Orientation at Night by High-Flying Insects

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6 Orientation at Night by High-Flying Insects

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1 Introduction

The substance of this paper deals with one striking feature of insect migration - common orientation at night by larger-sized (30-2000 mg), high-flying insects. This phenomenon was unsuspected before it was made dramatically obvious by the fortuitous sensitivity of simple scanning radars to non-random orientation in populations of airborne insects (Schaefer 1969). Since then, common orientation has been widely observed in many radar studies (J. Roffey, personal communication 1972; Riley 1975; Schaefer 1976; Reid et al. 1979; Riley and Reynolds 1979, 1983; W.W. Wolf, personal communication 1980; Greenbank et al. 1980; Drake et al. 1981; Drake 1983, 1984) and it appears to be a very common feature of nocturnal migratory flight. All authors agree that orientation occurs in both the presence and absence of moonlight.

There is clear evidence that the mean direction of collectively oriented night-flying insects is often related to wind direction (Schaefer 1976; Riley and Reynolds 1979, 1983; Drake 1983), but this relation appears to be a complex one. The only general rule to emerge is that in winds above the insects' flying speed, the angle between mean orientation and the downwind direction seems to be always less than 90° and is sometimes very small. In contrast to this wind-dependent behaviour, Schaefer (1976) has also reported common orientation by Sudan grasshoppers and noctuid moths in a fixed (SSW) direction, irrespective of the direction of the (light) wind.

In spite of the widespread nature of common orientation almost nothing is known about the factors which control either the mean direction or the degree of orientation of nocturnally migrating insect populations. There has been only one systematic study of the phenomenon published to date, and this has largely served to emphasise the lack of any consistent relation between orientation and obvious directional cues - at least in the case of the Australian plague locust, *Chortoicetes terminifera* (Walker) (Drake 1983). In this paper we compare earlier observations with new results obtained using improved radar techniques, and we describe some mechanisms which might be adopted by migrating insects to orientate themselves. The adaptive value of common orientation will be discussed in a later paper (D.R. Reynolds and J.R. Riley, in preparation).

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2 Methods

Three methods of using radar to study collective orientation are outlined below. Many of our results were obtained by the complementary use of all three.

2.1 Trajectory Measurements

When a flying insect is detected by a scanning radar it produces a string of dots or "footprints" on the radar screen. Measurement of the sequential position of the "footprints" allows one to compute the insect's ground velocity (Riley 1974). Similarly, the "footprints" of a freely drifting balloon carrying metal foil give wind velocity. In cases where these wind soundings are available in the locality of airborne insects, vector subtraction of wind velocity from an insect's ground velocity gives its air speed and orientation. A rough measure of general orientation direction may be obtained in this way, but detailed descriptions of heading distribution require many such measurements and the method becomes very tedious. It also becomes inaccurate when the wind speed substantially exceeds the insect air speed, and in addition is subject to complex bias effects which can be corrected only if the target's scattering properties are known (Riley 1979).

2.2 The Sector Patterning Method

A uniformly distributed aerial population of insects which has a degree of common orientation will produce a striking alternate quadrant (or dumb-bell shaped) pattern on the Plan Position Indicator (PPI) screen of a scanning radar. This is because the insects presenting side views to the radar reflect radio waves more effectively than those seen head or tail on, and they are consequently more readily detectable (Riley 1975). In the case of unimodal heading distributions, sector patterning is a very sensitive indicator of non-random headings, and the mean alignment direction of the insects can be readily determined. The method yields the average axis of *alignment*, but normally leaves a 180° ambiguity about the mean *heading*. This ambiguity may be resolved by comparing the mean direction of target displacement with that of a drifting balloon at the same time and altitude, and thus determining the general direction of flight. In instances where the target insects show differences in front/rear radar reflectivity, as well as the (much larger) side/end differences, it is also possible in principle to resolve the 180° ambiguity from the fine detail of the sector patterning (J.R. Riley, unpublished).

PPI sector patterns are not generally suited to quantitative measurements of the *degree* of alignment because interpretation of the patterns depends on a detailed knowledge of the angular dependence of the targets' radar reflectivity and on assumptions about the form of their heading distribution. These patterns have nevertheless been used to estimate heading distributions on several occasions when the identity of the targets was known, and where experimental measurements of cross-section were available (Schaefer 1976; Drake 1983; Riley et al. 1981, 1983). The method will, however, lead to misleading results if the heading distribution being observed is not unimodal.

2.3 *Vertical-Looking Radar*

This method uses a stationary, vertically-pointing radar beam in which the plane of (linear) polarisation is rotated. Insects displacing individually through the beam normally produce maxima in the radar signal when the rotating plane of polarisation of the electric field becomes aligned with their longitudinal body axes. Measurements of the position of these maxima in the rotation cycle allow estimation of the geographical alignment of the body axis with an accuracy of ±1.25° (J.R. Riley, unpublished). The technique also allows the acquisition of wing-beat frequency, displacement speed and parameters related to the body shape of each target (Riley and Reynolds 1979).

In the case of the largest insects (mass ~1 g), the longitudinal maxima may be replaced by circumferential ones which occur when the body axis is at right angles to the electric field. Fortunately these cases are readily detectable because the rotational modulation is then relatively shallow (Riley 1985). The few signals displaying this characteristic have been excluded from our analysis.

3 Results

We present here a small, but representative selection of the results we have acquired during the past 12 years in both East and West Africa. The selection has been chosen to illustrate different aspects of the phenomenon and to emphasize some new facets made particularly evident by the simultaneous use of vertical-looking (VLR) and scanning radars.

