Parameters used in the model

The receptive field of an ommatidium is the patch of the outside world which is imaged by the ommatidial lens onto the rhabdom, defined by the acceptance angle of the rhabdom, which varies from species to species, and can vary according to light/dark adaptation. Receptive fields of neighbouring ommatidia overlap (Fig. 1). The inter-ommatidial angle is the angle between optical axes of adjacent ommatidia. The fused rhabdoms of nocturnal and crepuscular mosquito species, including most of the *Anopheles* and *Aedes* genera that have been studied, provide a wide acceptance angle to gather as much light as possible, at the expense of image resolution.

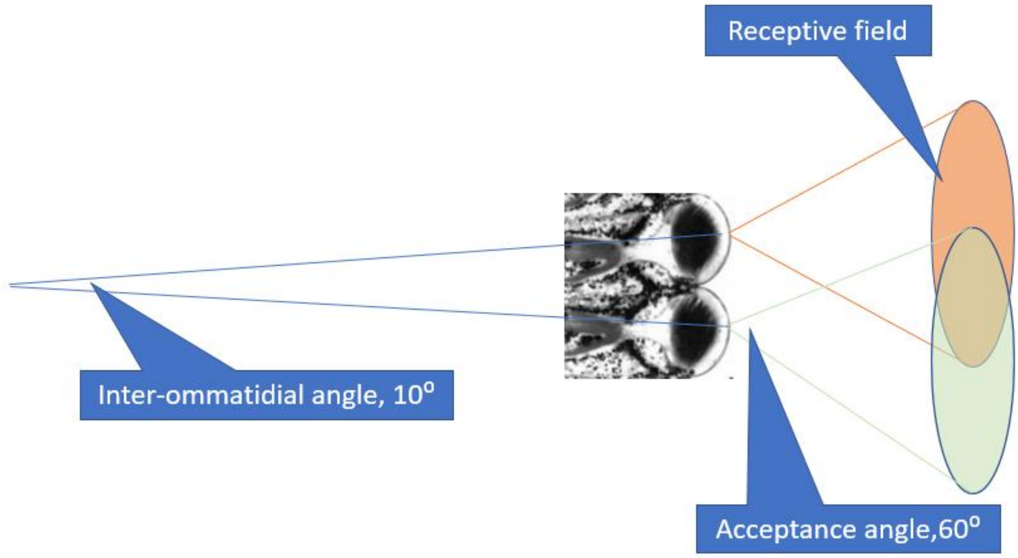


Fig 1. Two adjacent ommatidia, showing that receptive fields overlap (adapted from Land *et al.*, 1997).

We measure the size of objects in the visual field in terms of the angle they subtend at the eye (Fig. 2). The angle that is subtended by a target is a function of its size and the distance between the target and the eye.

