

## DIRECTIONAL CHANGE IN A FLYING BEETLE

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Rhinoceros beetles of the genus *Oryctes* turn in flight by a differential change in the stroke angle, or amplitude, of the wings of the two sides. This method of turning has been briefly described (Burton, 1964) and what follows is a fuller account of the turning mechanisms in these beetles.

### MATERIAL AND METHODS

Rhinoceros beetles of the species *Oryctes boas* and *O. monoceros* were used in this investigation. Both species are large, weighing about 3.5 g and having a wing span of about 10 cm. There appears to be no difference in the flight motors of the two species.

The beetles are common in sugar-cane fields and in well-established compost and manure heaps in Natal. The animals were kept in compost in metal bins in the laboratory at a temperature of about 25 °C.

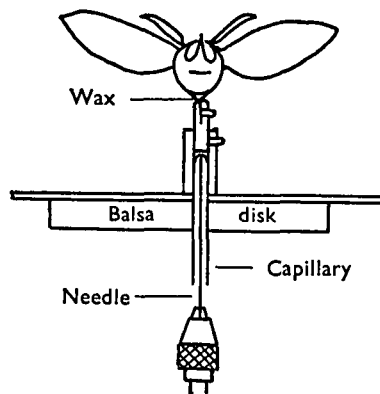


Fig. 1. The yaw apparatus.

Only yawing phenomena were investigated.

A very simple apparatus was constructed which allowed the beetle to rotate freely about its vertical axis (Fig. 1). Rhinoceros beetles do not display the tarsal reflex shown by many other insects and cannot readily be induced to fly. It was discovered by chance, however, that a reasonably reliable method of starting flight was to wax a stiff wire to the beetle and rotate the insect rapidly about its transverse or vertical axis beneath a red light. When a steady wing-beat of good amplitude was achieved the usual procedure was to cool the insect to immobility in a deep-freeze unit (about 15 min at -5 °C). This

made it easier to mount the insect on the apparatus and appeared more readily to induce the beetle to fly again after warming up from the cold.

Mounted on the yaw apparatus at a body angle of  $+30^\circ$ , a flying beetle could be induced to turn towards a lamp, to follow the movement of a striped disk rotating beneath it, and to make compensatory changes in the wing stroke such as would resist forcible spinning of the apparatus.

Dorsal photographs of the yawing phenomena were taken by means of a modified Cossor oscilloscope camera running continuously at 25 in/s, stroboscopic illumination being provided by a Dawe Stroboflood flashing at a frequency calculated to display apparent slow motion of the wings.

The part played by the nervous and muscular systems in yaw was investigated by recording junctional potentials from the flight muscles. Fine copper wires, insulated to the tip, were used as extracellular electrodes and were connected by screened leads to conventional pre-amplifiers and oscilloscope. The electrodes were made sufficiently long, *c.* 25 cm, to allow them to coil about the axle of the yaw apparatus and so permit five or six complete rotations. An earthed metal cage was required to minimize electrical interference.

#### I. OBSERVATIONS

##### *Observed differences between the behaviour of right and left wings during yaw*

Obvious disparities between the right and left wings were observed from tracings of the film negatives. These differences may best be detailed by treating each of the wing variables separately. For the sake of brevity the wings on the outside and inside of the yawing turn will be called the outer and inner wings respectively.

##### 1. *Differences in stroke angle (amplitude)*

Comparisons of the amplitudes of the wing strokes in straight flight and in yaw, for three beetles, are given in Fig. 2, a correction having been made for the fact that the stroke plane does not lie in the plane of the paper (see Appendix *a*, p. 583).

It is clear from the diagrams that during yawing rotation the amplitude of the outer wing is greater than that of the inner wing. This difference in amplitude may be achieved in three ways as exemplified by the three selected beetles.

Subjected to yaw, Beetle 1, flying at maximal stroke angle, decreased the amplitude of both outer and inner wings, but that of the inner wing was more drastically reduced.

