

Modelling mechanisms of animal behaviour

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The human brain is often quite incapable of appreciating the consequences of the theories it is able to propose. It is all too easy to make mistakes in logic when proposing an explanation in words, and to pass over the mistake repeatedly. A computer model that embodies our assumptions will ruthlessly expose any weaknesses that are inherent in our theorising. . . on the otherhand it will also reveal unexpected explanations. The computer will present us with an unbiased account of our assumptions, something we might be quite incapable of doing with the most honest intentions. (*Toates, 1975*).

I shall use the word model to mean *a working version* of a theory or hypothesis. Because it is a working version, a model has to be complete and unambiguous. It is therefore a reliable and accurate way of working out the consequences of our ideas. If there is a fault, it is usually with our ideas.

The model may consist of equations which can be explored by algebra but, more often it is a computer program which must be checked to see that the assumptions are properly built into the model and then run to prove their consequences.

I suspect that there is a useful role for modelling in most research programmes and the aims of the lecture are to focus on one particular program and find

1. the kind of questions that needed further experiments,
2. those that were helped by modelling,

3. the new questions that were raised by the modelling work
4. and something of the steps in the modelling process

To do this I have chosen our work on moth orientation and the session will be divided into three phases

1. A brief account of the way ideas developed during our research on male moths in a pheromone plume. This will illustrate the questions we could answer experimentally and those that needed modelling
2. A session in which the group tries to find answers to the modelling questions
3. A review of the modelling we did during the work, and of the questions it answered and raised

1 Moths in a pheromone plume

1.1 The development of ideas

You have already had the conclusions of our work on moth orientation, together with more recent work. My aim here is to describe the way our ideas developed over time.

Kennedy (1940) Reported that mosquitoes flying in still air over moving stripes tended to fly in the same direction as the stripes. This is equivalent to turning up wind and he showed that the

turning tendency depends on *both the speed and obliquity of image movement*. He used the term retinal velocity to mean speed and direction of image movement.

Wright (1958); Kellogg et al. (1962) described upwind flight by *Drosophila* in response to food odours.

Kennedy and Marsh (1974) demonstrated that male moths (*Plodia interpunctella*) in a wind-tunnel turned upwind in response to floor pattern in a plume of female sex-pheromone. They flew upwind in a series of zig-zags. A change in apparent wind direction could be introduced by moving the floor pattern downwind faster than the wind. The moth's response was to reverse the direction of flight and fly away from the source in what now appeared to be the upwind direction.

Marsh et al. (1978, 1981) Described tracks of *Plodia interpunctella* in pheromone in a wind-tunnel and showed that the ground tracks had the same angle to wind and the same ground-speeds in three windspeeds (0.1, 0.2, 0.3 m s⁻¹). This was the observation that started the modelling work.

Ludlow and Marsh (1978) Proposed that moths resolved image movement into longitudinal and transverse components, instead of angle and velocity of movement. They suggested that turning upwind was achieved by turning in the direction of the transverse image movement and showed that control of track angle required control of airspeed as well as longitudinal and transverse image movement.

Kennedy et al. (1980, 1981, 1982) Described the flight behaviour of moths in a wind tunnel: in uniform pheromone; in a plume on its own; and in a plume superimposed on a background of uniform pheromone. The moths made an initial upwind surge in uniform pheromone and then cast from side to side, but with narrower casts than when pheromone was withdrawn.

At this stage we had a complete theory of moth orientation in pheromone, based on wind-tunnel experiments. At the onset of pheromone a male moth would surge upwind in a series of zigzags. On losing the pheromone it would cast from side to side at approximately 90° to the wind.

In uniform pheromone the moth ceased to make upwind progress but turned from side to side more frequently, so *the casts were shorter*. When the plume from a single female was superimposed on a uniform background of pheromone the male could find the female without difficulty. In other words, the male responded to increases in pheromone by surging upwind, even when these increases were superimposed on a cloud of pheromone. In nature, with thousands of females upwind the male's task is to find the nearest female and this mechanism would allow him to do that.

David et al. (1982) used smoke plumes and demonstrated that individual parcels of air travelled in straight lines for several metres over rough grass in quite turbulent winds. This experiment arose from a seminar given by Wall and Perry who had been told by a meteorologist that parcels of air travelled in straight lines even in turbulent winds. The Silwood contingent did not believe it so we did experiments with a smoke generator videoed from a 30 m high tower. Wall and Perry were right and we published the results together.

Figure 1 shows the results and at once you can guess the efficiency of the system we had worked out in wind-tunnel experiments. You can also understand why a dog (or a polar bear) has a wet nose.