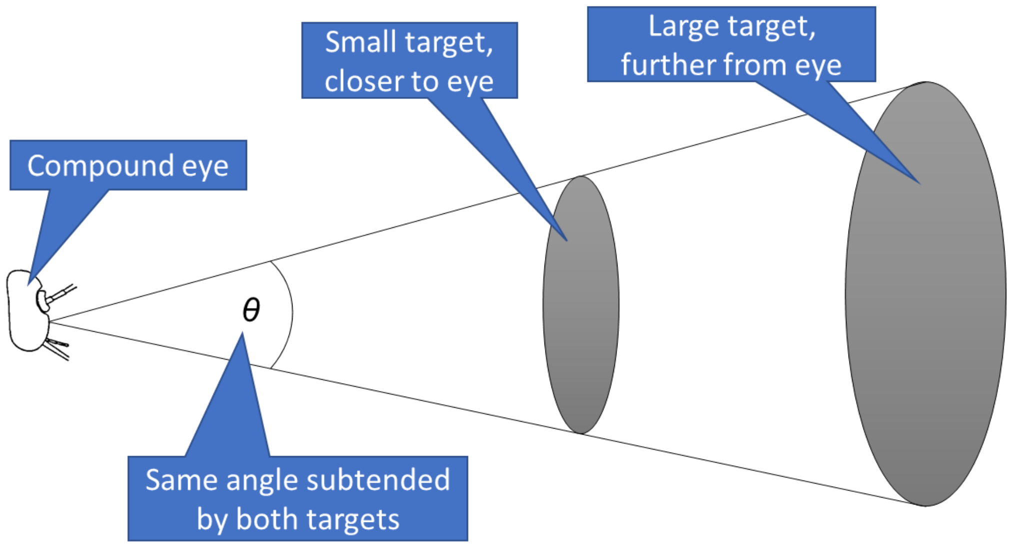


Fig. 2. The angle subtended by two targets at the eye. The subtense is the information transmitted to the brain.

The eye in the model is simplified as a group of 37 adjacent ommatidia. The R script works out the signal from each ommatidium when the flying insect looks at a circular target. The target can either be vertical, i.e. forming a 90° angle with the ground, or horizontal, i.e. lying flat on the ground (Fig. 3).

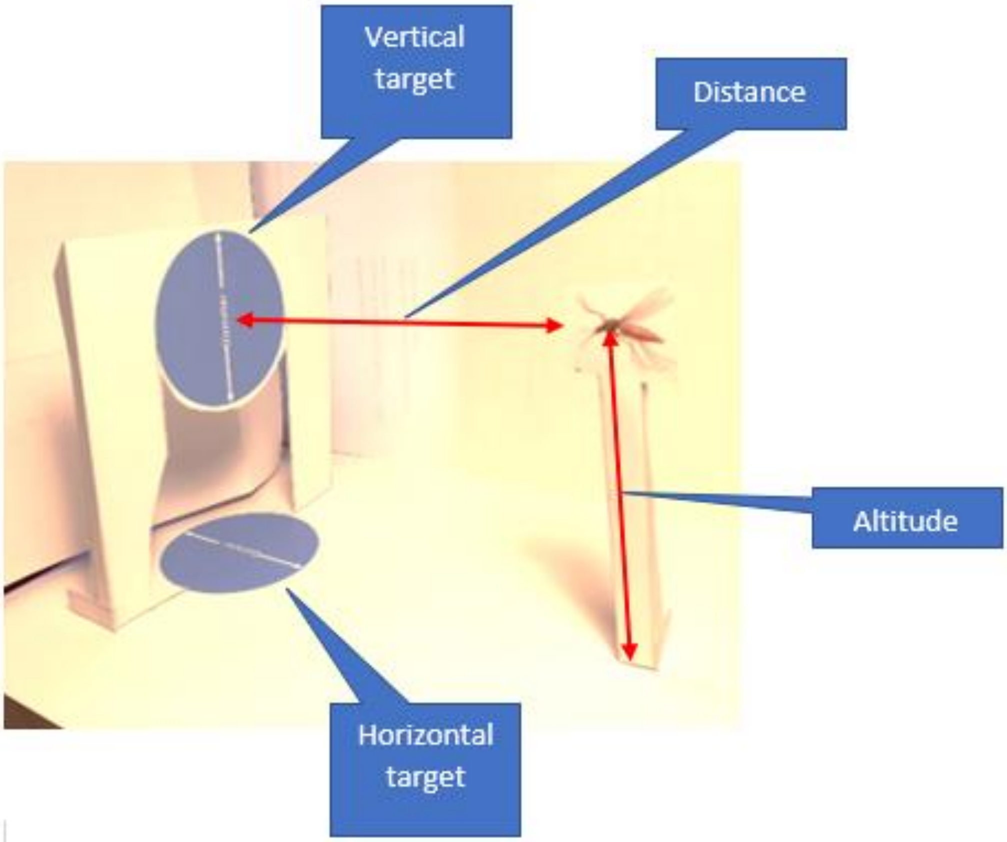


Fig. 3. Vertical and horizontal targets for the visual world model.

The model is designed to work on a wide range of settings. The parameters can be adjusted to reflect species-specific characteristics and target characteristics. A definition of the parameters that the model requires to function and that can be modified ad hoc is provided in Table 1.