The alignment distributions obtained from the vertical-looking radar data are plotted as equi-areal polar diagrams (Batschelet 1965) with arbitrarily selected 10° bin widths, and their mean values were computed using the method of doubling the angles (Batschelet 1981). The parameters, however, used as a measure of dispersion, was calculated using the expression in Mardia (1972) for double angles:

$$s = [-\ 2 \ln (r)]^{1/2}/2 \text{ radians}$$

because this expression produces values which correspond closely to the standard deviation in linear statistics, up to s values of 45° [r is the root of the mean value of the sum of squares of the sines and cosines of twice the individual orientation angles (Batschelet 1981)].

The term used by Batschelet for double angles:

$$s = [2 (1 - r)]^{1/2}/2 \text{ radians}$$

is equivalent to standard deviation only up to 25° ($r > 0.9$) and thereafter becomes a progressively less sensitive indicator of dispersion.

The precision of alignment measurement (±1.25°) meant that no correction for grouping was necessary. The "forward" or heading halves of the alignment distributions were usually identified by comparison of balloon and mean insect trajectories as observed simultaneously with a scanning radar, and are shown hatched. In cases where ambiguity remained (for example, instances of small groups aligned at large angles to the bulk of the distribution) no attempt was made to determine heading. The direction of mean insect displacement (D) and of balloon movement (W) (when available at the appropriate altitude) are shown on the histograms, as well as the moon's azimuth (M).

3.1 Downwind Unimodal Distributions

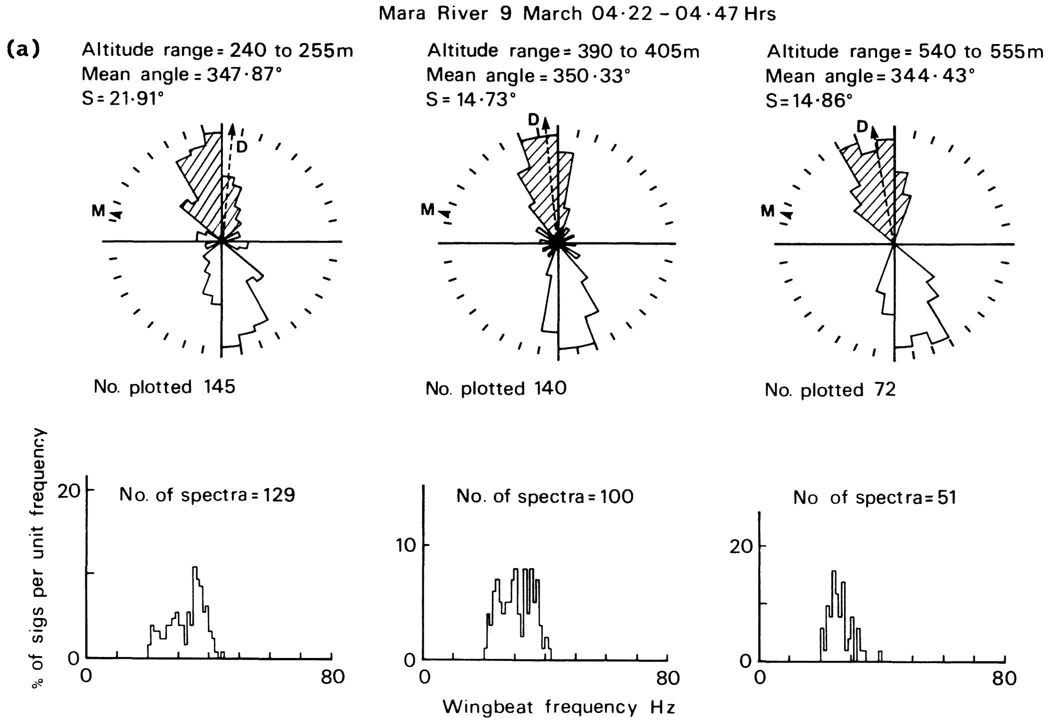
The distributions shown in Fig. 1a were obtained in southwestern Kenya at a site near Mara River (1° 03′ S, 35° 15′ E) and are typical of many observed. They are symmetrical about the mean and are not significantly different from the circular normal by the Chi^2 test (Batschelet 1981). The aerial density was of the order of one insect per 10^4 m^3. Overall displacement was nearly parallel to the alignment axis and observed to be at 5.1 ± 1 m s^{-1} at 250 m above ground level (agl), and at 6.1 ± 1 m s^{-1} at 460 m agl. We deduce from this that the insects were oriented close to the downwind direction, and as they were flying with an average air speed of 2.5 m s^{-1} (J.R. Riley and D.R. Reynolds, unpublished) the wind would have been $\cong 3$ m s^{-1}. Balloon soundings were not made during this period, but the alternative possibility that the insects were heading into an 8 m s^{-1} wind and displacing backwards was ruled out because of the presence of a small number of very slowly moving (< 1 m s^{-1}) insects (an 8 m s^{-1} headwind would give minimum ground velocities of ~ 5 m s^{-1}). In the many simultaneous observations we have made of balloon and insect trajectories, overall backwards displacement has never been detected for oriented groups.

It may be noted that orientation was not directed towards the full moon which was clearly visible at an elevation of 26°. The identity of the insect targets was not definitely established, but it seems certain from the wide range of wing-beat frequencies (20–42 Hz) extracted from their radar signatures that the common orientation was shared by a mixture of different species, perhaps noctuid and sphingid moths. The wing-beat frequency histograms in Fig. 1a show that the species with the higher frequencies were dominant at low altitudes, but were outnumbered in the 540–555 m range by larger insects with lower wing-beat frequencies. At the intermediate level of 390–405 m both groups seem equally represented. It is to be noted that although some decrease in frequency with altitude would be expected because of decreasing air temperature, the decrease over 300 m would be much smaller than that observed. For example, in the case of the noctuid moth, *Spodoptera exempta* (Walker) with a temperature coefficient of 1.2 Hz $°C^{-1}$ (Farmery 1982), even an extreme lapse rate of 1 °C per 100 m would produce only a 3–4 Hz decrease in frequency.