David et al. (1983) took the moth experiments into the field using the 30 m tower again and a bubble generator to mark where the pheromone was likely to be. The moths behaved exactly as we had predicted heading upwind when in bubbles and across wind when it lost the pheromone. However, we added the discovery that when the moth relocated the plume on a cross-wind cast,

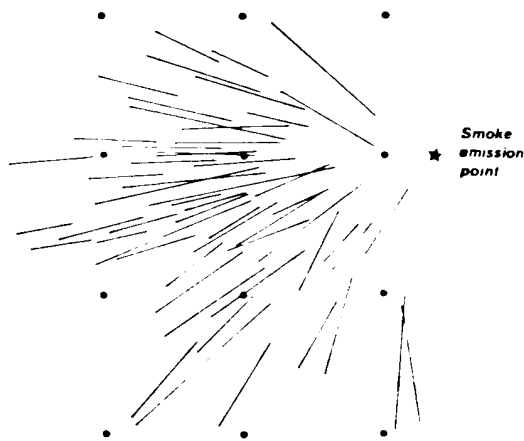


Figure 1: Segments of tracks of smoke puffs recorded within a 10-min period. Grid markers 5 m apart (From David *et al.*, 1982).

it usually found the plume closer to the source than when it had lost it. This is a consequence of geometry, and should have been shown by modelling, but we had overlooked it.

1.2 Points of surprise

Following the early work by [Kennedy \(1940\)](#); [Kellogg et al. \(1962\)](#) we expected the moths to show upwind flight in response to pheromone, although the rest of the world probably did not. The common theory at the time was that moths followed concentration gradients. We had expected flight to depend on wind direction, but the zig-zag flight in a plume came as a surprise. So did the cross-wind casting when pheromone was withdrawn.

Later, the control of groundspeed and track-angle in different windspeeds came as a surprise. So did the behaviour in uniform pheromone. We had expected the moth to fly straight upwind in uniform pheromone *because we thought the zig-zagging was*

due to rapid loss and gain of pheromone as the moth sampled the edge of the plume.

I think most people at the time thought that strong enough uniform pheromone would jam the system but, instead, we found the moth able to locate a single female against a uniform background. That was a surprise at the time but it should not have been. A male needs to be able to cope when the air is full of pheromone so we should have expected moths to have evolved a strategy for coping.

We were stunned by the information that individual packages of air travel in straight lines. When we finally accepted that it was true, after trying to disprove it, the accuracy and power of the moths' orientation system was obvious. We were surprised to discover that the moths were closer to the source when they lost the plume and found it again after casting. But apart from that, were not a bit surprised by their behaviour in the field. However, it was the field demonstration that convinced the readers.

1.3 Generalising to other insects

These points of surprise show that our mental models, at every stage, were wrong or incomplete and it is instructive to ask how well we could now predict the behaviour of other insects. Other species use upwind orientation to find odour sources. I have watched a wasp casting a few inches from side to side, just above the ground, before it pounced on an insect larva. In all respects it behaved like a male moth in pheromone but there are other species where we may expect differences in orientation behaviour.

For example, many forest insects use pheromones. Does air behave in the same way in a forest as it does on open ground? The answer is almost certainly no. In particular, individual parcels of air no longer move in straight lines. They may do so at first, but a later gust in a different direction will probably change the direction of a parcel so that an insect going upwind when it gets the scent may head in the wrong direction. Do forest insects use different mechanisms, or do they simply have a harder task? There is evidence that the mechanisms are the same, but they are less efficient in forest because the information in the wind is less accurate. **A model could show how much**

less efficient.

Tsetse fly live in areas where the wind is often 0.1 m s^{-1} , and they fly so much faster than this that it may not be worth their waiting for the wind to bring the odour to them. It may be quicker for the fly to search out an odour source by trial and error.

Slow-flying insects, like mosquitoes, *Drosophila*, and so on, may use anemotaxis as moths do, but the efficiency may be very different. Sources of food odour may be very large compared with a single female, and there is no race to food, as there is when the first male to mate wins. The insect must minimise cost of flight not time.

Some insects, such as aphids fly so slowly, that it may be most efficient to drift down-wind and land in response to a food scent.

There are many questions about how well a strategy works, and which is the optimal strategy, in different conditions. Some progress on these questions could be made by quantitative modelling, especially the difference between forest and open ground insects. Experimental work would be essential but field experiments are expensive and modelling could be used to reduce some of this cost by targeting the field work. An example is given by [Belanger and Arbas \(1998\)](#) who compared several different models of zig zagging flight and the models were less efficient at finding the source than real moths.

Please ponder how you would model the effectiveness of different strategies of orientation? What inputs would a model insect need? What responses would we have to build in? What questions might such a model answer?

2 How does the nervous system work?

Throughout the work we were funded by the Agricultural Research Council (later AFRC) and the central questions were: **How does a male moth find a female emitting sex pheromone? Can we jam the system or is it better to try to attract and kill the males?** However, as we made progress, an additional question emerged: “What do our ob-

servations tell us about the way the nervous system works?”.