Parameter	Definition	Unit	Name on csv file
Distance	Horizontal distance from target.	cm	targetdistance
Altitude	Insect height above ground. If the parameter is set, the model assumes the target is placed horizontally, otherwise if left blank, it assumes the target is placed vertically and the insect is approaching the target head on.	cm	altitude
Diameter	Diameter of the target.	cm	targetdiameter
Inter-ommatidial angle	Angle between two adjacent ommatidia.	degrees	interommatidialangle
Receptive field	Portion of the external world that is captured by each ommatidial lens, determined by the acceptance angle of the rhabdom.	degrees	receptivefield

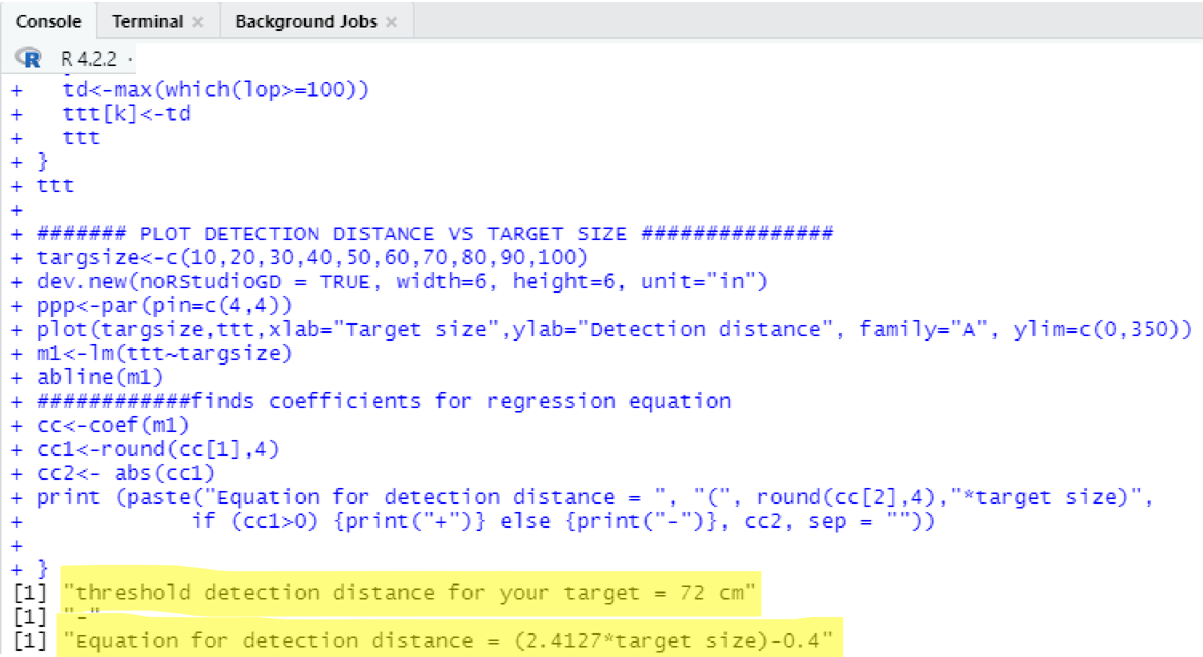
Ommatidium stimulation	Level of stimulation of a single ommatidium, determined by the extent of overlap between the receptive field of the ommatidium and the target. At 100%, the target fills the receptive field.	%	N/A
Detection distance	Maximum theoretical distance at which the target can be detected, determined by running the mosquito eye model with target distances ranging from 500 cm to 1 cm, and determining the distance at which the total eye stimulation (for all ommatidia whose receptive fields include at least a part of the target) exceeded the total eye threshold value.	cm	N/A
Total eye threshold	Minimum percentage of stimulation required for the target to be detected. This comes from the sum of all the different levels of stimulation of the ommatidia in which the receptive fields are covered by the target by at least the value selected in the individual ommatidia threshold parameter. We suggest leaving this value at 100%.	%	teye
Individual ommatidia threshold	For each ommatidium, this is the minimum percentage of stimulation needed for it to count towards the total eye threshold. If an ommatidium is stimulated (i.e. its receptive field is at least partially covered by the target) in a measure below the threshold, the ommatidium is counted as "not stimulated" and its value is not added towards the total eye threshold.	%	tom

Table 1. Parameters used by the model.

