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Variable wind directions and anemotactic strategies of searching for an odour plume

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Abstract. This paper deals with anemotactic strategies of searching for odour plumes under conditions of variation in wind direction and equal energy costs involved in moving a unit path length in any direction in the x, y plane. It is generally accepted that cross-wind searching is the best searching strategy to acquire a maximum amount of information. This is of course true, if the wind is unidirectional. A geometrical model of anemotactic searching is presented that takes into account variation in wind direction. It is shown, that, if wind direction fluctuates over a range larger than 30 degrees from the mean wind direction, then upwind or downwind searching is the best strategy and cross-wind searching is the worst of all possibilities.

Odour plumes can play a major role in animals locating mates or food. Once an animal enters the odour plume, it will find the odour source by performing a complex repertoire of behavioural responses to the odour gradients and the wind directions. This aspect has been subject to detailed investigations (Kennedy 1977, 1978, 1983; Bell and Tobin 1982). Much less attention has been paid to the problem of how an animal finds an odour plume.

It is generally accepted that cross-wind searching is the best strategy to acquire the maximum of information (e.g. Linsenmair 1969, 1973). Of course, this is true if the wind is unidirectional, but does this hypothesis also hold when wind direction varies, a situation more likely to prevail under natural conditions? This question can be answered by considering the size of the area from which the searching animal receives information by scent, further referred to as the inspected area. We will show by simple geometry that the best anemotactic strategy depends on the range of variation in wind direction.

Geometry of the inspected area

For reasons of simplicity the searching animal is represented by a point and the odour source by a point source. The odour is assumed to be displaced only in the wind direction prevailing at that moment. Moreover, it is assumed that the searching animal will find the odour source if downwind within a distance r from its target source. The final most critical assumption is that the animal can estimate the range of variation in wind direction ($=2\alpha$; $0^\circ \leq \alpha \leq 180^\circ$). Hence, if A in Fig. 1 is the starting position

Fig. 1. A Geometrical representation of the area inspected by a searching animal moving downwind (from A to a; $\beta=0^\circ$) or cross-wind (from A to a; $\beta=90^\circ$) over a distance p (---). The circle sectors ABDC, abdc and abdc (—) indicate the upwind area inspected by scent over a distance r , as a result of the wind direction varying between $+\alpha$ and $-\alpha$ around the mean wind direction indicated by the arrow. The dashed lines indicate the rectangles BCcb and ADda referred to in the text (---). These rectangles are equal to the area inspected by moving downwind ($\beta=0^\circ$) or cross-wind ($\beta=90^\circ$). The value of α used in drawing this Fig. is larger than 30° . B But the value of α is taken smaller than 30°

of the animal, the circle sector ABDC, limited by the range of variation in wind direction and the length scale r , is already inspected even before any movement is made. The question is: How much inspected area will be added by moving away from A over a distance p in direction β ? By taking the mean wind direction as a reference direction a polar coordinate system is defined with parameters p and β . In Fig. 1 the inspected area has been drawn for the case of negative anemotaxis ($\beta=0^\circ$) and of cross-wind taxis to the right ($\beta=90^\circ$), using a large value and a small value of α (α and α' in Fig. 1A and B respectively). If α is large and β is zero, the inspected area I is equal to the sum of the areas formed by two parallelograms (BAab and CAac), i.e. $I=2.p.r.\sin(\alpha)$. Since the triangles abc and ABC are congruent, the inspected area is equal to the rectangle BCcb. If α is still as large, but β has changed to 90° , the inspected area is ACDdca, i.e. $I=p.r.$ These geometrical considerations show that when α is large, the amount of information gained by moving downwind (BCcb) is much larger than by moving cross-wind (ADda). In the same way it is shown in Fig. 1B that the opposite is true if α is taken small (α'): then the area of rectangle B'C'c'b' is smaller than ADda. If α equals 30° , the areas of these rectangles equal each other.