It seemed that we might get a handle on the nervous system by looking in detail at the following questions:

1. How does a moth turn upwind?
2. How does it achieve a similar cross-wind ground track in winds of different speed?
3. Why does it keep the same groundspeed in different windspeeds? Presumably, *it could achieve a higher groundspeed in low windspeeds but it chooses not to*. This seems strange when the male is racing other males to the female.

In the next sections we examine these questions in turn but first, we need to examine the triangle of velocities and agree some definitions.

2.1 Wind drift and the triangle of velocities

Figure 2 shows a triangle of velocities. The moth flies at an airspeed, A , into a wind of speed, W , and the angle between course and wind is the course angle, α . In these circumstances, the moth will make some headway into the wind but will be drifted back so that its track over the ground is given by G . Since its body is pointing in the direction of A and it is moving over the ground in the direction of G , the images move over the moth’s retina at the drift angle, δ . Image movement is in the opposite direction to G while the retinal velocity of images will depend on G and the moth’s height above ground, h .

Notice that the track angle to wind is θ and that

$$\theta = \alpha + \delta \tag{1}$$

$$\theta = \alpha + \delta$$

$$\theta = \alpha + \delta$$

I suggested, in 1978, that the image movement might not be stored in the nervous system as G and δ but it might be resolved into two components: along the body axis, L , and across the body axis, T_r . The question arose while trying to model the system but, since then, neurons responding to longitudinal and

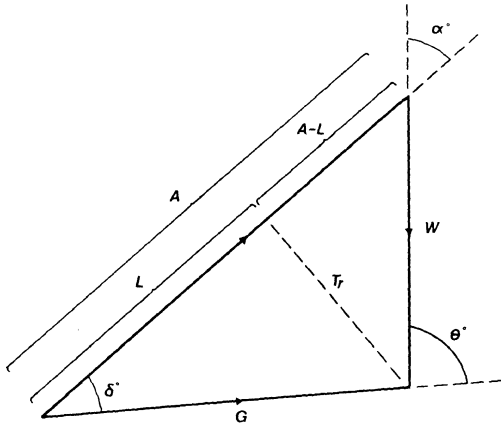


Figure 2: Triangle of velocities for an insect flying to the right of the wind-line, showing the notation used throughout. The sides of the triangle are proportional to the moth's airspeed, A , the windspeed, W , and the resultant groundspeed, G . α is the angle between the insects long axis and the wind; θ is the angle between ground track and wind while δ is the angle between the insect's long axis and the direction of the ground track. L and T_r are the longitudinal and transverse components of the insects groundspeed.

transverse components of image movement have been found (Hausen, 1982a,b). It is still sensible to consider models with δ and G as well as those based on T_r and L .

It is important to note that the moth has no direct measure of wind speed, W , α or θ . To control these it must calculate them in some way from the variables it can measure directly. These are: A , G and δ or, alternatively, A , L and T_r .

2.2 Turning upwind

The first observation is that moths turn upwind in response to pheromone onset. Kennedy (1951) reviewed his mosquito work saying:

Similarly, it was suggested that when the images pass transversely, say from left to right, instead of directly from front to back over the eye, owing to a cross-wind from the right, the insect compensated by following the direction of the transverse image movement, that is by turning toward the right until it is facing into the wind, and transverse image movement has therefore ceased.

This sounds like a suggestion that left to right image movement, T_l , causes the insect to turn right but Kennedy (pers. comm.) always thought in polar coordinates and used the term retinal velocity to mean speed and direction of image movements.

Nevertheless, Kennedy's mechanism works perfectly well. All we need to think about is the mechanics of turning. Let us assume that the thrust of the right and left wings can be varied. The moth will turn to the right when the left wing-thrust is greater than the right and vice versa. Figure 3 shows a simple model which turns upwind. The thrust command, P , increases wing-thrust on both sides but the left wing-thrust is reduced by right→left movement detectors while the thrust of the right wings is reduced by left→right detectors.

This simple model can be translated into a computer program (written in the language DARE P) as shown in Table 1

Figure 4 shows output from the turning program in Table 1. The torque has a maximum when the course