Model output

The signal level from an ommatidium depends on the percentage of its receptive field which the target fills and is colour-coded as a shade of grey on the output chart.

The model also calculates at which distance the target would produce an overall ommatidium stimulation of over 100%. This could be produced by a single ommatidium stimulated at 100% or by the sum of multiple ommatidia partially stimulated. Thus, for a given set of eye and target parameters, the model produces the maximum distance at which the target could be detected. This will be printed out in the console, together with the general equation that can be used to extrapolate the distance at which, considering the specific eye parameters used, targets of different dimensions could be detected (Fig. 4).



```
Console   Terminal ×   Background Jobs ×
R 4.2.2 ·
+    td<-max(which(lop>=100))
+    ttt[k]<-td
+    ttt
+ }
+ ttt
+
+ ####### PLOT DETECTION DISTANCE VS TARGET SIZE ###############
+ targsize<-c(10,20,30,40,50,60,70,80,90,100)
+ dev.new(noRStudioGD = TRUE, width=6, height=6, unit="in")
+ ppp<-par(pin=c(4,4))
+ plot(targsize,ttt,xlab="Target size",ylab="Detection distance", family="A", ylim=c(0,350))
+ m1<-lm(ttt~targsize)
+ abline(m1)
+ ############finds coefficients for regression equation
+ cc<-coef(m1)
+ cc1<-round(cc[1],4)
+ cc2<- abs(cc1)
+ print (paste("Equation for detection distance = ", "(", round(cc[2],4),"*target size)",
+            if (cc1>0) {print("+")} else {print("-")}, cc2, sep = ""))
+
+ }
[1] "threshold detection distance for your target = 72 cm"
[1] "-"
[1] "Equation for detection distance = (2.4127*target size)-0.4"
```

Fig. 4. Model output that presents the general equation for the detection distance and the maximum detection distance for the target size introduced in the model. Model parameters were set as follows: Inter-ommatidial angle 8°; Receptive field 40°.

The model also produces a graph that displays the relationship between the distance of detection and the target size (Fig. 5).

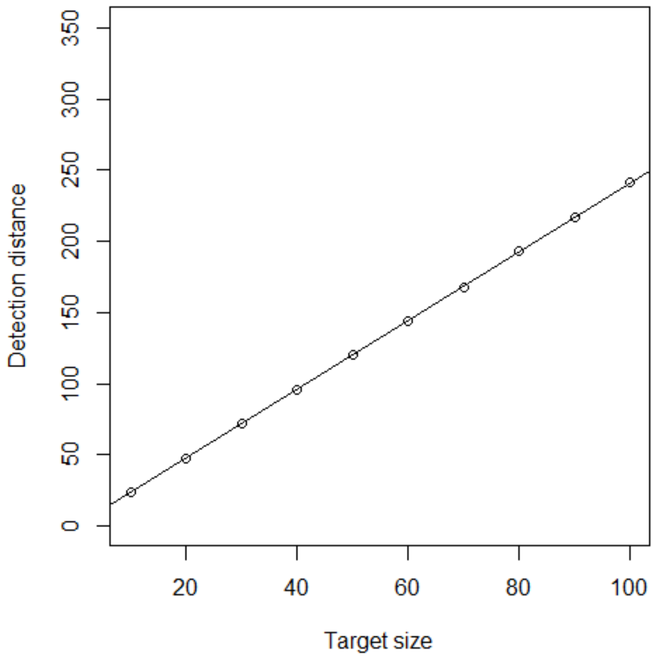


Fig. 5. Model output that indicates the maximum detection distance for ten different target sizes for *Anopheles* mosquitoes. Model parameters were set as follows: Inter-ommatidial angle 8°; Receptive field 40°.