3.2 Crosswind Unimodal Distributions

In contrast to the example shown in Fig. 1a, the orientation distributions in Fig. 1b are aligned at 63° to the direction of average insect movement, which in this case was

Fig. 1a,b. Alignment distributions, at three altitudes, for insects showing orientation in: (a) the downwind, and (b) a crosswind direction, together with corresponding wing-beat frequency distributions for each altitude. *D* = direction of displacement; *M* = moon's azimuth. *Shaded* section indicates deduced heading distribution


Mara River 9 March 04·22 – 04·47 Hrs
(a)
Altitude range = 240 to 255m
Mean angle = 347·87°
S = 21·91°
D
M
No. plotted 145
Altitude range = 390 to 405m
Mean angle = 350·33°
S = 14·73°
D
M
No. plotted 140
Altitude range = 540 to 555m
Mean angle = 344·43°
S = 14·86°
D
M
No. plotted 72
% of sigs per unit frequency
No. of spectra = 129
20
0
0
80
No. of spectra = 100
10
0
0
80
No of spectra = 51
20
0
0
80
Wingbeat frequency Hz

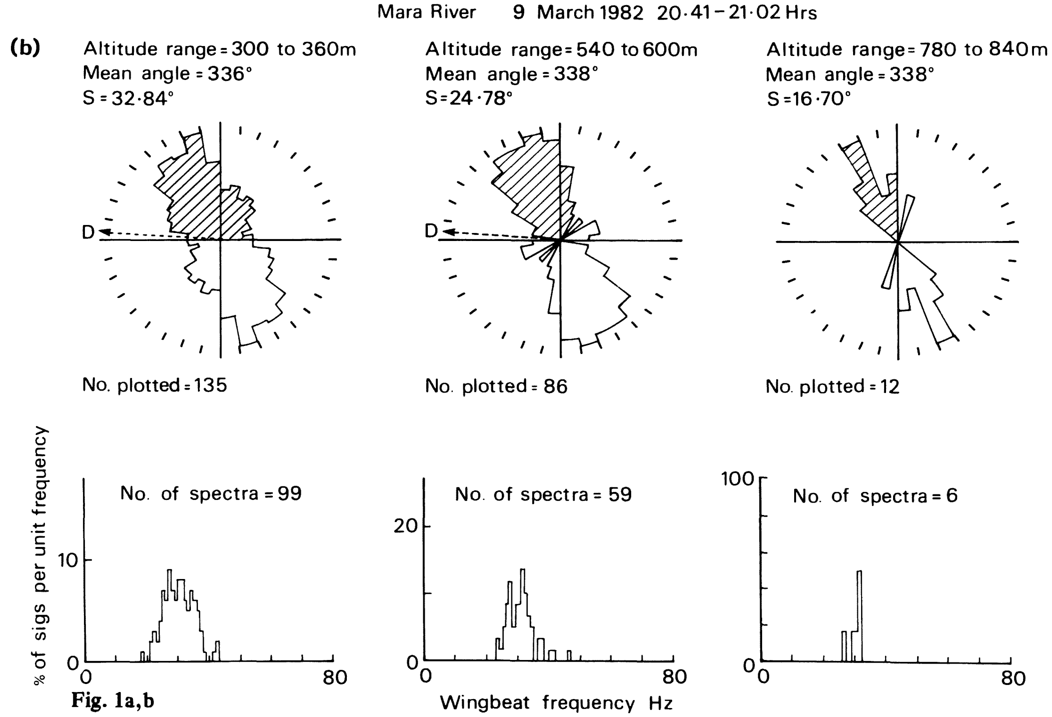

Mara River 9 March 1982 20·41 – 21·02 Hrs
(b)
Altitude range = 300 to 360m
Mean angle = 336°
S = 32·84°
D
No. plotted = 135
Altitude range = 540 to 600m
Mean angle = 338°
S = 24·78°
D
No. plotted = 86
Altitude range = 780 to 840m
Mean angle = 338°
S = 16·70°
No. plotted = 12
% of sigs per unit frequency
No. of spectra = 99
10
0
0
80
No. of spectra = 59
20
0
0
80
No. of spectra = 6
100
0
0
80
Wingbeat frequency Hz

Fig. 1a,b

seen on the PPI to be towards 270°-280° at 11 ± 2 $\mathrm{m\ s^{-1}}$. The insects were thus aligned largely across the wind. If it is assumed that a representative individual flying speed is 2.5 $\mathrm{m\ s^{-1}}$ directed to the northwest quadrant, then the average air speed for a population with a standard deviation, s, of 25° would be 2.3 $\mathrm{m\ s^{-1}}$. Vector subtraction of this figure from the observed displacement velocity gives an average wind of 10 $\mathrm{m\ s^{-1}}$ directed *towards* 264°, i.e. the downwind direction is some 74° away from the mean insect orientation direction. As in Fig. 1a, the broad spread of wing-beat frequencies shows that a mixture of species was present, especially at the lowest altitude (300-360 m agl).

It was noted from the PPI display that in the altitude range 230-570 m agl the average insect displacement direction had changed from 310° to 275° at some time between 20.34 and 20.48 h, and that the mean orientation had also moved from approximately 005° to 335° during the same period. Vector subtraction of an assumed flying speed of 2.3 $\mathrm{m\ s^{-1}}$ from the observed displacement vectors indicated that the wind had backed from towards 300° to towards 264° and slackened slightly from 10.5 to 10 $\mathrm{m\ s^{-1}}$. *Thus the average orientation appeared to be at rather similar angles to the downwind (65° and 71°) before and after the wind shift.* The difference between these figures and the value of 74° found from the VLR results probably occurred because the PPI results are spot measurements, whereas the VLR produced a value averaged over 25 min.