Table 1: Computer program of the upwind-turning model

```

$D1
*
*   UPWIND TURNING MECHANISM
*   *****
*
*   Let ALPHA be the angle, in degrees, between the insect's long axis
*   and the upwind direction (wind from left to right is positive).
*   ALPHA' is the turning rate (degrees per second, right positive)
*
ALPHA' = DELAY(TORQUE,  TORLAG,  1,  0.0 )
*
*   where DELAY(...) is a function which makes ALPHA' equal to the
*   value that TORQUE had exactly TORLAG seconds before
*
TORQUE = C1*(THRUSTL - THRUSTR)
*
*   where C1 is a constant of proportionality, and where THRUSTL and
*   THRUSTR are left and right wing-thrust respectively.  These are
*   given by
*
THRUSTL = P - TR
THRUSTR = P - TL
*
*   where P is a signal increasing wing-thrust on both sides.
*   TR and TL are the rates of right-left and left-right image
*   movement. (NOTE: it could be THRUSTL = P + TL; THRUSTR = P + TR.
*   What difference would that make and how could we test the model?
*
*   Right-left image movement is proportional to the transverse
*   wind drift (WIND*SIN(ALPHA)) but the neurons carrying this signal
*   cannot go negative, so the signals carrying TR and TL are given by:
*
TR = WIND*MAX( SIN(ALPHA*RADIAN), 0.0)
TL = WIND*MAX( SIN( -ALPHA* RADIAN), 0.0)
*
*   where MAX(...) is a function that ensures that TL and TR
*   never go negative.
*
*   An initial value for ALPHA must be set elsewhere in the program,
*   as must values for the parameters TORLAG, C1, P, WIND and RADIAN
*
END
*-----

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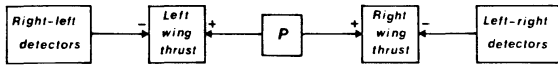


Figure 3: A model which turns upwind.

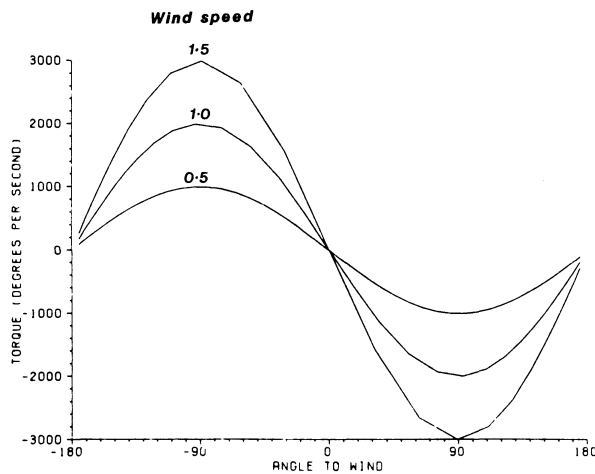


Figure 4: Turning tendency, TORQUE, plotted against angle to wind, ALPHA in three windspeeds

angle to wind is $+90^\circ$ or -90° . It is zero at 0° or 180° but the downwind direction (180°) is unstable so that the slightest turn away from down wind and the moth will continue turning until it reaches the upwind heading. This model behaves exactly as the mosquitoes described by Kennedy (1940).

I have assumed that the right \rightarrow left detectors reduce left wing-thrust but they might increase right wing-thrust instead. **How would this affect the model and how could it be tested?**

2.3 The problem of maintaining cross-wind tracks

Figure 5c shows a moth casting at 90° to the wind. The broad arrows show that the wind direction changed in mid-cast, and yet the moth was able to adjust its track to about 90° to the new wind direction. The windspeed, too, may have varied during the

cast, although we cannot tell because there were no bubbles nearby from which to calculate windspeed. Certainly, moths do maintain the same track angles in different wind speeds (Fig. 6). As Fig. 7 shows, the constant track angles were achieved by altering both course angle, α , and airspeed, A .

Baker and Kuenen (1982) have shown that moths which have experienced wind and pheromone can perform manoeuvres, such as casting or flying up a hanging plume, even after the wind has dropped. Moreover, the orientation of these manoeuvres is closely related to the former wind direction. In the case of casting there can be no question of chemotactic orientation to the remaining plume, because there isn't one. Thus, the moths must have fixed and retained the former wind direction. The model described below does this.

2.4 A proposed mechanism of track angle control

Ludlow (1983) reviewed and explored several theories that might explain control of track angle in different wind speeds but found that most of them required extremely complex connections within the nervous system. In contrast, the following theory places few demands on the nervous system or on its evolution (Fig. 8). It has the added attraction that it is approximate and predicts that moths will not control their track angles or groundspeeds at exactly the same values in different windspeeds. Instead the theory predicts that they will make 'mistakes'. The observed distribution of angles and groundspeeds shows evidence of these 'mistakes'. The theory also explains why groundspeed is controlled.

The track angle, θ , is the sum of course angle, α , and drift angle δ . The theory proposes that track angle control is in three parts:

1. The moth identifies the upwind direction as the direction in which there is zero transverse image movement.