In Beetle 2, at submaximal amplitude, the stroke angle of the outer wing was increased and that of the inner wing decreased during yaw.

In Beetle 3, again at submaximal stroke angle, the amplitude of the outer wing increased whilst that of the inner wing remained constant.

##### 2. *Differences in the paths traced by the wing-tips*

We are here dealing with the wing variable usually referred to as the *angle of the stroke plane*, defined by Weis-Fogh (1956) as 'the angle between the vertical axis and the plane which includes the extreme positions of the wing-tips'. It is necessary, however, to make a more detailed comparison between the paths of the two wings than would be provided merely by consideration of the angle of the whole plane of the wing beat.

Since the photographs of yaw were taken from directly above the beetles it was necessary to devise a method of constructing a graph of the wing-tip path in the vertical plane from the dorsal photographs (see Appendix *b*, p. 583).

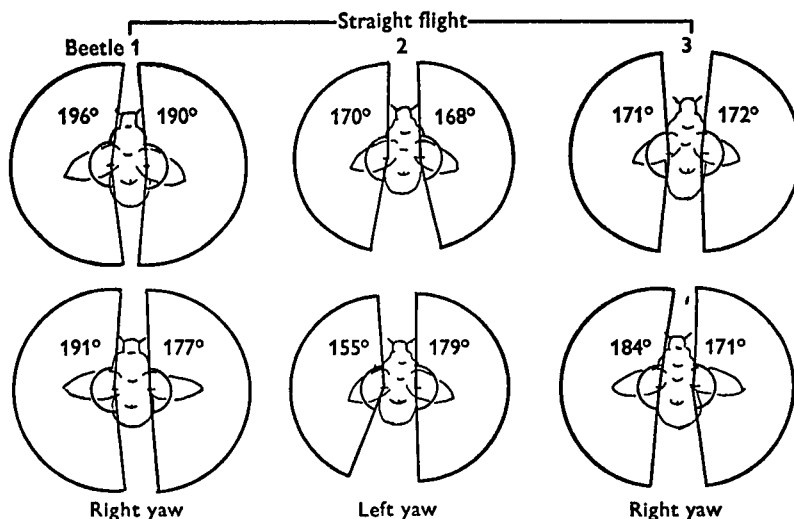


Fig. 2. Comparisons of the amplitudes of the wing strokes of three beetles, in straight flight and in yaw.