3.3 Bimodal Distributions

As well as the more common unimodal distribution to the type illustrated in Fig. 1 we have occasionally observed clear instances of bimodal or split distributions. One example observed in Mali in West Africa has been described previously (Riley and Reynolds 1979) and another more recent observation, also from Mali (at Daoga, 15° 53′ N, 0° 14′ E), is shown in Fig. 2. In this example, a fairly tight distribution centred on 41° between 225 and 270 m agl is largely replaced by a northwards orienting group at 675-720 m, but the groups clearly overlap at the intermediate heights. This pattern is reflected in the wing-beat frequency histograms which show a dominance of higher frequencies (33-42 Hz) at the lowest altitude, and of lower frequencies (26-33 Hz) above 675 m. It would thus appear that several different species were present, with overlapping vertical density profiles and with two different mean orientation directions. PPI observations of a balloon trajectory at 20.40 h showed that the wind was towards 348° at 7 $\mathrm{m\ s^{-1}}$ up to 600 m, the highest altitude observed, thus the northwards group was heading close to the downwind direction. The mean direction of insect displacement at all altitudes seen on the PPI was very close to northwards, the lowest fliers having a mean ground direction towards only 002° in spite of their northeast heading. This result is consistent with the vector addition of a mean air speed of 3 $\mathrm{m\ s^{-1}}$ (found to be typical for the insects we were observing in the area) at 41° to the wind vector. The mean orientation direction deduced from PPI sector patterning backed steadily with altitude from 45° to 360° but as would be expected, gave no indication of the heading split made evident from the VLR records.

The identity of the targets contributing to both the orienting groups was not certain. However, comparing the wing-beat frequencies of the Acridid species taken at our light

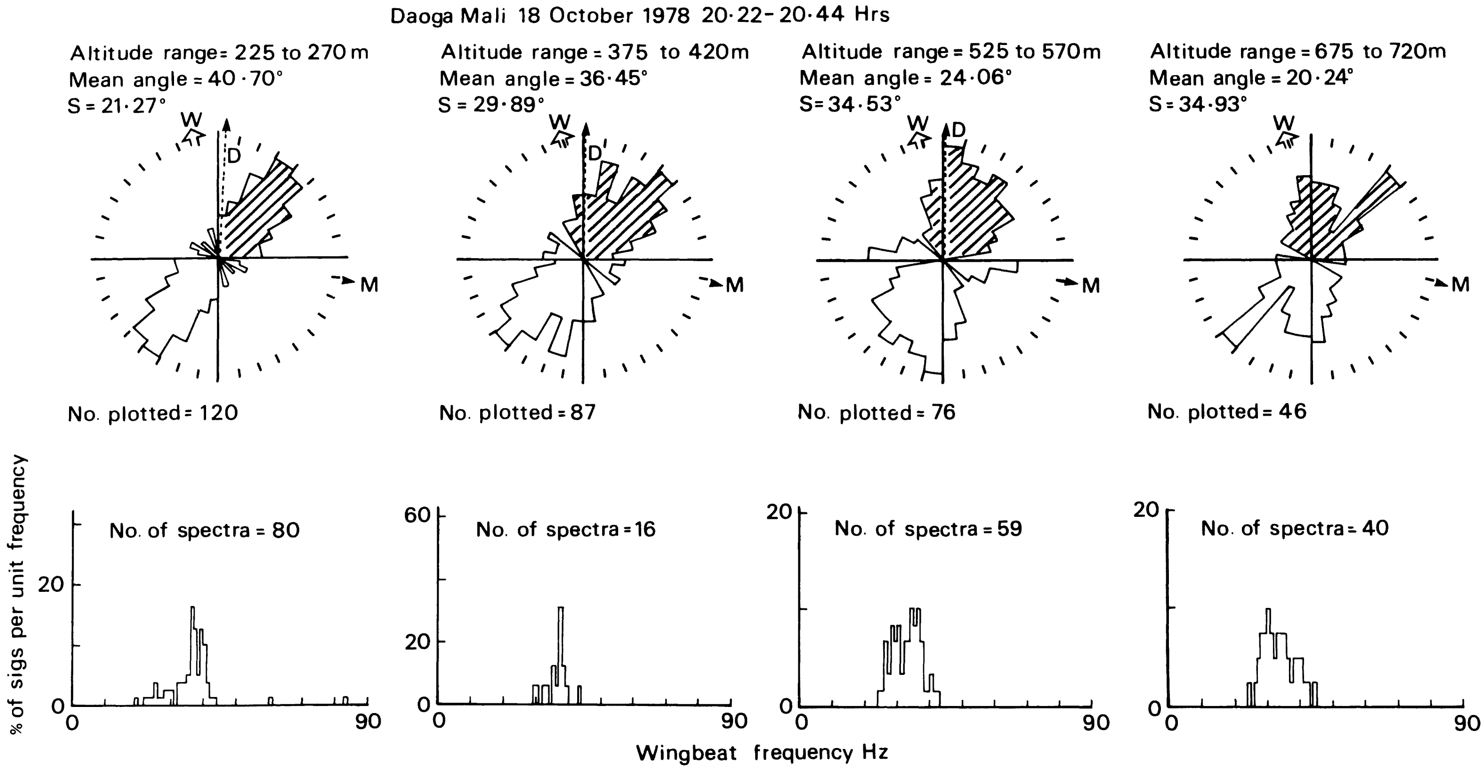


Fig. 2. Alignment distributions at four altitudes, for insects (probably Acridids) showing collective orientation about two different mean headings, together with corresponding wing-beat frequency distributions for each altitude. D = direction of displacement; W = direction towards which wind was blowing; M = moon's azimuth. *Shaded* section indicates deduced heading distribution

traps with those measured from the overflying insects, we consider it likely that *Oedaleus senegalensis* Krauss was predominant in the low frequency group, and that smaller grasshoppers such as *Acrotylus* spp. and *Pyrgomorpha conica* (Ol.) might have been the dominant species in the higher frequency, northeast-heading population.