2. It 'commands' a given track angle with an excitatory signal

Table 2: Effect of three windspeeds on a variety of measures of straight ‘legs’ of moth tracks, *Plodia interpunctella*. Note, if moths were controlling a variable across windspeeds we should expect $\chi_r^2 = 1.39$ and $T = 25$.

Variable	Friedman two-way analysis of variance		Wilcoxon matched pairs test	
	χ_r^2	P	T	P
Track angle to wind, θ	5.4	> 0.05	5	< 0.02
Groundspeed, G	3.8	> 0.1	9	N.S.
$L + T$	1.4	0.5	25	N.S.
$L^2 + T^2 = G^2$	4.2	> 0.1	10	N.S.
Longitudinal component of groundspeed, L	5.6	> 0.05	2	< 0.01
Transverse component of groundspeed, T	20.0	< 0.001	0	< 0.01
Airspeed + Longitudinal component of groundspeed ($A + L$)	1.4	0.5	27.7	N.S.

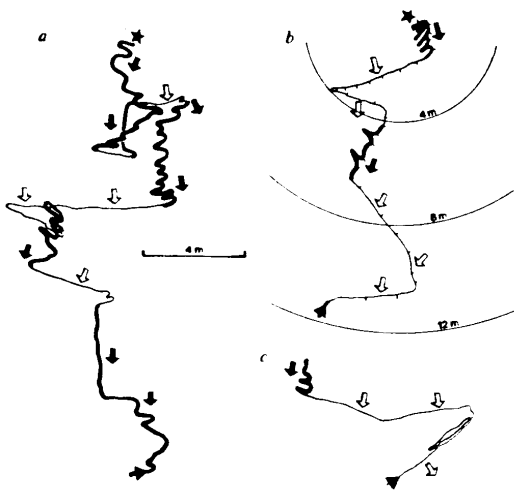


Figure 5: Selected tracks of male gypsy moths approaching a source of both sex pheromone and bubbles (Star). Thick line, track apparently among bubbles, with associated wind direction (solid arrows). Thin line, track away from bubbles, with associated wind direction (open arrows). a. progress towards source mainly by upwind flight among bubbles and pheromone (duration of track 50 s, windspeed when moth among bubbles $0.8\text{--}2.0\text{ m s}^{-1}$); b. progress towards source mainly during cross-wind casting away from bubbles (time marks 0.5 s, windspeed when moth among bubbles $1\text{--}3\text{ m s}^{-1}$) c, portion of track 12 m from source showing change direction with change of wind direction (wind speed among bubbles 1.7 m s^{-1}) (From David, Kennedy and Ludlow, 1983).

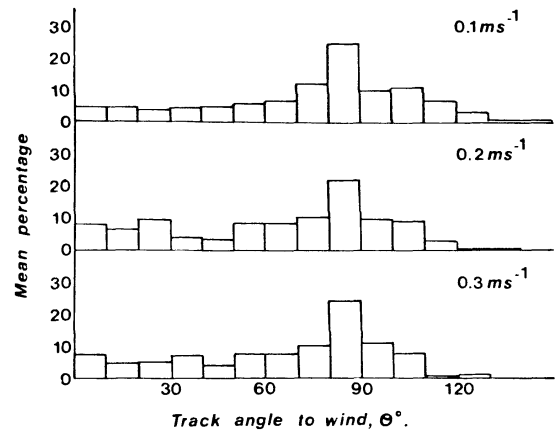


Figure 6: Frequency distribution of track angles to wind along straight legs in three windspeeds.

3. Opposed to the command signal are two feedbacks. The first increases as the moth turns from the upwind direction. *In effect, the moth counts the angle turned from this position by an optomotor system and the signal opposes the command signal.* Optomotor systems have been well established in insect research
4. The upwind turning mechanism is ‘left on’ and compensates automatically for wind drift by opposing the command signal so that the track angle reached is a compromise between the command and the two negative feedbacks.
5. Such a system will not give constant track angle unless the moth divides by groundspeed *or controls groundspeed at a constant value.* In other words, dividing by groundspeed can be avoided if the moth controls groundspeed at a constant value. It also needs to maintain a constant height. Both height and groundspeed were kept within close limits in the wind tunnel experiments and wild moths appear to control these variables too.

The full model is shown in Fig. 8 and, returning to the idea of right and left wing thrust, the thrusts are given by:

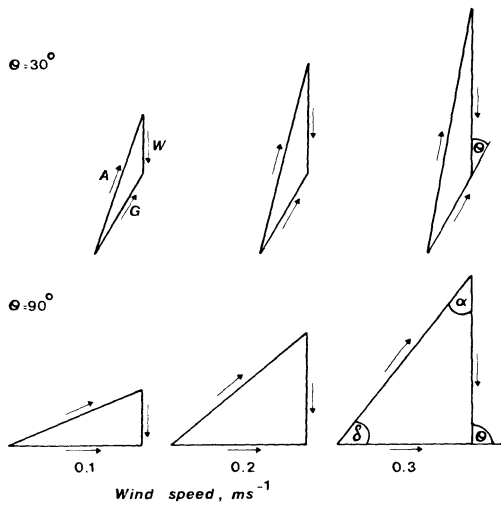


Figure 7: Triangles of velocities summarising the observed behaviour of moths flying at two sample track angles, 30° and 90° to the right of the wind-line. Note how the moths maintained the same track angle and associated course angle by adjusting their course angles to wind and their airspeeds, according to windspeed. At each track angle the groundspeed and therefore the speed of image movement was the same in all windspeeds, but the direction of image movement was different between windspeeds (angle of image movement is the angle between course and track) (from Marsh, Kennedy and Ludlow, 1978)

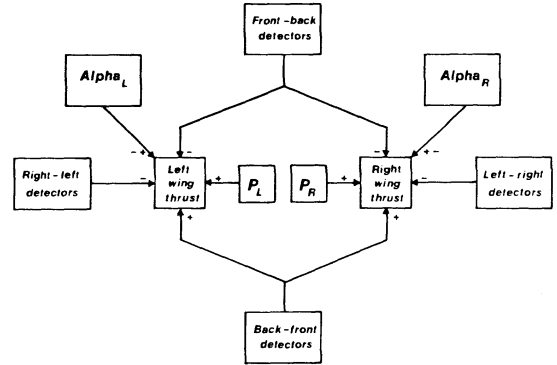


Figure 8: The full model

$$\begin{aligned} \text{THRUSTL} &= P_L - \text{ALPHAL} - \text{TR} - L/2.0 \\ \text{THRUSTR} &= P_R - \text{ALPHAR} - \text{TL} - L/2.0 \end{aligned}$$

where P_L and P_R are command signals. When equal the moth will fly upwind, when different it will fly at some angle to the wind. ALPHAL and ALPHAR are signals proportional to the number of degrees since the moth last faced upwind. TR and TL are right→left and left→right components of image movement and L is the longitudinal component.

Instead of controlling groundspeed, this model controls the sum of $L + T$ which is an approximation to groundspeed, and instead of controlling the track angle at the same values for each windspeed it controls $A + L$. As Table 2 shows, these two sums were more consistent across windspeeds than any of the other variables considered.