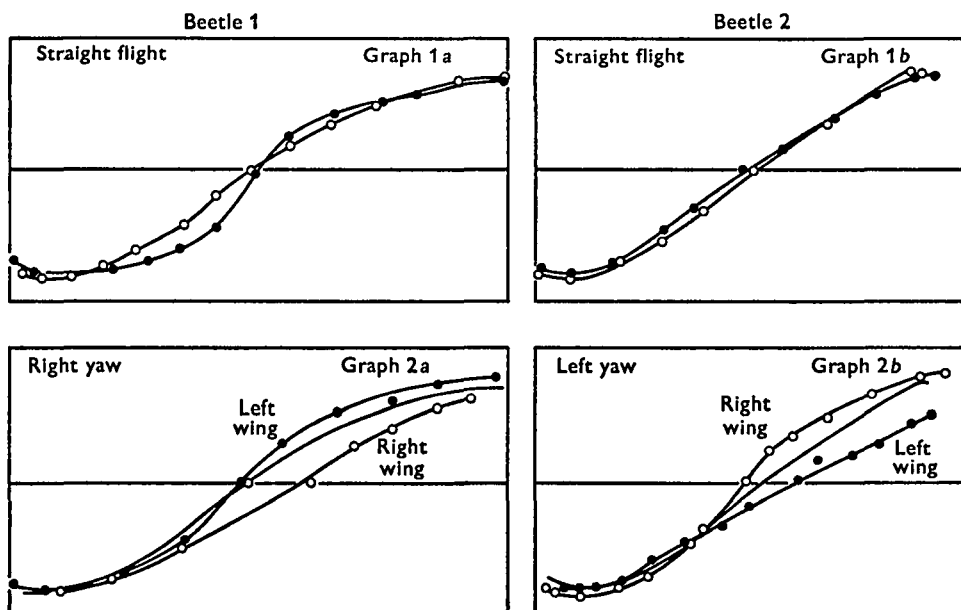


Fig. 3. Graphs of the downstroke paths of two beetles, in straight flight and in yaw. (For Method, see Appendix *b*, p. 583.)

Only the downstroke paths were considered as it was found that the upstroke path was invariant both in straight flight and in yaw.

In Fig. 3 the wing paths of Beetles 1 and 2 are displayed. Graphs 1 *a* and *b* show the

downstroke paths of the left and right wing-tips during straight flight. The paths differ in the two beetles, but the left and right wings of each individual follow very similar curves.

Graphs 2*a* and *b* compare the left and right wing-tip paths during yaw: Beetle 1 in right yaw and Beetle 2 in left yaw. It can be seen that, in both beetles, the outer wing is elevated in relation to its fellow during the first half to two-thirds of its path. Furthermore, the outer wing adopts a steeper trajectory than that of the inner wing during the middle of the stroke. It can also be seen that the outer wing-tip traverses a longer path than its fellow.

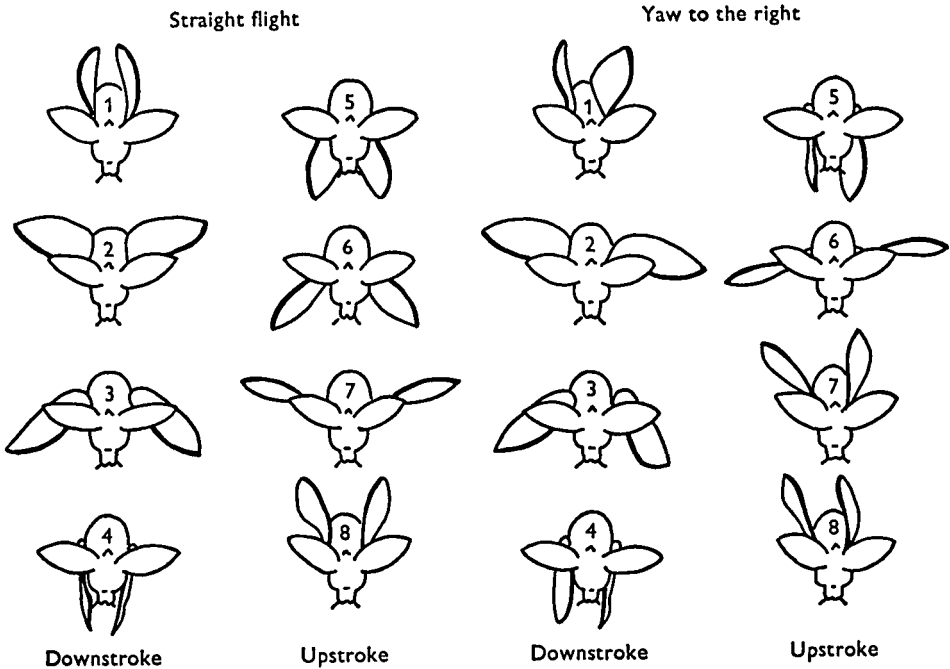


Fig. 4. Comparisons of the wing strokes in straight flight and in yaw.

The interpolation of the respective straight-flight downstrokes in Graphs 2*a* and *b* (continuous line) makes it clear that during yaw the outer wing-path is elevated and the inner wing-path depressed relative to the path followed in straight flight.

### 3. Other differences in the wing stroke during yaw

The following further differences between the movements of the wings of the two sides during yaw may be observed from the tracings illustrated in Fig. 4.

