Eristalis nemorum male aerobatics

Wopke Wijngaard
Dahliastraat 9, 5271 HB Sint-Michielsgestel, The Netherlands,
E-mail: wopke.wijngaard@home.nl (http//www.insect-behavior.nl)

Eristalis nemorum (L.) males show a characteristic hovering behaviour above females feeding on a flower. A male may hover 1-2 cm above a female for minutes. When the female leaves, the male will follow swiftly. This following behaviour is described by a control model with velocity control. When a male is hovering above a female with more males in the neighbourhood, clusters of hovering males may come into existence. Sometimes even four males are hovering in a column above a female. The existence of columns of hovering males is explained by the males obeying a small set of simple behavioural rules.

Keywords: hovering, hoverfly, position control

Eristalis nemorum (L.) males show a characteristic hovering behaviour above females feeding on a flower (Stubbs & Falk 1983, Iliff 2003, Reemer *et al.* 2009; Figure 1). A male may hover 1-2 cm above a female for minutes. In a previous paper a quantitative characterization of the hovering of a male hoverfly *E. nemorum* has been given (Wijngaard 2010). In this paper an overview is given of various aspects of the movement of the males. When a female is leaving, the male will react swiftly. A conceptual model will be used to quantify the timing of this reaction.

In the summer of 2012, clusters of hovering males have been filmed, even a column of four hovering males above a female. The way in which a column of hovering males arises is also investigated here.

MATERIALS AND METHODS

The flies have been filmed near Sint-Michielsgestel, The Netherlands, from May until July 2012. The behaviour is very characteristic, therefore the flies have not been kept for further identification. Two cameras were used: a Casio EX-F1 or a Canon SX-40HS. Both cameras filmed in a high speed mode (HS) with 300

(Casio) or 120 (Canon) frames per s. The camera is held in hand. Parts of the film with much movement along the line of sight have been discarded. The films have been analysed in small sequences of several seconds (*i.e.*, tracks), using 'Tracker', short for 'Tracker video analysis and modelling tool' (http://www.cabrillo.edu/~dbrown/tracker/). The 'tracks' are coded by the date and time of recording plus a track-specific code; for example, track '300512_1557A' indicates track A of the film recorded on May 30, 2012, at 15:57 hours. As unit of distance the length of the male or female is chosen, *i.e.*, approximately 1 cm.

EXPERIMENTAL RESULTS

At first some general observations about the behaviour of male *E. nemorum* are described. Males may be found searching for females in a patch of flowers. The

Figure 1. A male *Eristalis nemorum* hovering above a female.

males are looking for dark objects of the size and shape of a female. The object of interest will be approached and touched with the legs. When this check is positive the male may start hovering.

One hovering male

In the field the hovering males *E. nemorum* are apparent by the emission of a characteristic humming sound of approximately 280 Hz, the frequency of the wingbeat. A hovering male may do so for minutes, but every now and then, the male is touching the female with its legs. This may function to test whether the object is a female *E. nemorum*. A real copulation does not occur in these circumstances.

Horizontal position control has been investigated in a previous paper (Wijngaard 2010). The control of vertical distance is somewhat more complicated. When the male is touching the female, the vertical distance is at first enlarged with a jump and afterwards diminished with a time constant of the order of 0.5 s. An example is given in Figure 2. In Figure 2 the male is at first hovering approximately 1 unit above the female. At time t = 0.9 the female is touched by the legs and the distance is increased to 3.5 units. Afterwards the distance is decreased exponentially with time constant 0.77 s. At t = 2.8 s the distance is again increased due to some unknown cause.

In hovering above the female the male is performing a wobbling oscillation with a frequency of approximately 7 Hz. Perhaps this oscillation is of use to determine the distance to the female (Wijngaard 2010).

Many times the male is not hovering above a female but above some other object. Hovering has been observed above a honeybee, a soldier beetle, a white clover flower head (*Trifolium repens*), and a male *E. nemorum*.