Another prediction of the theory is that the accuracy of the system will depend on the availability of optomotor cues needed for measuring the course angle, α after last heading upwind.

3 Subsequent work

When our work started, we assumed that zig-zagging occurred because the moth was repeatedly ‘reaching the edge of the plume’ and turning back on losing the pheromone. That view had to be rejected at an early stage, especially when zigzagging was seen in uniform pheromone. Tom Baker introduced the

term ‘counter-turning’ to describe this feature and any model of moth orientation should include a submodel to simulate counter-turning.

Such a submodel would explain how the ‘preferred directions’ or ‘command directions’ changed with pheromone and other stimuli, while the orientation submodel (described above) explains how these command directions may be achieved. In the model by Ludlow (1983) the command signal for groundspeed is the sum of $P_L + P_R$ while the command for turning to the right is the difference $P_L - P_R$. Subsequent work has thrown light on the factors that affect these signals.

Clearly the onset of pheromone, which leads to upwind flight, would do so in the model by reducing the difference $P_L - P_R$. Charlton et al. (1993) used different concentrations of pheromone from 10 ng to 1000 ng and found that the moths steered significantly smaller course angles as concentration increased. The overall width of the flight track was also reduced inspite of the fact that at the higher concentrations the detectable pheromone plume was wider. Charlton et al. (1993) also found that the moths flew at progressively slower airspeeds and groundspeeds as pheromone concentration increased, which would happen if pheromone reduced the sum $P_L + P_R$.

Increasing temperature from 20°C to 26°C had the opposite effect: it increased groundspeed and course angles. This is consistent with a higher sum ($P_L + P_R$) and difference ($P_L - P_R$).

But neither temperature nor pheromone concentration seemed to affect the mean turning frequency (c. 4 turns s^{-1}), even though the moth’s thoracic temperature differed by 5°C. So the counter-turning submodel should be insensitive to temperature and pheromone concentration.

Mafra-Neto and Cardé (1994) found that the fine-scale structure of the plume had a profound effect on the track, with high frequency turbulence leading to almost straight upwind movement. Many sense organs and neurones respond more strongly to high frequency intermittent input than to continuous stimulation. Mafra-Neto and Cardé (1994) also found that the moth could respond to individual pulses of pheromone and, in a later paper, they ‘dissected’ the flight of moths in terms of single-pulse responses. A

more recent study by Lei and Hansson (1999) looks at the central processing of pulsed signals.

In a more recent study still, Zanen and Cardé (1999) repeated the three windspeeds experiment of Marsh et al. (1978) but with many more details recorded, including direct measurement of the moth’s body angle. They showed that the longitudinal axis of the moth was not always along the axis of its course and deduced that the moth was ‘rolling’ so that its thrust was directed slightly to one side (as well as downward and backward). This manoeuvre allows the moth to slip sideways while it is facing more or less upwind.

Zanen and Cardé (1999) reject my model and propose a mechanism of their own. You need to read the paper yourselves and form your own view, but I must point out one or two things that are wrong or difficult to understand.

- They say that my model controls the vector sum of $L + T$, whereas it is the arithmetic or scalar sum.
- They claim that my model was not designed to simulate flight in still air, whereas the whole point of introducing α_l and α_r was to explain how the moth can cope with still air.
- They seem to think that the model controls only $L + T$ and make no reference to it measuring the the number of degrees since last pointing upwind.
- Wherever they refer to rolling or yawing (eg. page 25 of their paper) they mean *pure* rolling and *pure* yawing. This leads to misleading statements such as: “A very small percentage of flying time is spent yawing.” (p27). In fact, nearly 50% of the moths time is spent in banking (which is yawing and rolling simultaneously (their Fig. 7)