It can be seen that the outer wing: (i) pronates ahead of its fellow, (ii) leads throughout the downstroke, (iii) supinates earlier, and (iv) leads throughout the upstroke.

The earlier pronation and supination might seem to suggest that the outer wing would gradually become more and more out of step with the inner wing, but this clearly does not happen. The number of wing positions from any point in the stroke cycle to the corresponding point in the following cycle is the same for both wings. The two wings take the same time to complete each half stroke, but are out of phase with one

another, the outer wing starting down whilst the inner wing is still completing the upstroke, and starting up whilst the inner wing is still completing the downstroke. In fact, the outer wing beats through a greater arc in the same time that is taken by the inner wing to beat through a lesser arc.

## II. MECHANISMS

### *The probable effect of the above-described wing-beat differences in bringing about yawing rotation*

#### 1. *Differences in stroke angle (amplitude)*

The wings of insects are in some respects analogous to the rotor blades of helicopters, where:  $\text{Lift} = m \times w$ ,  $m$  being the mass of air influenced per second and  $w$  the downwash velocity induced.

The mass of air influenced per second clearly depends upon the area swept by the rotors or wings and the frequency of their rotation or oscillation. The downwash velocity will depend upon frequency only. Whereas, in the helicopter, only the frequency of rotation can be varied, in some insects the area swept can also be altered by change of amplitude of the wing beat. It therefore appears that, in the yawing beetle, the increased amplitude of the outer wing provides increased lift and propulsion by the increased velocity of the wing and also by the increase in the area swept by the wing. This would seem to be all that is required to bring about a banked turn.

#### 2. *Differences in the wing-tip paths of the two wings*

The elevation of the path of the outer wing and the depression of the path of the inner wing during the first half to two-thirds of the downstroke probably gives rise to a rolling rotation. In addition to this the steeper trajectory of the outer wing about the middle of its path, where the wing is travelling at its maximum velocity, would produce greater propulsion and therefore a yawing rotation.

#### 3. *Other differences in the wing stroke during yaw*

Although the earlier pronation and supination of the outer wing during yaw are quite striking phenomena they do not, in themselves, have any special significance, but are brought about by the increased stroke angle and greater velocity of the outer wing.

## III. THE ROLE OF THE NERVOUS AND MUSCULAR SYSTEMS IN YAWING ROTATION

In *Oryctes* all the flight muscles, including the basalar and subalar muscles, are of the fibrillar type in which the junctional potentials are of a lower frequency than that of the muscle contractions, there being no obvious temporal relationship between them. It follows that, in contrast with non-fibrillar motors, it is not possible to obtain any information about the timing of muscle contraction by electrical recording. Fortunately, a few clues and a chance observation pointed the way out of this apparent impasse.

Roeder (1951), whilst recording the muscle potentials and thoracic movements of flies, observed that periodic increases in amplitude of the thoracic movements appeared to bear some relation to increases in the frequency of the muscle spikes.

Machin & Pringle (1959) also observed a frequency-dependent effect in the oscillation of *Oryctes* basalar muscle. The amplitude of oscillation of the muscle decreased if the stimulus frequency was reduced below a certain figure. Later, Wilson & Wyman (1963) suggested that frequency control may operate in the regulation of parameters like direction of locomotion.

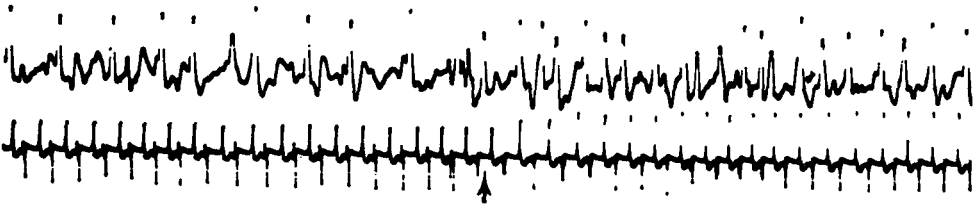


Fig. 5. Sudden increase in light intensity (at point marked by arrow), leads to increase in muscle spikes and to enhanced frequency and amplitude of the flight vibrations.