It will be clear that the conclusions derived for β values of 0° and 90° will also apply to the opposite directions; positive anemotaxis ($\beta=180^\circ$) being equivalent to negative anemotaxis ($\beta=0^\circ$) and cross-wind taxis to the right ($\beta=270^\circ$) being equivalent to cross-wind taxis to the left ($\beta=90^\circ$). A more elaborate representation of the areas that are inspected for different values of α and β is given by the following formulas for the first quadrant of β ($0^\circ \leq \beta \leq 90^\circ$):

If $0^\circ \leq \alpha \leq 90^\circ$ and
 $\beta \leq \alpha$ and $\beta \leq 90^\circ - \alpha$, then $I = r.p.(\sin(\alpha + \beta) + \sin(\alpha - \beta))$
 $\beta \leq \alpha$ and $\beta \geq 90^\circ - \alpha$, then $I = r.p.(1 + \sin(\alpha - \beta))$
 $\beta \geq \alpha$ and $\beta \leq 90^\circ - \alpha$, then $I = r.p.\sin(\alpha + \beta)$
 $\beta \geq \alpha$ and $\beta \geq 90^\circ - \alpha$, then $I = r.p.$
 If $90^\circ \leq \alpha \leq 180^\circ$ and
 $\beta \geq \alpha - 90^\circ$, then $I = r.p.(1 + \sin(\alpha - \beta))$
 $\beta \leq \alpha - 90^\circ$, then $I = r.p.2$

The values of I in the remaining three quadrants of the β circle are found by symmetry:

$I(\beta_1; 90^\circ \leq \beta_1 \leq 180^\circ) = I(\beta = 180^\circ - \beta_1; 0^\circ \leq \beta \leq 90^\circ)$
 $I(\beta_2; 180^\circ \leq \beta_2 \leq 270^\circ) = I(\beta = \beta_2 - 180^\circ; 0^\circ \leq \beta \leq 90^\circ)$
 $I(\beta_3; 270^\circ \leq \beta_3 \leq 360^\circ) = I(\beta = 360^\circ - \beta_3; 0^\circ \leq \beta \leq 90^\circ)$

In Fig. 2 the areas of α and β are drawn in a scheme indicating the appropriate formulas for calculation of the inspected area.

Reconsidering the basic assumptions it will be clear that if source and animal are represented by circles instead of points, or if real odour plumes instead of odour tracks are considered, the repercussions will be similar to enlarging the value of α . Hence, the conclusions still hold qualitatively. However, these conclusions are invalidated, if the searching animal cannot somehow estimate α , and if the wind does not blow in one direction long enough to transport the odour over a distance r .

The latter condition may seem not to be fulfilled, because variation in wind direction causes the odour plume to meander and 'snake' (David et al. 1982). However it has been established by atmospheric physicists (Pasquill 1974) that over short grass in open country each single 'parcel' of smoke (or other material) composing a plume

Fig. 2. Graphical representation of the regions of α values and β values in which the inspected area I is a function of α (half the range of variation in wind direction), β (the animal's direction of movement), p (the distance travelled) and r (the maximum distance of odour source detection), and in which the capitals A–G indicate the appropriate formulas to calculate I. These formulas for I_A to I_G are:

- A $I_A = p.r$
- B $I_B = p.r.2$
- C $I_C = p.r.(|\sin(\alpha + \beta)| + |\sin(\alpha - \beta)|)$
- D $I_D = p.r.|\sin(\alpha + \beta)|$
- E $I_E = p.r.|\sin(\alpha - \beta)|$
- F $I_F = p.r.(1 + |\sin(\alpha - \beta)|)$
- G $I_G = p.r.(1 + |\sin(\alpha + \beta)|)$

is carried away from the source in a relatively straight line for a considerable distance while the plume as a whole may be snaking to and fro across wind. The snake is not the path of the wind: the plume snakes simply because the wind direction varies (Murlis and Jones 1981; David et al. 1982).

Optimal searching strategy

Optimal search for odour plumes is achieved by maximizing the amount of information per unit of energy spent in searching. If the effort of searching is equal in all directions (β), the maxima can be readily found from the above formulas, as shown in Fig. 3. However, it is probable that searching upwind or cross-wind is energetically more expensive than searching downwind, especially in flying animals (Gillies and Wilkes 1974). This means that the critical value of α , below which cross-wind searching is the best strategy, will be lower than 30° . Hence, it is increasingly likely that downwind searching will prevail! Another distinct advantage of downwind searching is that a downwind sector of odour tracks is entered *on average* at a distance of $r/2$, whereas upwind searching for an upwind sector always results in a distance r from the odour source on arrival in the sector (Fig. 4). In contrast, the strategy of moving downwind places the searching animal at a disadvantage, if the target animal escapes after scenting the searcher (Bell and Tobin 1982).