Model output for vertical targets

The signal level of the ommatidia stimulated by a vertical target depends on the intercept of the circular receptive field and the circular subtense of the target image. The model output is a chart representing the 37 ommatidia individually coloured depending on the signal level (Fig. 6). The model also produces a red circle overlay that shows what a high-resolution image of the target would look like.

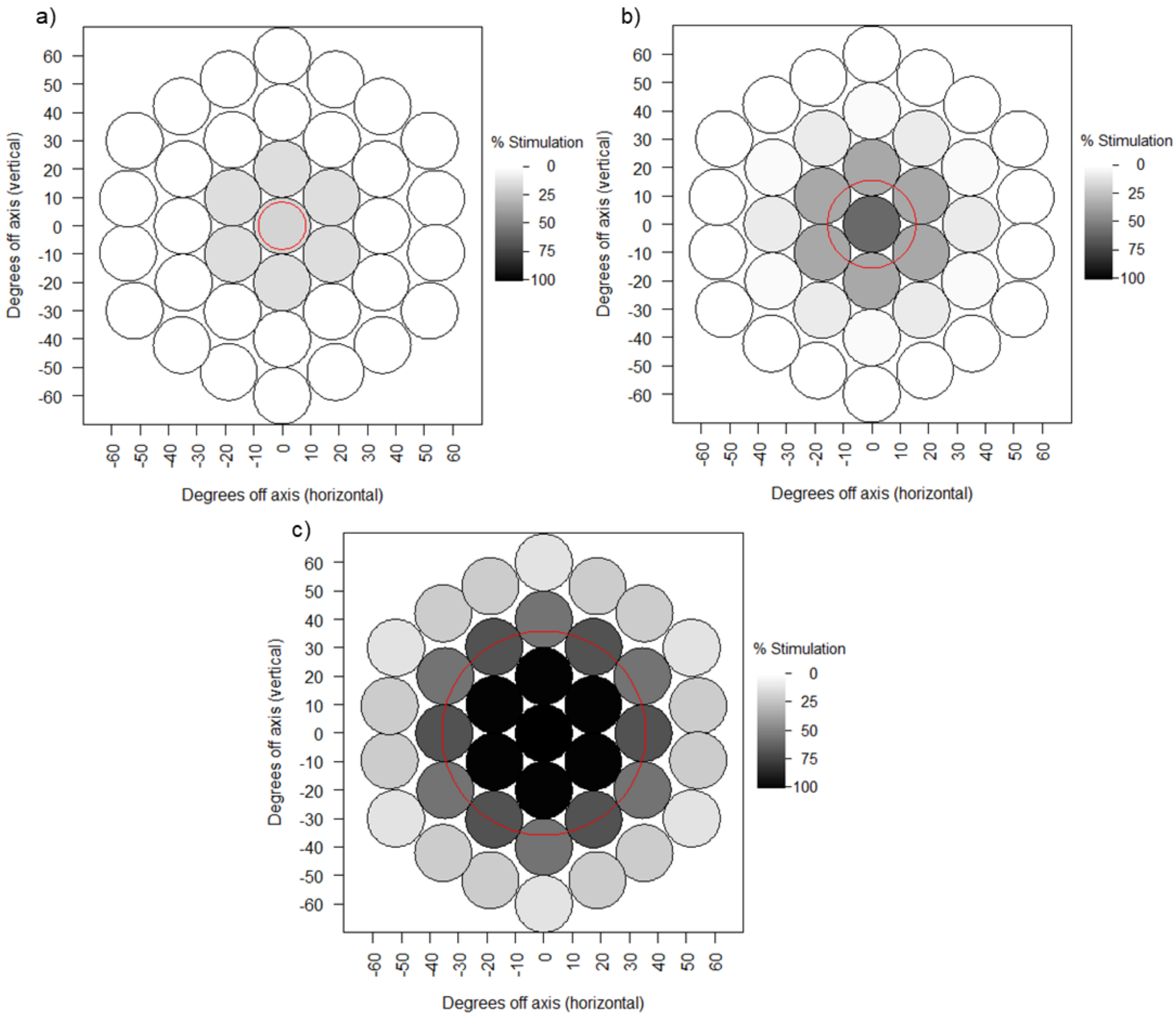


Fig.6. Model output of how an *Anopheles* mosquito sees a vertical target at different distances: a) 100 cm away, b) 50 cm away, c) 10 cm away. Model parameters were set as follows: Diameter 30 cm; Inter-ommatidial angle 8°; Receptive field 40°. Axis scales are in 10° units.