- What really matters is the percentage of steering angle that is due to rolling and what due to yawing. Calculations from their Table 3 show that 70–90% of the mean track angle flown by the moths was due to wind drift; 12–24% was due to yawing and only 2–3% due to rolling.

- For course angles the figures are 9–15% of course angle due to rolling, and the rest due to yawing. For the true angle of visual movement only 2.1–3.5% was due to rolling, with the rest due to wind drift.
- In other words, their data show that rolling can be important, in those cases where yawing does not happen, but most of the moth’s steering is done by yawing.

With these caveats, it is an excellent experiment and a paper well worth reading. Zanen and Cardé (1999) propose that Gypsy moths control zigzagging flight in two steps: they find the wind direction on a counter turn (as proposed by Ludlow, 1983). Then, coming out of the turn with their bodies aligned with the wind, the moth’s roll away from the wind toward a preferred slip angle. (Slip angle is the true angle of image movement allowing for the fact that the moth may be pointing and flying in slightly different directions. Slip angle equals the sum of the drift angle and the angle induced by rolling).

In practice, this is very similar to my model because they assume that the roll-induced angle is a measure of the deviation between wind and body angle, while I assume simply that the moth measures this deviation by counting the degrees it has turned since last upwind, using either optomotor or kinaesthetic cues. Zanen and Cardé (1999) point out that, in high wind-speeds, a very small roll will reach the preferred true angle of image movement, so their system has built-in compensation for wind speed.

The crucial questions are whether this compensation is enough (which needs to be modelled); how much of the steering is due to yawing and how much due to rolling; how the moth measures the sum of yawing and rolling, because it cannot compensate for wind drift unless it does. It would be particularly interesting to find what happens in still air: is all steering by rolling or is yawing still important?

Finally, there is nothing in the data they present that tests my model, although they cite Willis and Cardé (1990) who have data that do challenge it.

A number of other papers cite the modelling work and make useful reading. They include: Belanger and Arbas (1998);

Li et al. (2001); Mafra-Neto and Cardé (1996); Mafra-Neto and Cardé (1998); Vickers and Baker (1996); Willis and Arbas (1991, 1998); Willis and Baker (1988)

4 Conclusion

The importance of modelling is that it forces you to define all your assumptions and to work out the consequences of your ideas properly. Orientation is an area where the mind cannot cope, but there is a danger that we may be overconfident in other areas if we do not test our ideas by building a model. The literature contains examples of theories which never did predict what people thought they did.

The process of modelling also raises new questions and triggers new research. For example, I suggested the idea that insects resolve image movement into longitudinal and transverse components while trying to model the orientation system. Again, it was modelling that led us to ask whether moths use Pythagoras’ theorem to control groundspeed, ($G^2 = L^2 + T^2$) and then led us to check whether the moths use an approximate measure ($L + T$) instead.

The benefits of modelling start when you are forced to think about your research in new ways and to be more thorough and consistent. The model is a working version of your ideas and if your ideas are not complete the model won’t work.

References

- T.C. Baker and L.P.S. Kuenen. Pheromone source location by flying moths: a supplementary non-anemotactic mechanism. *Science*, 216:424–427, 1982.
- J.H. Belanger and E.A. Arbas. Behavioral strategies underlying pheromone-modulated flight in moths: lessons from simulation studies. *Journal of Comparative Physiology*, 183:345–360, 1998.
- R.E. Charlton, H. Kanno, R.D. Collins, and R.T. Cardé. Influence of pheromone concentration and ambient temperature on flight of the gypsy moth,

- lymantria dispar* (l.), in a sustained-flight wind tunnel. *Physiological Entomology*, 18:349–362, 1993.
- C.T. David, J.S. Kennedy, and A.R. Ludlow. Finding of a sex pheromone source by gypsy moths released in the field. *Nature, Lond.*, 303:804–806, 1983.