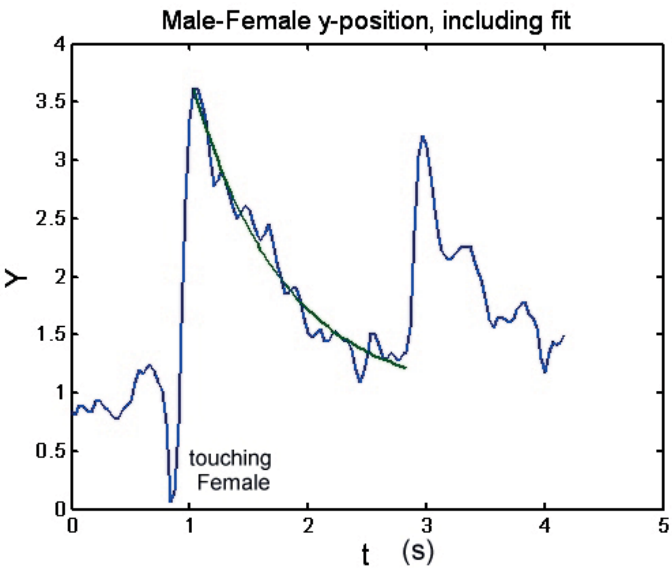

Figure 2. Vertical distance after touching. Exponential fit (green) with time constant 0.77 s. Track 280612_1613.

Following behaviour

When the female is flying away the male in general will follow the female. The reaction of the male is very fast. To gain more insight the conceptual model from the previous paper will be used with added velocity control.The model given here is meant to be of use for the following behaviour in one dimension, either in the horizontal x-direction or in the vertical y-direction. The proposed model is given in Figure 3. For generality the model does not mention a male or female, instead a 'Follower' is following a 'Leader'. For a male hovering above a female, the male is the Follower and the female the Leader. The physical distance x_F-x_L between Follower and Leader is filtered by a first order system to obtain the distance d_{estim} as seen by the insect. The filter is modelling sensory and neural delay. The estimated distance is compared with the internal reference d_{ref} and amplified by the proportional gain K_r. In parallel the estimated distance d_{estim} is differentiated to obtain the estimated velocity. The velocity is amplified by a parameter K_d. The resulting control signal is the sum of a proportional and derivative (velocity) part. The control signal is filtered by a first order system, modelling the mechanical part of the system, to obtain the physical velocity. By integrating the velocity the position x_F of the Follower will be obtained.

As an example the model has been used to fit the experimental results for a male following a female. In this case male and female were both stationary at the start of the track. The results for the vertical y-direction are given in Figure 4. The parameters of the model have been chosen to fit the experimental results visually. The chosen parameters are therefore only indicative.

Two males hovering above a female

Sometimes two males are hovering above one female, one male above the other (Figure 5). The highest male, to be called male2, may follow either the female or the lower male, to be called male1.

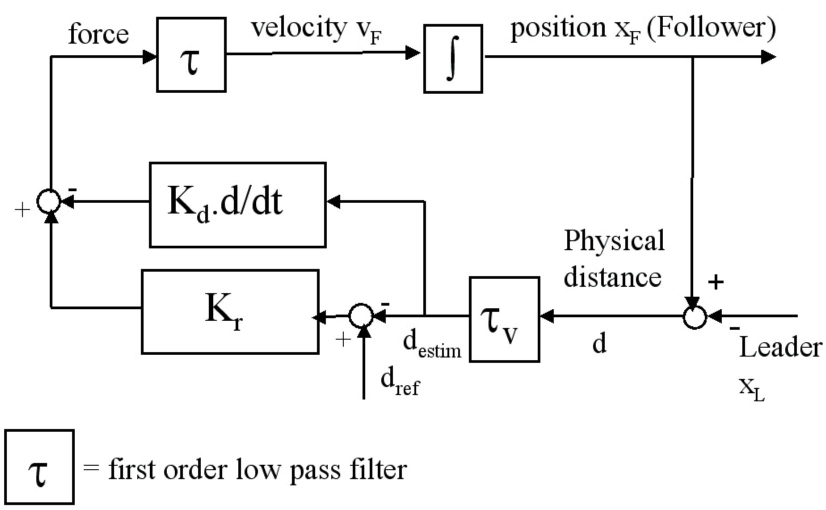

Figure 3. The conceptual model with proportional and derivative (velocity) control.