In the present investigation, it was found that a change from the low-intensity illumination of a neon Stroboflash to the high-intensity light of the Stroboflood brought about an audible change in the wing-beat of the beetles. Simultaneous recordings of the flight vibrations and of the electrical potentials from one of the tergo-sternal muscles revealed that there was a correlation between muscle-spike frequency and the frequency and amplitude of the flight movements.

The trace shown in Fig. 5 demonstrates that the change in light intensity was quickly followed by a considerable increase in amplitude of the flight vibrations: a 5% increase in the frequency of the flight movements, and a 50% increase in the number of muscle spikes.

Having established the fact that fibrillar muscle can be driven to greater degrees of contraction by an increase in the frequency of firing of the motor nerves, it remained to be seen whether or not the muscles of the left and right sides were independent. Preliminary extracellular recordings from the left and right members of a pair of muscles showed that, during yaw to the right, there was a marked increase in the frequency of the nervous input to the left muscle of the pair. Subsequently, recordings were obtained from the left and right members of all six pairs of fibrillar muscles during straight flight and yawing rotations of tethered beetles.

The insects were afterwards frozen and dissected to confirm the correct positioning of the electrodes.

The recordings from the muscle pairs are displayed graphically in Fig. 6. Here the abscissa represents 2 s of flight, the initial second being a control flight in which rotation of the beetle was prevented, the subsequent second being the experimental flight in which the beetle was forcibly rotated in the yaw plane.

The ordinate provides a measure, not of the total number of junctional spikes from the left and right muscles of a pair, but of the difference obtained by subtracting the lesser number from the greater for each interval of 0.2 s along the abscissa.

Unfortunately, only three control flights (3, 5, 6) showed an equal number of spikes on the two sides. In the other graphs the control flights showed a bias to the left or right, probably due to misalignment of the beetle on the support, so that compensatory

movements of the wings were already being made. In all the experimental flights, however, an excess of spikes was recorded from the flight muscle on that side of the insect which was expected to be compensating for the forced rotation.