3.4 Accumulated Results

We found that in four particularly clear examples of bimodal distribution, the mean orientation of one of the groups was within ±5° of the downwind direction. It therefore seemed likely that these groups were perceiving wind direction and responding to

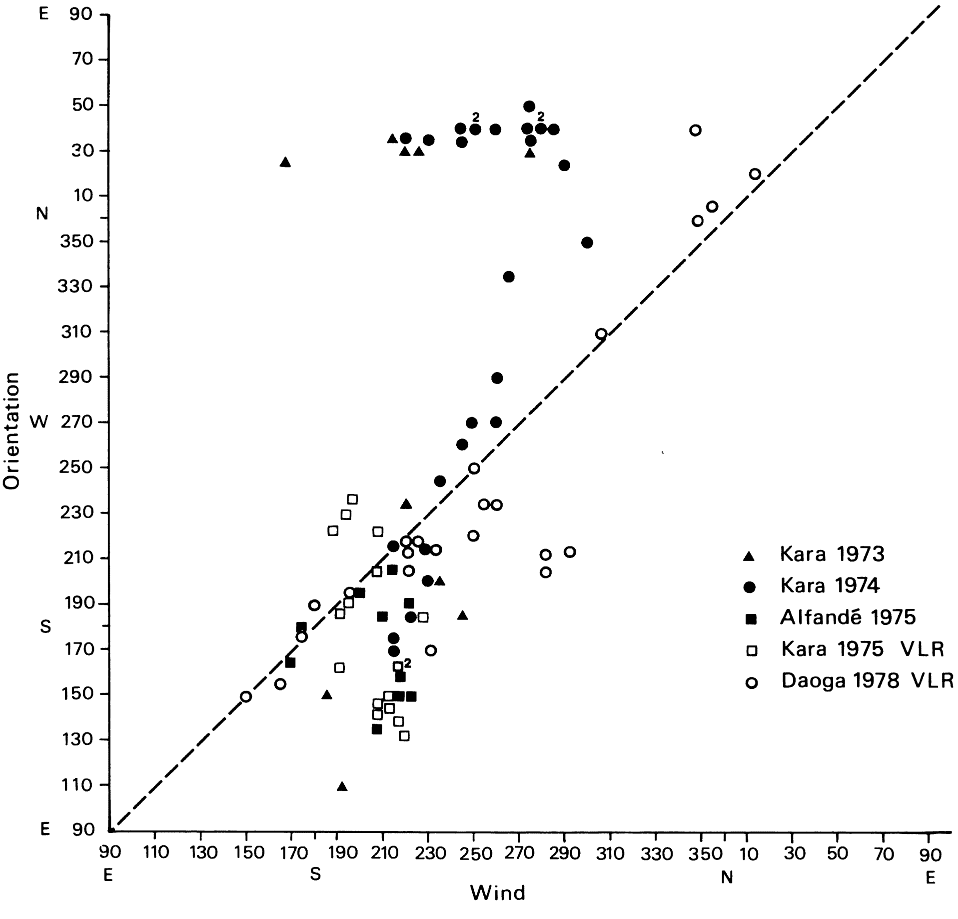


Fig. 3. Mean heading of orienting groups of insects (believed to be mainly Acridids) plotted against the direction towards which the wind was blowing. Wind direction was established from the movement of freely drifting balloons at the same altitude as the insects. The radar data was recorded in Mali, West Africa from three sites: Kara (14° 10′N, 5° 1′W); Alfande (15° 48′N, 3° 4′W), and Daoga (15° 53′N, 0° 14′E). The Daoga (1978) and Kara (1975) data are from a vertical-looking (VLR) radar, the rest are from PPI recordings from a scanning radar

it, and that the other groups were aligned to some other cues. In none of the cases was there an obvious cue like the moon's azimuth, the twilight arch or a significant feature on the horizon.

To determine the relative incidence of downwind orientation, we pooled both VLR and PPI results for several years and from three sites, and plotted orientation against wind direction. The data from Mali produced a total of 87 points (Fig. 3) of which only 24% were within ± 10° of the downwind line. There was strong evidence of a preferred orientation towards 25°–50° in light winds blowing towards a wide variety of directions (165°–350°), and in both the presence and absence of moonlight. There was also some concentration of off-wind headings within the much wider range of 130°–210° in winds towards the southwest.

4 Discussion

In most of the examples of nocturnal collective orientation which we have seen, the aerial density of the insects has been well below one insect per 10^4 m^3 and the average separation between individuals has ranged from 30 to 150 m, so it seems most unlikely that the insects maintained common orientation by visual reference to each other. This conclusion is supported by the observation that degree of orientation is not affected by moonlight nor, in our experience, by variations in aerial density. In any event, mutual references of any type would not provide a mechanism by which a non-random mean heading could be selected and sustained over large areas and for long periods without the accumulation of drift due to systematic errors or biases in the reference process. It is therefore necessary to invoke an environmental directional cue (or hierarchy of cues) to which the insects individually respond, and in the sections below we discuss a number of candidate cues. Throughout the discussion we assume that different species may on occasions simultaneously respond to different cues in the same environment [as implied by Fig. 2 and by our earlier results (Riley and Reynolds 1979)].