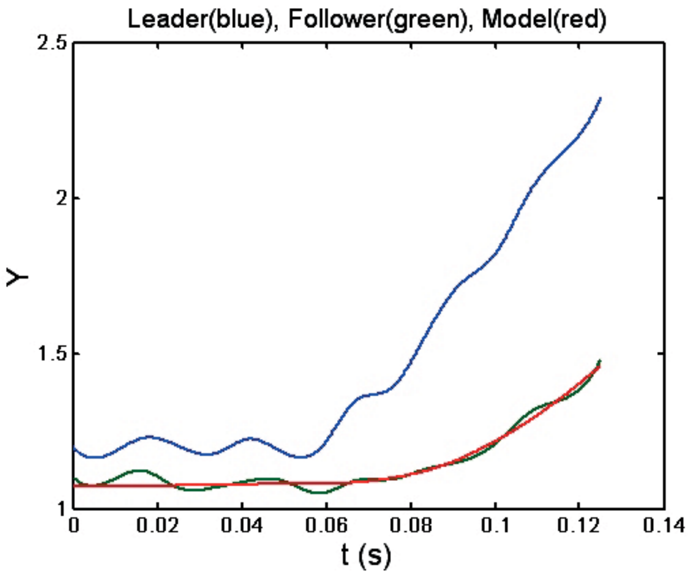

Figure 4. The vertical position of female (blue) and male (green) as a function of time along with the fitted results of the model (red). K_r = 13, K_d = 0.7 s, $\tau_v = \tau$ = 0.02 s.

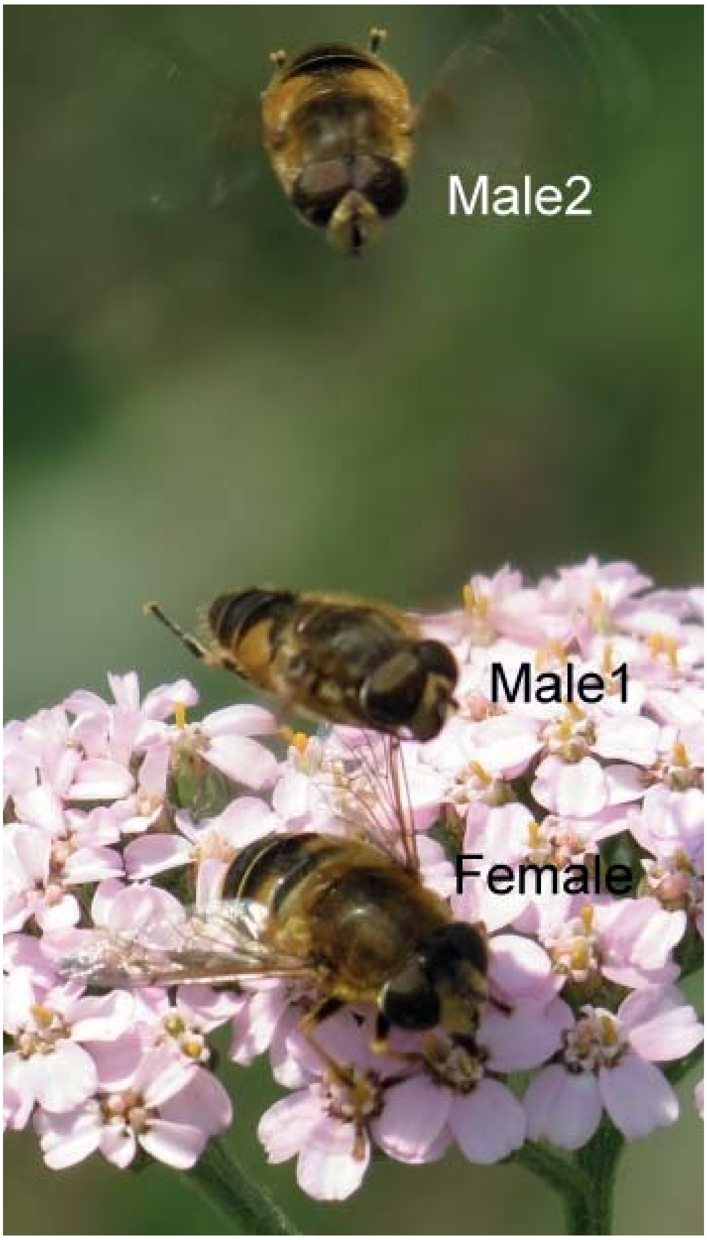

Figure 5. Two males hovering above a female.