Model output for horizontal targets

The horizontal target is seen in perspective as an ellipse, and the extent of overlap is approximated from the intersection of polygons fitted to the circle and the ellipse. The model produces two charts, one shows how the target looks to the group of ommatidia it impinges on, and the second (a polar plot of the eye surface) shows how the image moves across the visual world as the insect flies over the target, i.e. which part of the eye is stimulated depending on the position of the insect with respect to the target. On the second chart, the red circles show the image a high-resolution eye would produce, whilst the red spider web lines are a polar plot of the eye surface (Fig. 7).

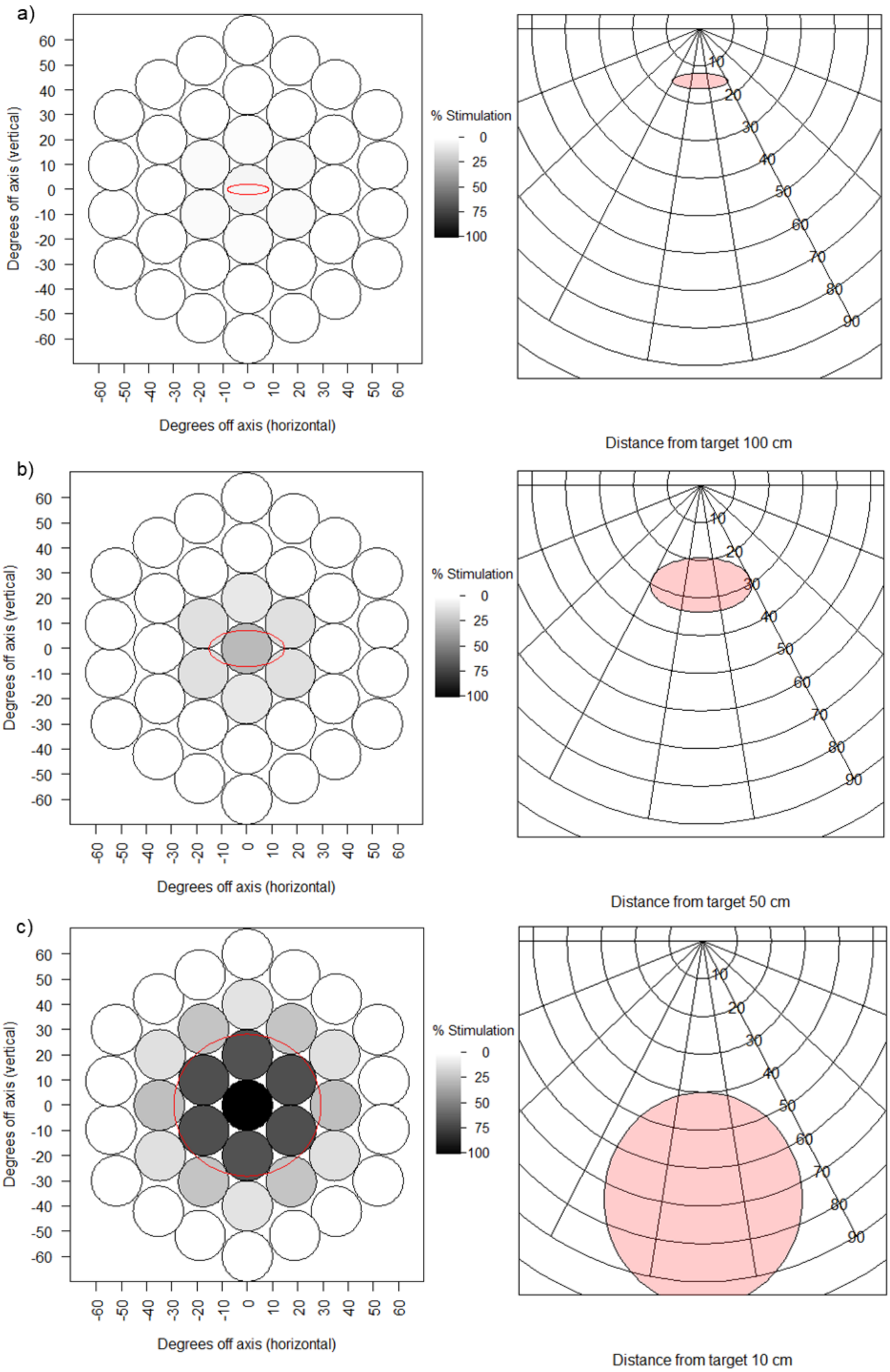


Fig. 7. Model output of how an *Anopheles* mosquito sees a horizontal target. The chart shows the portion and the level of stimulation of the 37 modelled ommatidia, whilst the right chart shows the position of the target

imaged on the eye and the dimension of the target resolved. Model parameters were set as follows: Target diameter 30 cm; Altitude 25 cm; Receptive field 40°; Inter-ommatidial angle 8°.

User manual of model

The model is written in R and requires the following files to work: the R script (Full_eye_model), the data file that contains the model instructions on the 37 ommatidia (eye_model_design_do_not_modify), and the file that contains all the parameters that can be modified ad hoc depending on specie-specific and target characteristics (parameters_to_modify). Note that these files must be in the same folder for the model to run, and whenever a parameter is modified the "parameters_to_modify.csv" file should be saved as CSV over the old file.

To run the model:

1) Open ommaparams.csv in Excel, insert your chosen parameter values, and Save as CSV file. Note: is important to note that the parameter "altitude" should be left blank in case of vertical targets (the insertion of the value zero would give false results).
2) Open R or RStudio and set the session working directory to the folder where all the model files are saved.
3) The script uses 3 packages (conicfit, gpclib and plotrix) – these will need to be installed on your computer: use Packages, Install Packages, then select a CRAN mirror site, and browse for these 3 packages. Once installed they remain available to R. This step only needs to be carried out once.