4.1 Orientation to the Wind

There is now a weight of evidence to suggest that at least on some occasions, orientation direction is related to wind direction. For example, we have described an observation in which the orientation of Sahel grasshoppers veered with altitude and time in a similar way to wind direction, so that orientation was maintained close to the downwind (Riley and Reynolds 1983). Schaefer (1976) has reported similar behaviour in spruce budworm moths, although in this case the maintainance of downwind direction became less accurate above 400 m agl. Wind-related orientation is not always, however, close to downwind, as we demonstrated in Sect. 3.2. In this observation mean orientation was maintained at 65° to 71° to the downwind direction after the wind had backed by 36°. Drake (1983) noted a similar effect when the orientation of migrating *Chortoicetes* apparently remained at some 40° to the wind after a wind shift of more than 90°.

These observations prompt enquiry into the mechanisms by which the wind might provide cues to which insects could orientate themselves. As we have pointed out previously (Riley and Reynolds 1983), any ability on the part of the airborne insects to establish geographical direction (using for example, celestial cues or the earth's magnetic field) would not have enabled them to deduce the direction of the wind. To do this they must either have been able to detect the direction of apparent ground movement relative to their own alignment, or else have been able to sense some accelerative anisotropy of air movement associated with wind direction.

4.1.1 Visual Perception of Relative Ground Movement

Kennedy (1951) has hypothesised that visual perception of wind-induced movement relative to the ground is a factor which governs the orientation of locusts flying at low altitude during the day. The conditions for which this optomotor response was postulated were, however, very different from those in which we detected wind-related orientation. The illumination levels were very much higher (ca. 10^4 lx compared to ca. 10^{-2} lx) and the angular rates of wind-induced movement were also higher. For example Kennedy (op.cit. p. 218) gives a rough estimate of preferred retinal velocity as that produced by a displacement speed of 3 m s^{-1} at 6 m agl, i.e. 27° s^{-1}, whereas our observations typically relate to insects at several hundred metres agl and experiencing longitudinal angular rates of ca. 0.2° to 3° s^{-1}. If insects maintain their heading with respect to the wind by observing relative ground movement, it might be hypothesised that they do so by orienting themselves so that the transverse angular velocity of ground features remains within preferred limits. An estimate of required limits of this type may be obtained from the downwind distribution described in Sect. 3.1. Thus the estimated wind speed at 545 m agl was 3 m s^{-1} along the mean orientation direction, and the component of this speed transverse to the longitudinal axes of those insects near the edges of the distribution (±15°) would be $\pm 3 \sin(15)$ m s^{-1}. Insects at 545 m agl would therefore have to maintain their transverse angular velocities within the range of $0 \pm 0.08°$ s^{-1} to achieve the observed heading distribution.

It is perhaps more instructive to examine the case of wind-related, off-wind headings. Consideration of the example described in Sect. 3.2 shows that the observed distribution with a standard deviation of ±25°, at some 74° to a wind of 10 m s^{-1} at 570 m agl, would produce lateral angular velocities within the range 0.759° to 0.993° s^{-1}, with a mean of 0.966° s^{-1}, i.e. *the angular velocity distribution would be highly skewed.* Trigonometric considerations show that this is generally the case for symmetrical off-wind distributions when the mean heading is greater than 45° away from the direction towards which the wind is blowing. Conversely, if the insects oriented themselves so as to produce a symmetric distribution of transverse angular rates about a preferred mean (as one might expect), a skewed heading distribution would result. Our observations show, however, that both downwind and crosswind headings are usually symmetric about the mean. Furthermore, the maintainance of off-wind headings by the adoption of a 'preferred' lateral angular velocity would introduce an altitude dependence into the resultant heading, i.e. the higher the insects were flying, the more they would have to head off-wind to maintain the same lateral angular velocity. This is clearly *not* the case in the example shown in Fig. 1b where the same mean heading was maintained at all altitudes, even though the lateral angular velocity experienced by the lowest group was more than twice that seen by the highest group. (The displacement speed and direction were virtually unchanged over this altitude range.)

Overall it seems clear that the transverse angular velocity hypothesis does not account for observed off-wind orientation. Nor is it consistent with the independence of standard deviation on altitude which is often observed in both crosswind and downwind heading distributions (Fig. 1a and b; and Riley and Reynolds 1983).

An alternative hypothesis for the maintainance of off-wind headings is that the *ratio* of lateral to forward angular movement might be used as an orientation cue (Baker et al. 1984). This would not predict symmetrical distributions for off-wind headings, but provided that angular rates remained high enough to be quantitatively perceived, it *would* explain the altitude independence of both standard deviation and the direction of off-wind headings.

4.1.2 Laboratory Measurements of Response to Angular Movements

It is of interest to enquire whether there is any evidence from the laboratory that insects can visually perceive and respond to the angular rates required to explain wind-related orientation. Thorson (1966) has shown that rigidly mounted desert locusts *(Schistocerca gregaria)* respond to very small (5×10^{-3} deg) angular movements of boldly striped patterns. These movements corresponded in his experiments to maximum angular rates of 4×10^{-3} deg s^{-1}, and the response was achieved at an average pattern brightness of 1 L. Decreasing the brightness lowered sensitivity to movement, and at 10^{-4} L a response was just perceptible to a pattern movement of 0.1° ($0.08° s^{-1}$). This is comparable to the rates that we have seen are necessary to maintain wind-related headings and it is therefore pertinent to compare the laboratory visual stimuli with those available to insects in the field.

The pattern used by Thorson was of higher contrast (86%) and regularity than that likely to be found in the natural landscapes in which we have made our observations, but it is possible to make a comparison of the brightness of the visual environment in the two cases. If one assumes that a reflectivity of 0.2 in the wavelength range of 400-700 nm is representative of the terrain in which we obtained our results (M.B. Allenson, personal communication), then a full moon at zenith and a clear starlit sky, giving illuminations respectively of 3×10^{-1} and 10^{-3} lx, would produce surface brightnesses of 6×10^{-6} and 2×10^{-8} L. It would appear from these figures that to achieve by visual means the wind-related orientation that we have observed when the moon was at low elevation or below the horizon, the insects concerned would have had to respond to ground patterns whose brightness levels were at least two orders of magnitude below those at which a response could be elicited from locusts in the laboratory.

