

**SUPPLEMENTARY INFORMATION: A GENERALISED RANDOM ENCOUNTER MODEL  
FOR ESTIMATING ANIMAL DENSITY WITH REMOTE SENSOR DATA**

S1. TABLE OF SYMBOLS

Symbol	Description	Units
$v$	Velocity	$\text{m s}^{-1}$
$\theta$	Angle of detection	Radians
$\alpha$	Animal call/beam width	Radians
$r$	Detection distance	Metres
$\bar{p}$	Average profile width	Metres
$p$	A specific profile width	Metres
$t$	Time	Seconds
$z$	Number of detections	
$D$	Animal density	animals $\text{m}^{-2}$
$x_i$	Focal Angle $i \in \{1, 2, 3, 4\}$	Radians
$T$	Step length	Seconds
$N$	Number of steps per simulation	
$d$	Time step index	

TABLE S1. List of symbols used to describe the gREM

## S2. SUPPLEMENTARY METHODS

**S2.1. Introduction.** This supplementary methods derives all the models used in the paper. For continuity, the gas model derivation is included here as well as in the main text. The derivation of all models is included in the Python script S2.

**S2.2. Gas model.** We assume that animals are in an homogeneous environment, and move in straight lines of random direction with velocity  $v$ . We allow that our sensor can detect animals at a distance  $r$  and that if an animal moves within this detection region they are detected with a probability of 1, independent of distance from the sensor while animals outside the region are never detected.

We then consider movement from the reference frame of the animals so that now, all animals are stationary and randomly distributed in space, while the sensor moves with velocity  $v$ . If we calculate the area covered by the sensor during the study period we can estimate the number of animals it should encounter. We calculate this as the average width of the sensor region  $p$  multiplied by  $v$ . The average width of the profile is the integral of the profile width over a full circle, divided by  $2\pi$ . We use  $x_i$  to denote the focal angle which is the angle we integrate over. The subscript  $i$  distinguishes different angles (see Figure S2) but here we use  $x_1$ . As all models are bilaterally symmetric, we can integrate over a half circle, and divide by  $\pi$ .

$$p_{\text{Gas}} = \frac{1}{\pi} \int_{\frac{\pi}{2}}^{\frac{3\pi}{2}} 2r \, dx_1 \quad \text{eqn S1}$$

$$p_{\text{Gas}} = 2r \quad \text{eqn S2}$$

The number of expected encounters,  $z$ , for a survey of duration  $t$ , with an animal density of  $D$  is then

$$z = 2rvtD. \quad \text{eqn S3}$$

However, in practice we have the opposite situation. We know the number of encounters and want to estimate the density. We do this by simply rearranging to get

$$D = z/(2rvt). \quad \text{eqn S4}$$

For different values of  $\theta$  and  $\alpha$ , the only thing that changes is that the area covered per unit time is no longer given by  $2rv$ . Instead of the sensor having a diameter of  $2r$ , the sensor has a complex diameter that changes with approach angle. The rest of the derivation is just calculating this value for all values of  $\alpha$  and  $\theta$ . However, different regions of this two dimensional parameter space have noncontinuously different models, with different derivations. Therefore we have to identify the regions for which the derivation is the same, and then separately derive  $p$  for each region. The separate regions are shown in Figure S1.

**S2.3. Model SE1.** SE1 is very similar to the gas model except that as  $\alpha \leq \pi$  the profile width is no longer  $2r$  but is instead limited by the width of the animal call. We therefore get a profile width of  $2r \sin(\alpha/2)$  instead (see Fig S3b).

$$p_{\text{SE1}} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}}^{\frac{3\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_1 \right) \quad \text{eqn S5}$$

$$p_{\text{SE1}} = 2r \sin\left(\frac{\alpha}{2}\right) \quad \text{eqn S6}$$

**S2.4. Model NE.** For regions with profiles that are more complex than a circle we need to explicitly write functions for the width of the profile for every approach angle. We then use these functions to find the average profile width for all approach angles by integrating across all  $2\pi$  angles of approach and dividing by  $2\pi$ .

There are three regions within cell NE. Note that NE1 covers the area  $\alpha = 2\pi$  as well as the triangle below it as these two models are specified exactly the same, rather than happening to have equal results.

These models have up to five regions. 1) The profile width starts, from  $x_1 = \frac{\pi}{2}$  as  $2r$ . 2) At  $x_1 = \theta/2$ , the right hand side of the profile cannot be  $r$  wide as the corner of the 'blind spot' (see Fig. S3a) limits its size to being  $r \cos(x_1 - \theta/2)$  wide (see Fig. S4a).