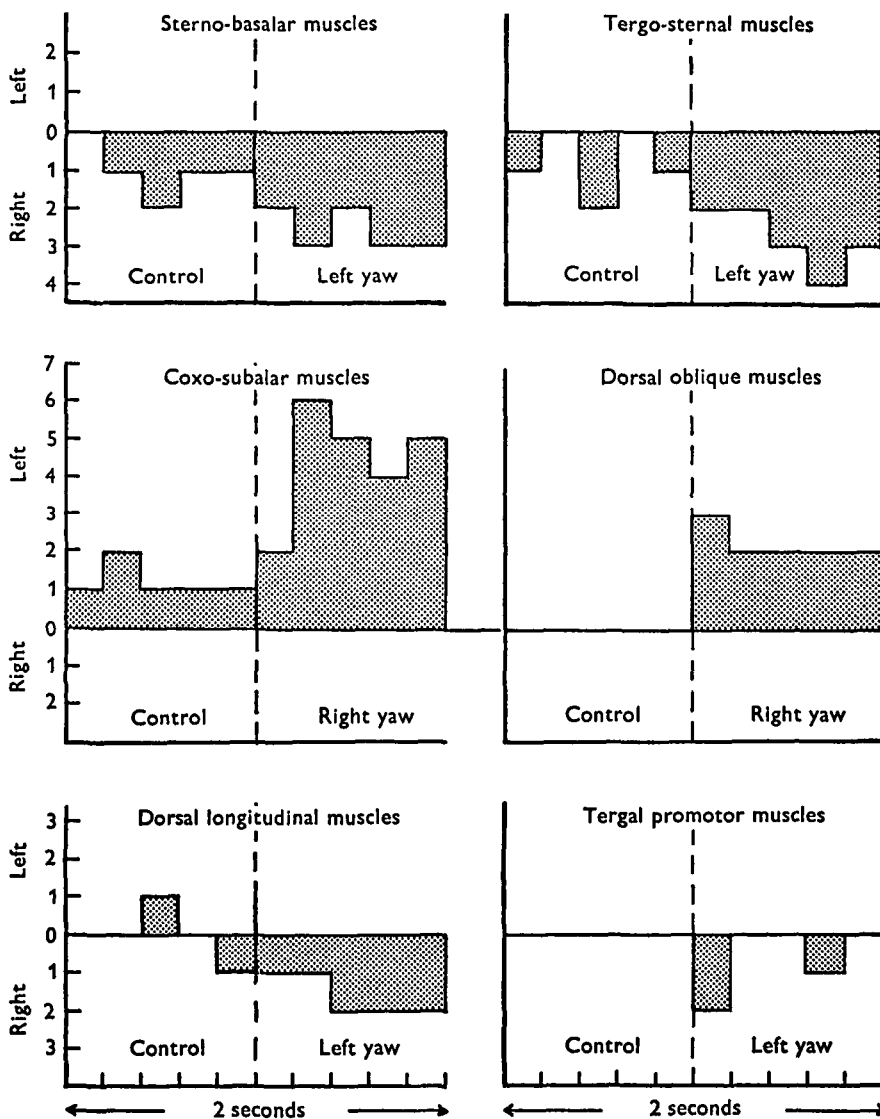


Fig. 6. Histograms of muscle spikes from each pair of fibrillar flight muscles after having subtracted the lesser spike numbers from the greater.

DISCUSSION

The ability to fly would be of very limited use without the additional capacity for changing direction in flight. This being so, it would be reasonable to suppose that the ability to turn would have been one of the earliest modifications in the evolution of insect flight. The mechanics of turning in flight might therefore be supposed to be

essentially similar in all orders of flying insects. This supposition, however, is very far from being the case, at least four different turning mechanisms having been described thus far.

Theoretically, turning movements may be brought about by a change in one or more of the following parameters: (i) the frequency of the wing-beat, (ii) the angle of the stroke plane, (iii) the angle of attack of the wings, (iv) the stroke angle, or amplitude.

No observation has as yet been reported of a flying insect capable of unilateral alteration in the wing-beat frequency.

One of the earlier flight observations was made by Stellwaag (1916) on the honey bee, which was shown to have the ability to alter the angle of the stroke plane differentially on the two sides. This sophisticated turning mechanism has been described as being a feature peculiar to the wing mechanism of the bee.

Turning by alteration of the angle of attack of the wings has been described by Faust (1952). He induced yaw in the fly *Calliphora* by rotating the insect about its vertical axis. Compensatory changes in the angle of attack of the wings were observed during the downstroke, the inner wing being supinated whilst the outer wing was pronated to a lesser degree than in straight flight. According to Pringle (1968) the effect would be to produce greatly increased drag from the inner wing and some increase of lift from the outer wing, thus generating the torques required to compensate for the forced rotation.

Dugard (1967) observed an apparently similar turning mechanism in *Schistocerca* flying at the mouth of a wind-tunnel and induced to turn by greater illumination of one-half of the visual field. The chief effector action was again a change in the angle of attack of the wing, in this case an earlier and greater pronation of the left forewing during a left turn. This action presumably has the effect of increasing the drag of the inner wing, thus bringing about a yawing turn.

Although, in the observations of Faust and Dugard, yawing rotations were achieved chiefly by increasing the drag produced by the inner forewing, the mechanisms whereby this was brought about in the two insects must have been radically different. In *Schistocerca*, pronation of the forewing was brought about by the firing of one or both of the motor units in the second basalar muscle, the motor discharge to the subalar muscle remaining constant (Dugard, 1967). In *Calliphora*, however, the differential torsion of the inner and outer wings could only have been produced by different 'settings' of the wing articulation on the two sides, presumably brought about by the non-fibrillar direct muscles.