- C.T. David, J.S. Kennedy, A.R. Ludlow, J.N. Perry, and C. Wall. A reappraisal of insect flight towards a distant point source of wind-borne odor. *Journal of Chemical Ecology*, 8:1207–1215, 1982.
- K. Hausen. Motion sensitive interneurons in the optomotor system of the fly I. The horizontal cells: structure and signals. *Biological Cybernetics*, 45: 143–156, 1982a.
- K. Hausen. Motion sensitive interneurons in the optomotor system of the fly. II. The horizontal cells: receptive field organisation and response characteristics. *Biological Cybernetics*, 46:67–79, 1982b.
- F.E. Kellogg, D.E. Frizel, and R.H. Wright. The olfactory guidance of flying insects. *Canadian Entomology*, 94:884–888, 1962.
- J.S. Kennedy. The visual responses of flying mosquitoes. *Proceedings of the Zoological Society of London*, 109:221–242, 1940.
- J.S. Kennedy. The migration of the desert locust (*schistocerca gregaria* forsk.). *Philosophical Transactions of the Royal Society*, 235:163–290, 1951.
- J.S. Kennedy, A.R. Ludlow, and C.J. Sanders. Guidance system used in moth sex attraction. *Nature, Lond.*, 288:475–477, 1980.
- J.S. Kennedy, A.R. Ludlow, and C.J. Sanders. Guidance of flying male moths by wind-borne sex pheromone. *Physiological Entomology*, 6:395–412, 1981.
- J.S. Kennedy, A.R. Ludlow, and C.J. Sanders. Guidance system for pheromone orientation in moths — reply to Tobin and Bell. *Nature, Lond.*, 295:263, 1982.
- J.S. Kennedy and D. Marsh. Pheromone-regulated anemotaxis in flying moths. *Science*, 184:999–1001, 1974.
- H. Lei and B.S. Hansson. Central processing of pulsed pheromone signals by antennal lobe neurons in the male moth *agrotis segetum*. *J Neurophysiol*, 81: 1113–1122, 1999.
- W. Li, J.A. Farrell, and R.T. Cardé. Tracking of fluid-advection odor plumes: strategies inspired by insect orientation to pheromone. *Adaptive Behaviour*, 9 (3/4):143–170, 2001. ISSN 1059-7123.
- A.R. Ludlow. *Applications of computer modelling to behavioural coordination*. PhD thesis, University of London, 1983. URL <http://www.modelresearch.com/science/thesis>.
- A.R. Ludlow and D. Marsh. Mechanisms of moth orientation. Presentation at SEB meeting, Reading University, December 1978.
- A. Mafra-Neto and R.T. Cardé. Fine-scale structure of pheromone plumes modulates upwind orientation of flying moths. *Nature*, 369:142–144, 1994.
- A. Mafra-Neto and R.T. Cardé. Dissection of the pheromone-modulated flight of moths using single-pulse response as a template. *Experientia*, 52:373–379, 1996.
- A. Mafra-Neto and R.T. Cardé. Rate of realized interception of pheromone pulses in different wind speeds modulates almond moth orientation. *Journal of Comparative Physiology*, 182:563–572, 1998.
- D.M. Marsh, J.S. Kennedy, and A.R. Ludlow. Anemotactic zigzagging flight in male moths stimulated by pheromone. *Physiological Entomology*, 3: 221–240, 1978.
- D.M. Marsh, J.S. Kennedy, and A.R. Ludlow. Analysis of zigzagging flight in moths: a correction. *Physiological Entomology*, 6:225, 1981.
- F.M. Toates. *Control theory in biology and experimental psychology*. Hutchinson, London, 1975.

- N.J. Vickers and T.C. Baker. Latencies of behavioral response to interception of filaments of sex pheromone and clean air influence flight track shape in *heliiothis virescens* (f.) males. *Journal of Comparative Physiology*, 178:831–847, 1996.
- M.A. Willis and E.A. Arbas. Odor-modulated upwind flight of the sphinx moth, *manduca sexta* I. *Journal of Comparative Physiology*, 169:427–440, 1991.
- M.A. Willis and E.A. Arbas. Variability in odor-modulated flight by moths. *Journal of Comparative Physiology*, 182:191–202, 1998.
- M.A. Willis and T.C. Baker. Effects of varying sex pheromone component ratios on the zigzagging flight movements of the oriental fruit moth, *grapholita molesta*. *Journal of Insect Behavior*, 1: 357–371, 1988.
- M.A. Willis and R.T. Cardé. Pheromone-modulated optomotor response in male gypsy moths, *lymantria dispar* l.: upwind flight in a pheromone plume in different wind velocities. *Journal of Comparative Physiology, A*, 167:699–706, 1990.
- R.H. Wright. The olfactory guidance of flying insects. *Canadian Entomology*, 90:81–89, 1958.
- P.O. Zanen and R.T. Cardé. Directional control by male gypsy moths of upwind flight along a pheromone plume in three wind speeds. *Journal of Comparative Physiology, A*, 184:21–35, 1999.