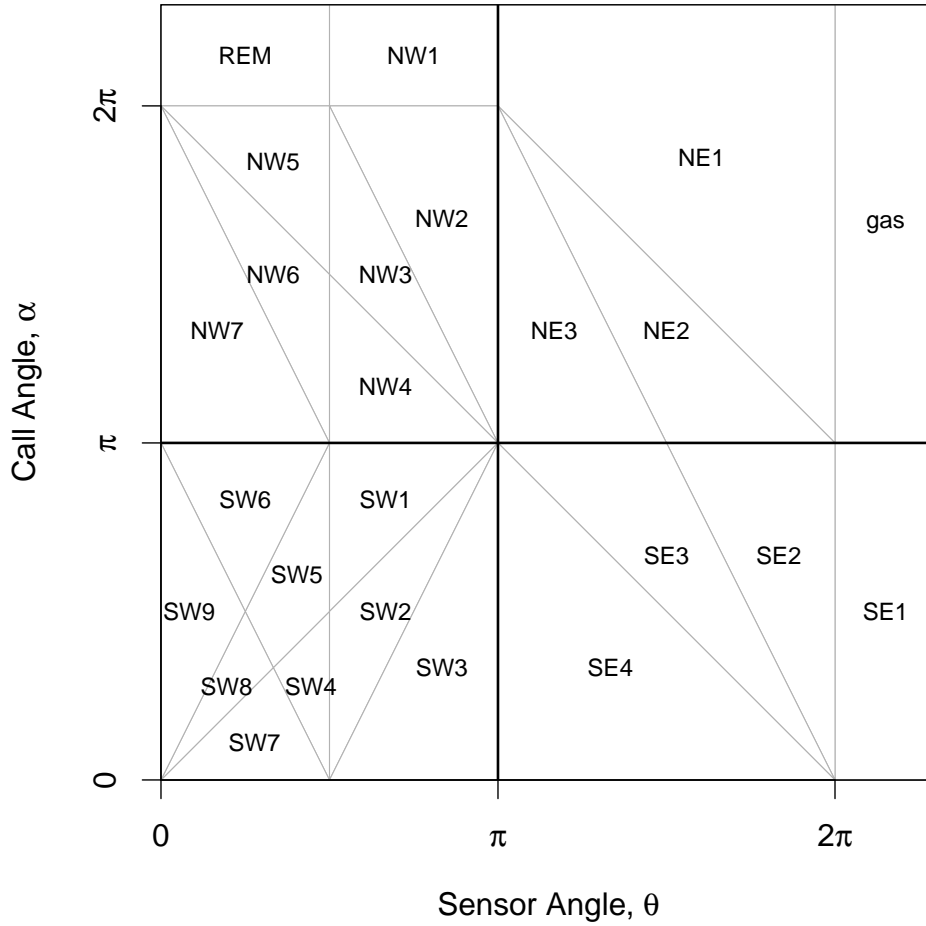


FIGURE S1. The location of each model in parameter space. Each named model must be derived separately. However, the results of the different models are often the same; areas coloured the same have the same result. Other than the gas model and the REM model, individual models are named after the compass point of the quadrant they are in. The region extends past  $\alpha, \theta = 2\pi$  to clearly display the models that are defined for only  $\alpha = 2\pi$  or  $\theta = 2\pi$  (e.g. the REM model is only defined for  $\alpha = 2\pi$ ).

3) The third profile is only found in NE3. If  $\alpha < 4\pi - 2\theta$ , then at  $x_1 = \theta/2$ , when the profile is perpendicular to the edge of the blind spot, the whole right side of the profile is invisible to the sensor (see Fig. S4b). This gives a profile size of just  $r$ .

4) At some point, the sensor can detect animals once they have passed the blind spot giving a profile width of  $r + r \cos(x_1 + \theta/2)$ . From  $x_1 = \pi$ , if the animal call is wide enough to be detected in this area, this is the wider profile. This then defines the split between NE1 and NE2. In NE1, with  $\alpha > 3\pi - \theta$ , the animal call is wide enough that at  $x_1 = \pi$  the animal can already be detected past the blind spot and so this profile is used. In NE2, with  $\alpha < 3\pi - \theta$ , the latter profile is reached at  $5\pi/2 - \theta/2 - \alpha/2$  and is therefore dependant on the sizes of  $\alpha$  and  $\theta$ .

5) Finally, common to all three models, at  $x_1 = 2\pi - \theta/2$  the profile becomes a full  $2r$  once again.