A male may hover above another male, so male2 will follow male1. In most cases male1 is following the female, but sometimes male1 is following male2. This hypothesis is supported by a few tracks where the two males are drifting away from the female. An example is given in Figure 6. Here for some time male1 and male2 are drifting away from the female until the distance, approximately at time t = 3, is too large and the vertical distance to the female is decreasing to normal values. The conceptual model has been used to model this behaviour. The parameters of the model have been chosen to obtain a reasonable fit with experiment.

Development of a column of hovering males

The development of a column of hovering males has been filmed. Here, as an example, it will be described how a column of two hovering males may arise from one male hovering above a female. In Figure 7 four frames from a film are given. The female is indicated by a red dot. At first only one male, indicated by a green dot, is hovering above the female. Then another male, the orange male, is coming in the field of view. The orange male is touching the green one with its legs and then going on until the female will be touched. After touching the female a second time, the orange male is entering the hovering phase. The green

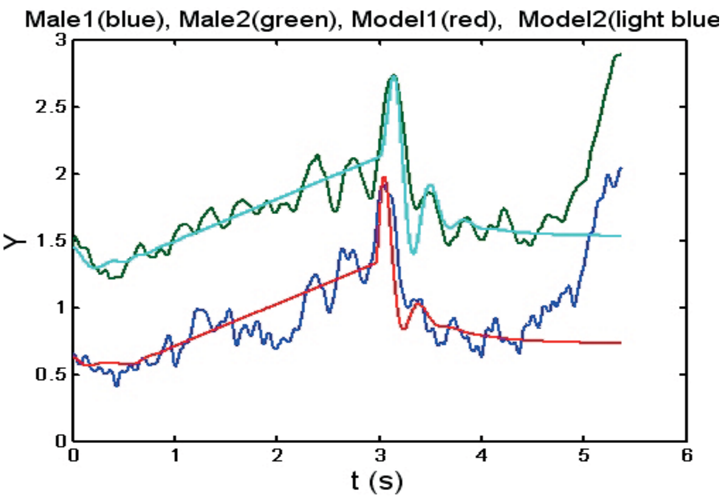

Figure 6. Track 190612_1654. For 0.5<t<2.97 the males are following each other and the distance to the female is drifting away. Model: K_r = 18, $\tau_v = \tau$ = 0.03 s, K_d = 0. At time t = 5 both males are leaving the female to hover above a nearby fly.

Figure 7. Pictures from a film, with the first picture at the left. A second male is added to the first hovering male forming a column of two hovering males above a female. The total time between the first and the last picture is 2 s. Track 190612_1654Film.

male is at first pushed forward to the female and then continues hovering. So at the end two males are hovering in a column above the female.

Generalizing results of this kind, components of behaviour related to hovering are now integrated to obtain the rules to be used by *E. nemorum* males to obtain a column of hovering males. The rules which a male will obey are: (1) Search for a dark object on a flower. (2) Touch the object of approximately your own length with your legs. (3) When a female is encountered enter the hovering phase. (4) When a hovering male is encountered look for a female below the hovering male. If a female is found enter the hovering phase somewhere in the column of hovering males. Otherwise leave the scene.

DISCUSSION

The trajectories are in reality three dimensional, but only the position in a plane perpendicular to the line of sight has been measured. This will not be a problem when the movements in the plane and perpendicular to the plane are independent. Parts of the results with much movement along the line of sight have been discarded. The camera has been held by hand, therefore the camera has not been completely stationary. This has been partly, but not completely, compensated in some cases by choosing a point in the background as a reference. The unit of distance is the length of a male or female, this is approximately 1 cm. However the analysis in terms of the model will not depend on absolute distance, so this choice of the unit of distance does not have consequences for the analysis.

Conclusion

Eristalis nemorum males are capable of closely following a female feeding on a flower or leaving. The simple rules used by the males in following females are the cause of columns of males hovering above a female. The conceptual model has been helpful in analyzing this behaviour.

Acknowledgements

Tracker video analysis and modelling tool is a project of Open Source Physics (http://www.cabrillo.edu/~dbrown/tracker/).

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