4) For R users: click on File, Open File, and select "Full_eye_model". For RStudio users: click on the double-click on the script file to open it directly.
5) Select all the script.
6) Run the script using this button  or the button "Run" in RStudio. This will produce the outcome chart(s).
7) Once the program has finished all the calculations it will also print on the Console an equation that the user can use to determine the maximum detection distance at which a target can be detected. Only once the equation is printed the program has finished running. Thus the user should wait until the equation is printed to consider the results of each run.

To copy the chart(s) we recommend right-clicking on the chart's window and the use the command "Copy as a bitmap". Copying the graph as a metafile could result in losing some parts of the graph.

Note that for some of the functions (i.e. for the part that determines the maximum detection distance for horizontal targets) the program might take a few minutes to perform the calculations, depending on the speed of the processor used.

Limitations and assumptions

The model bases its calculations on the following assumptions:

- Mosquito eyes are intended as perfect spheres, where each ommatidium is identical to all other ommatidia. No anatomical nor physiological imperfections are taken into account.
- The eye model has been designed for ommatidia with receptive field of at least 10°. Thus, this model is not suitable for diurnal species or species with high-resolution vision.
- All targets must be of circular shape.
- When the target is positioned vertically, the mosquito is assumed to approach the target at its centre. Thus, the flights height is assumed to be the radius of the target.

- For targets positioned horizontally, due to mathematical calculations in the model, the maximum detection distance is calculated accurately only for targets > 20 cm of diameter. For smaller targets, the program only approximates the detection distance. Thus, we recommend caution when interpreting detection distances results for small targets positioned horizontally. Note that this is not the case for vertical targets, as here the model accurately calculates detection distances even for small targets.

References

Land, M. F., Gibson, G. and Horwood, J. (1997) 'Mosquito eye design: Conical rhabdoms are matched to wide aperture lenses', *Proceedings of the Royal Society B: Biological Sciences*, 264(1385), pp. 1183–1187.