A further point of relevance is that Thorson found responses only when the angular period λ, of the moving pattern exceeded 3° (most of his data were obtained with $\lambda = 8°$) and he noted that this result was compatible with a light- (or dim-)adapted visual acuity of ca. 3°. The implication of this is that dark-adapted locusts, with visual acuity of ca. 6° (Horridge 1965, quoted in Thorson op.cit.) and flying at 400 m agl, could respond only to movement relative to those features on the ground which showed substantial contrast over scales of $\geqslant$ 40 m. Individual trees and bushes would thus not provide a usable pattern. In the case of the moth *Manduca sexta* (Joh.), the minimum angular period required to induce a response in motion-detecting neurons in the dark-adapted eye is reported to be 16° (Rind 1983), so even if this moth could perceive ground contrast, it could presumably orient itself to the wind from an altitude of 400 m agl only when flying over contrasting features on a scale of $\geqslant$ 100 m.

The angular movements response experiments of Kien (1974) with single-edge patterns showed a very much higher threshold level (0.4° s^{-1}) for the Australian plague locust, *Chortoicetes terminifera* than Thorson found for the desert locust, and this was at quite high brightness levels (6.8×10^{-3} L). In Kien's experiments the locusts were able to move their heads and her results may therefore be more applicable to the conditions of free flight. If this is the case, then her work would indicate even more strongly that visual perception of the apparent direction of ground movement provides an inadequate explanation of wind-related common orientation.

Quite apart from constraints due to the limits of visual perception, the detection of low angular rates normally requires that the viewing platform be stabilised within much smaller limits than the rates to be detected. In the cases we have considered, this would seem to require the insects to control their head attitudes within, say 10^{-2} to 10^{-3} degrees about their roll axes – an improbable feat for an insect in free flight (Kennedy 1975, p. 112).

The presence of irregular, flight-induced movements may not, however, completely exclude the possibility that airborne insects can detect low angular rates of motion. Horridge (1966a) has shown that the eye of the crab *Carcinus* responds to pattern movements as low as 7×10^{-4} deg s^{-1}, in spite of the fact that the eye is subject to continual tremor movements of 0.04°–0.2°, at a frequency of 1 Hz. He also found evidence for a similar opto-kinetic memory in *Locusta migratoria* (L.) (Horrdige 1966b). It thus seems conceivable that some insects may be able to make very precise assessments of the average angular position of visible features, even when subject to flight perturbation. The average angular positions of the horizon and any visible ground features underneath the insect flight path might then presumably be compared to reveal small, relative angular rates associated with displacement.

We note in conclusion that the general absence of 'backwards' displacement would seem to imply that nocturnally flying insects can usually maintain enough visual contact with the ground to detect and avoid gross front-to-back movement of ground features. The threshold at which reverse angular rates become unacceptable has not been established, but careful examination of some of our balloon and insect trajectories suggests that it is at least 0.2° s^{-1} under starlight illumination (J.R. Riley, unpublished).

4.1.3 Anisotropic Air Movement

The use of anisotropic accelerations or gusts in the wind as a cue to fix wind direction was postulated many years ago by Williams et al. (1942) and Nisbet (1955) to explain wind-related orientation. Since then it has been invoked by a number of authors including most recently Larkin (1980) and Able et al. (1982) for birds, and ourselves in relation to insects (Riley and Reynolds 1983), but there has been a singular lack of experimental evidence to show that small-scale anisotropy is a widespread phenomenon.

The turbulence induced by wind shear at altitude is believed to be substantially isotropic below length scales of the order of a kilometre, except in cases where the shear produces Kelvin-Helmholtz (KH) waves (E.A. Gossard, personal communication).

Atlas et al. (1970) have described an example of KH instability in which insect horizontal displacement velocities apparently oscillated by ±2 to 3 m s^{-1} in the vicinity of the wave, and it was deduced that the maximum velocity perturbation was in the direction of wave motion. It seems very probable that the accelerations associated with velocity changes of 2–3 m s^{-1} occurring in a period of ca. 20 s (the average time for an insect to fly between a trough and a crest of the observed wave) would be perceptible to airborne insects, either directly, or because their inertia within the accelerating/decelerating air mass would produce cyclic changes in their air speed. Atlas et al. (1971) concluded that the insects were travelling (and therefore presumably orienting) in a direction opposite to that of the wave propagation, which in this case was downwind. The wind speed at the altitude of the waves (365 m) was 1 m s^{-1}, so upwind displacement would indeed have been possible for insects with an air speed of 3 m s^{-1}.

It would appear from the observations of Atlas et al., that wave-induced anisotropy provides a directional cue which could be used by insects to maintain wind-related orientation, and the fact that the direction of wave propagation (and therefore of maximum anisotropy) is often not downwind (E.A. Gossard, personal communication) could explain the occurrence of wind-related, but off-wind headings.

The lack of experimental evidence for the common occurrence of anisotropies may in part reflect the scarcity of instruments able to detect fine-scale structure in the wind at altitudes of several hundred metres. For example, the results of Atlas et al. were made possible only by the advent of a specially constructed, ultra-high resolution radar. On the other hand, subsequent use of this radar by Noonkester (1973) for a total of 849 h detected breaking KH waves for only 0.6% of the operational period, and Noonkester considered that meteorological conditions in the area in which he was working would generally favour wave phenomena. If this result is representative, then KH waves producing refractive index gradients severe enough to register on even the most sensitive radars must be considered rate. It remains *conceivable*, however, that "mild" wave events, which generate sufficient anisotropy for orientation but do not break, and so do not create the refractive index gradients required for radar detection, occur quite regularly (K.A. Browning, personal communication). We have therefore begun to re-examine our VLR data to see if there is any evidence from individual insect displacement speeds for anisotropies in the wind.