Clearly, these two turning mechanisms are quite distinct, the more so in view of Dugard's observation that, during yaw, *Schistocerca* extends the inner metathoracic leg into the air-stream and curves the abdomen in the direction of the turn.

Four insects, *Apis*, *Schistocerca*, *Calliphora* and *Oryctes*, have been discussed, the last in detail, and found to be distinctly different in their yawing mechanisms. It seems unlikely that all the possible permutations of the yawing mechanism could be exhausted by reference to only four of the orders of insects. This being so, it would appear that a thorough investigation of orientation phenomena would be fruitful, particularly in relation to the difficult problem of the origin of insect flight.



## SUMMARY

1. Stroboscopic photographs of tethered rhinoceros beetles executing yawing rotations show that yaw is achieved chiefly by a unilateral increase in amplitude of the wing stroke.

2. This change in amplitude is brought about by an increase in the frequency of the nervous input to all the fibrillar flight muscles of the appropriate side.

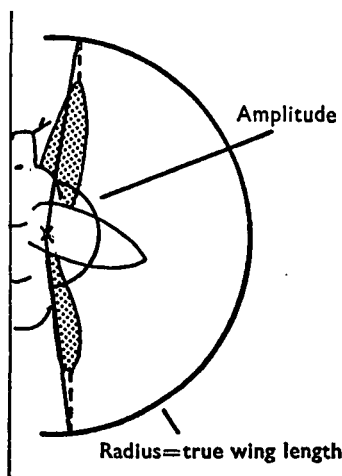


Fig. 7. Method of determining the true amplitude of the wing stroke.

## APPENDIX A

*Differences in amplitude during yaw*

Amplitudes were determined from enlarged tracings of the dorsal photographs taken during yawing rotations. Correction was made for the inclination of the plane of the wing-beat by projecting the wing-tip positions on to the arc of a circle of radius equal to the true wing length, and with the pleural wing process, as centre, as in Fig. 7.

## APPENDIX B

The path of the wing-tip is usually illustrated by plotting the successive positions of the tip of the wing from high-speed ciné or stroboscopic photographs of the flying insect in lateral view. Where the amplitude of the wing beat is large, as in *Oryctes*, the method has the disadvantage of virtually ignoring the extreme upper and lower portions of the stroke. Here, the wing-tip is travelling almost directly along the line of sight, towards, or away from, the mid line of the insect's body.

A method was therefore devised whereby graphs of the wing-tip paths could be constructed from the data provided by the available dorsal photographs.

It is clear that in the composite tracing of the wing positions (Fig. 8*a*), the inclination of the plane of the wing-beat results in the apparent shortening of the wings in all positions above and below the horizontal. But the true wing-tip position must be somewhere along a vertical line passing through the traced position.

