migration flights may benefit from use of harmonic radar to supplement other techniques such as mark resight and vertical looking radar (Osborne et al. 2002; Chapman et al. 2003). We note that two of the style D flights were from highly migratory species (V. atalanta and V. cardui). Both these flight tracks were straight and fast (figure 3c), and it is possible that these flights were migratory (sensu Kennedy 1986), in contrast to A. urticae and I. io that were searching for forage and hibernation sites at the time of this study.

Despite the small sample size of this pilot investigation, useful observations were made about *A. urticae* and *I. io* flight patterns. Firstly, the flights of these two species were classified into three styles (A, B and C), which significantly differed in flight distance, ground speed and straightness. Styles A and B (figure 3) are very similar to the two types of flight identified by Conradt *et al.* (2000). Their type 1 described a directed linear flight, and type 2 included a period of looping flight, recognized as being a systematic searching flight. Although within our dataset only one track out of 30 included a similar pattern of repeated loops returning to the release site, in B style flights, other loops were observed up to 570 m from the release point and the

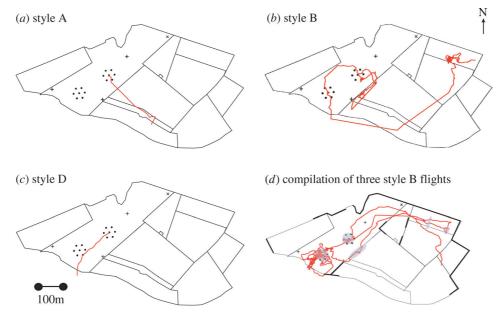


Figure 3. Digitized map of field arena with superimposed flights. Flight paths are indicated by red lines. Linear features, fence, hedge and treelines, field boundaries and farm tracks are indicated by black thin lines. X indicates location of radar, + indicates wind measurement sites and the hexagonal arrangement of black dots the two release points. (a) Example of style A linear flight and (b) example of style B: nonlinear flight, loops can be seen to return the butterfly to areas of forage (indicated on d), (c) example of style D flight (V. cardui), (d) compilation of three style B flights, avoiding dense tree/hedge lines (thick dark lines), between foraging bouts (grey shaded areas indicate presence of greater than 1 m² forage plants).

majority were associated with returning towards a familiar area containing suitable forage plants. Butterflies were also observed to be able to perceive and fly directly towards potentially suitable forage habitat. Bell (1991, p. 69) states that 'when an animal has no information about where resources are located it must attempt to move in such a way so as to optimize its chances of locating resources, but also to reduce the chances of covering areas already searched'. Thus perhaps this looped flight performs an orientation function for the butterflies, and this supports a non-random method of systematic searching during flight.

With respect to landscape geometry, there was no linear feature within the study arena that caused a butterfly to maintain linear flight along it. Dover & Fry (2001) suggested that more than one element is required to maintain, rather than just initiate linear flight along a feature. The strongest association between linear flight periods and linear features occurred for two flights, where abundant forage (C. arvense) was present along a fenceline. No linear flight was observed along this fence beyond the forage, and the fence was not followed on approach to the forage.

Dense treelines appeared to have the strongest influence on flight path directions and appeared to have an effect when the butterfly was up to a distance of 200 m away. Three times, butterflies (A. urticae) changed their direction from heading directly at the treeline to a more parallel path (figure 3d). It is also possible that the unsuitable habitats involving dense areas of trees channelled these same three tracks over a section of fence-line lacking trees. Haddad (1999b) noted that butterflies preferring open habitat (Eurema nicippe and Phoebis sennae) appeared to be 'reflected' off forest edges, while habitat generalists (Papilio trolius) were not affected by habitat edges or corridors. This suggests that the ability of corridors to channel butterfly movement between 'suitable patches' will only be effective where surrounding matrix is highly unattractive. Conradt et al. (2000) proposed that M. jurtina (Satyridae) when translocated into unsuitable habitat 'can detect and orient towards habitat from distances of 100-150 m'. In agreement with such hypothesized perceptual ranges, our data tentatively suggest A. urticae and I. io may be able to identify and avoid unsuitable areas of habitat from up to 200 m and locate potentially suitable forage habitat from up to 100 m. This is an area that deserves further investigation when considering critical levels of habitat fragmentation.

In summary, we have demonstrated the capability of harmonic radar to provide novel data on Nymphalid butterfly movement within the landscape. The 31 flights tracked support the notion of non-random dispersal, and search strategies influenced by landscape features and forage patchiness, but not related directly to wind direction. The components influencing direction of flight are thus likely to be a complex combination of factors, the weighting of which is likely to vary temporally and between species and sexes.

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