4.2 Orientation to Compass Directions

Our West African observations of persistent northeast headings in a wide range of wind directions provides convincing evidence that the insects concerned (probably Acridids), were orienting to a preferred geographical direction. Because these north-eastwards results were all obtained (with one exception) at one site (Kara), we cannot rigorously exclude the possibility that the effect was merely a localised, site-specific response to some distinctive topographical feature, but we consider this to be unlikely. By far the most striking topographical feature in the area was the River Diaka, and while this undoubtedly influenced the behaviour of some insects, the influence was highly localised and obviously associated with the outline of the river (Reynolds and Riley 1979). The northeast headings were on the other hand uniformly maintained over an area of 7 km^2 and showed no evidence of being related to any localised stimulus.

Overall, we consider that the data provide good evidence for the adoption of compass headings by some insects flying at high altitude in darkness.

In the following sections we briefly consider two of the mechanisms by which compass orientation might be achieved.

4.2.1 Use of Celestial Cues

Wehner (1984) has reviewed the evidence that nighttime skylight cues might be used for compass orientation, and notes that insects with apposition compound eyes can detect the moon as a point source, and that those with superposition eyes may in addition be able to detect the brightest stars. He draws attention to the fact that use of the moon as a compass presents formidable problems because of the complexity of its azimuth - time relationship.

Moon Compass. Sotthibandhu and Baker (1979) report observations of orientation at a fixed (non-time-compensated) angle to the moon's azimuth for tethered large yellow underwing moths (*Noctua pronuba* L.), but there is general agreement amongst radar observers that collective orientation in high-flying insects is unaffected by the presence of the moon. The northeast heading groups we described in Sect. 3.3 mainly occurred when the moon was well below the horizon so the apparent compass orientation exhibited by these groups was clearly not a moon-related phenomenon.

Stellar Compass. In the absence of moonlight, Sotthibandhu and Baker (1979) detected a response of *Noctua pronuba* to rotation of the celestial sphere and deduced that the moths were using stellar cues to maintain non-time-compensated orientation. Our observations of geographical heading could conceivably be explained if the insects concerned had been capable of *time-compensated stellar* orientation. However, stellar orientation of any type would presumably not have been available to the northeast heading Acridids we observed, because their apposition eyes are unlikely to resolve individual stars (Wehner 1984).

Polarised Light. A non-localised skylight cue to direction which is available to day-flying insects is the pattern of polarisation in the sunlight scattered from the atmosphere [see Wehner (1984) for a review]. Once the sun is more than 7° below the horizon (30 min after sunset), however, the atmosphere overhead is no longer effectively illuminated by the sun and polarisation information is lost. Insects which rely on polarisation patterns then become disoriented (R. Wehner, personal communication). Scattering of moonlight by the atmosphere generates similar patterns to those caused by sunlight, but the scattered light is of very low intensity (sky brightness $\sim 10^{-6}$ L). No experiments on the response of insects to low light polarisation patterns have been reported to date, so orientation to night-sky polarisation must for the time being be considered speculative. We note, however, that we have observed common orientation on occasions when the moon has been more than 7° below the horizon, and on moonless nights, so it is certain that night-sky polarisation cannot in itself account for the common orientation phenomenon.

4.2.2 Terrestrial Magnetic Cues

There is no doubt that a number of biological organisms exhibit great sensitivity to various features of the earth's magnetic field [see for example a summary by Gould (1980)]. Perhaps the most convincing evidence that this sensitivity is shared by at least one species of flying insect is provided by the behavioural experiments of Lindauer and Martin (1972). They showed that the error in the 'waggle' dance direction of bees on a vertical comb was apparently related to the rate of change of the magnitude of the earth's magnetic field. What is particularly surprising about this result is the tiny size of the field changes (ca. 200 gammas in a normal field of 50,000 gammas). Even greater sensitivity has been suggested (2-5 gammas or 0.3 gammas min^{-1}) to explain the maintainance of circadian rhythm in bees deprived of all temporal cues except the diurnal variations in terrestrial field strength (Martin and Lindauer 1977; Gould 1980). Sensitivity to changes as small as this suggests that simple orientation to the normal field would be easy to accomplish. Nevertheless, evidence that insect species orientate to magnetic cues appears to be limited to the work of Baker and Mather (1982) on *Noctua pronuba*.

In summary, the question of whether insects at large are able to use terrestrial magnetic fields for orientation remains unanswered. Given, however, the apparently extreme magnetic sensitivity of bees, it would not be surprising if at least some other insect species were able to perceive the gross features of the terrestrial field well enough to orientate to it.

5 Conclusions

The common orientation which insects regularly exhibit when flying at high altitude at night, has been shown to be sometimes related to wind direction, and sometimes to geographical direction. Occasionally, one species will adopt one of these strategies, whilst another, in the same aerial environment, adopts the other. Evidence has been given which demonstrates that wind-related common orientation is almost certainly not maintained by visual references to the ground, but ground reference may well be used to detect and avoid gross backwards displacement.

It has been argued that accelerative anisotropies of air movement associated with shear-induced (Kelvin-Helmholtz) waves in the atmosphere provide insects with directional cues related to wind direction, but it remains to be seen whether anisotropies of this type are widespread enough to account for wind-related orientation.

Of the candidate cues examined to explain compass orientation, perception of the earth's magnetic field, and time-compensated stellar orientation would seem to be the most plausible, although neither has been demonstrated for insects in free flight.

We would expect nocturnally migrating insects to adopt wind-related cues or compass orientation in an hierarchical manner which would depend on wind conditions and on their individual flight strategies.

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