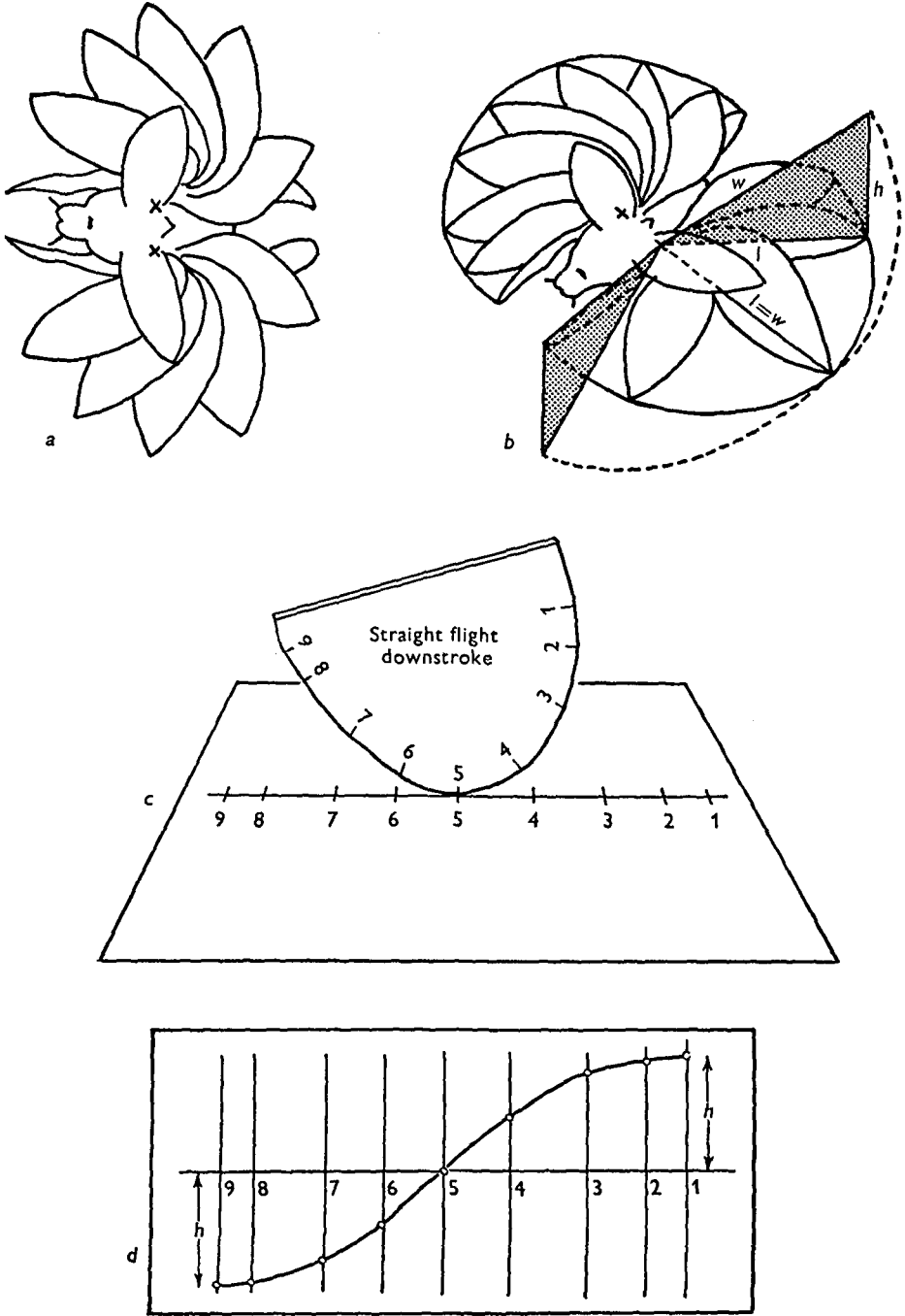


Fig. 8. Method of constructing a graph of the wing-tip path in the vertical plane from dorsal photographs of the insect in flight.

This true position may be obtained graphically, as in Fig. 8*b*, by constructing a right-angled triangle in which the hypotenuse = the true wing length, and the base = the apparent wing length. In practice, the vertical position of the wing-tip was obtained from the formula:

$$h = \sqrt{w^2 - l^2},$$

where  $h$  = the vertical distance above or below the horizontal,

$w$  = the true wing length,

and  $l$  = the apparent wing length.

The horizontal intervals between the wing-tip positions were plotted by making cardboard templates of the composite strokes of the left and right wings as traced in Fig. 8*a*, and marking off the tip positions along a horizontal line passing through the pleural wing process, as in Fig. 8*c*. The values of  $h$  were then inserted in their respective positions to construct the graph shown in Fig. 8*d*.

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