The above model is purely hypothetical, but nevertheless it raises some interesting questions for further research. The most challenging of all is whether animals are capable of estimating the range of variation in wind direction (α) and orient themselves to the mean wind direction. If they are not capable of estimating α , optimal search is determined by the mathematical expectation of the inspected area, given the frequency distribution of α ($=P(\alpha)$) sampled over a sufficiently long period of time in the habitat of the searcher. The optimal searching direction is then found as

Fig. 3. The upper graph shows the relation between the maximum area inspected and the range of variation in wind direction (α), when the product of path length p and the maximum distance of odour source detection equals unity ($p \cdot r = 1$). The lower graph shows the associated travelling directions (β) along which the area inspected is maximum (shaded areas and thickened lines)

Fig. 4. The circle sector represents the area over which the odour borne from a point source is spread in concentrations that elicit source location behaviour. It is determined by the range of wind directions (2α) and the maximum distance of source detection and finding (r). The arrows show where the sector is entered when searching downwind or upwind. The 'feathered' arrow indicates the mean wind direction

the value of β that maximizes the expectation value of the inspected area:

$$I_{\max}(\beta_{\text{opt}}) = \max_{\beta} \left(\sum_{\alpha} P(\alpha) \cdot I(\alpha, \beta) \right)$$

In this way, the model can still be useful in pinpointing the best average and/or the least risky strategy. Hence, whether or not the animals are capable of estimating α , it is still worthwhile testing theories emerging from the geometric model presented.

Discussion

We suggest that cross-wind searching is not always the best strategy and, as argued above, this does not necessarily depend on the ability of the animal to estimate the range of variation in wind direction. This view of the biological significance of anemotactic searching contrasts with the theory of Linsenmair (1973). He states that the searching insect should avoid moving in directions that correspond to the wind direction and prefer to move cross-wind because the largest amount of information is acquired in this way.

Fig. 5. Distribution of walking directions chosen by dung beetles (*Geotrupes* sp.) in response to an air stream without behaviour modifying chemicals. The length of the bar drawn within the circle corresponds to the frequency of 10 walking tracks. Mean wind direction is indicated by the arrow

For this reason Linsenmair (1969) was quite surprised to find that dung beetles moved upwind with only a small deviation relative to $\beta = 180^\circ$, as shown in Fig. 5. Nevertheless he considered this small angle to be advantageous, though less than larger angles that are close to cross-wind searching. It will be clear that the geometric model presented in our paper offers an alternative explanation for Linsenmair's results.

The anemotactic searching strategy should be subject to natural selection if it not only determines searching success, but also results in a contribution of progeny to the next generation. The evolution of anemotactic searching strategies, however, presupposes a genetic base. Spencer Johnston (1982) has shown this to be the case in drosophilid flies. He selected one line of *Drosophila melanogaster* Meigen for upwind response and one line for downwind response and found heritability values that led him to suggest that wind-oriented movement can be rapidly modified by selection under different habitat conditions. Most interestingly, he also found different wind responses in wild-caught individuals of different species. It would be worthwhile investigating the adaptive value of these responses in view of our theory.

Though the hypotheses emerging from our model can be tested easily, there are some important pitfalls in interpreting such tests. Firstly, the model is based on the assumption that the animal is actually searching for odour plumes. Irrespective of the test result one should keep in mind that the anemotactic behaviour may serve other goals than finding odour plumes. Secondly, to specify the model prediction of the optimal anemotactic strategy one should have estimates of the parameters of the model. Since the formulas that calculate the inspected area, all contain the parameters p and r as the product $p \cdot r$, it follows that the anemotactic strategy predicted ($=\beta_{\text{opt}}$) does not depend on these two parameters. Hence, the anemotactic strategy only depends on α . The problem is how to estimate this parameter. Clearly, fluctuations in wind direction may be rapid or slow. The meso-scale fluctuations that are always present in atmospheric flow, are characterized by a time scale between 10 min and a few h. However, in the turbulent air, that will be present e.g. in the most exposed part of a vegetation, the time scale of the fluctuations will be between

0.02 sec and 10 min. Deeper in the vegetation the air stream is expected to be much less variable and to closely resemble the meso-scale variations in the atmosphere. This is because (1) the air stream in the vegetation is retarded, which reduces turbulence, and moreover, because (2) there is a draught in the vegetation resulting from a negative gradient in static air pressure across the vegetation caused by the air stream being obstructed at the windward edge of the vegetation cover. Consequently, the time scale of the fluctuations in wind direction depends on wind speed, position of the animal in the vegetation etc. How animals cope with the problem of variable time scales and how they actually measure the range of variation in wind direction, is a problem that has to be solved in order to estimate the model parameter α in a meaningful way.

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