**S2.4.1. Model NE1.** Model NE1 exists within the area bounded by  $\alpha \leq 2\pi$ ,  $\theta \leq 2\pi$  and  $\alpha \geq 3\pi - \theta$ . It has four regions; it does not include the  $r$  profile at  $x_1 = \pi$ . Furthermore,  $\theta$  is wide enough that the  $r + r \cos(x_1 + \theta/2)$  profile starts at  $\pi$ . This then gives us

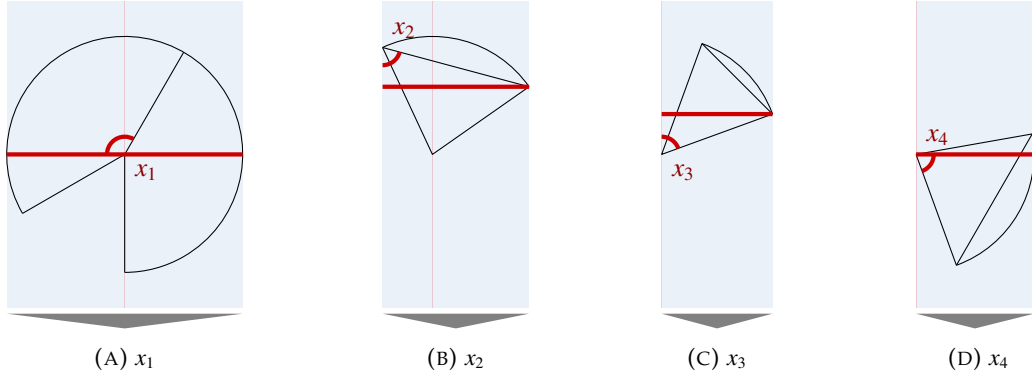


FIGURE S2. The location of the focal angles  $x_{i \in [1,4]}$ . In these figures, the segment shaped detection region is shown in black. The width of this region is shown with a thick red line and a blue rectangle. The direction of animal movement is always downwards, as indicated by the grey arrow.

$$\begin{aligned} \text{pNE1} = \frac{1}{\pi} & \left( \int_{\frac{\pi}{2}}^{\frac{\theta}{2}} 2r \, dx_1 + \int_{\frac{\theta}{2}}^{\pi} r + r \cos\left(-x_1 + \frac{\theta}{2}\right) dx_1 \right. \\ & \left. + \int_{\pi}^{2\pi - \frac{\theta}{2}} r + r \cos\left(x_1 + \frac{\theta}{2}\right) dx_1 + \int_{2\pi - \frac{\theta}{2}}^{\frac{3\pi}{2}} 2r \, dx_1 \right) \end{aligned} \quad \text{eqn S7}$$

$$\text{pNE1} = \frac{r}{\pi} \left( \theta + 2 \sin\left(\frac{\theta}{2}\right) \right) \quad \text{eqn S8}$$

S2.4.2. *Model NE2.* Model NE2 is bounded by  $\alpha \leq 3\pi - \theta$ ,  $\alpha \geq 4\pi - 2\theta$  and  $\alpha \geq \pi$ . It is the same as NE1 except that the third profile starts at  $5\pi/2 - \theta/2 - \alpha/2$  instead of at  $\pi$  which is reflected in the different bounds in the second and third integral.

$$\begin{aligned} \text{pNE2} = \frac{1}{\pi} & \left( \int_{\frac{\pi}{2}}^{\frac{\theta}{2}} 2r \, dx_1 + \int_{\frac{\theta}{2}}^{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}} r + r \cos\left(-x_1 + \frac{\theta}{2}\right) dx_1 \right. \\ & \left. + \int_{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}}^{2\pi - \frac{\theta}{2}} r + r \cos\left(x_1 + \frac{\theta}{2}\right) dx_1 + \int_{2\pi - \frac{\theta}{2}}^{\frac{3\pi}{2}} 2r \, dx_1 \right) \end{aligned} \quad \text{eqn S9}$$

$$\text{pNE2} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + \cos\left(\frac{\alpha}{2} + \theta\right) \right) \quad \text{eqn S10}$$

S2.4.3. *Model NE3.* Model NE3 is bound by  $\alpha \leq 4\pi - 2\theta$ ,  $\alpha \geq \pi$  and  $\theta \geq \pi$ . It is the same as NE2 except that it contains the extra profile with width  $r$  (third integral).

$$\begin{aligned} \text{pNE3} = \frac{1}{\pi} & \left( \int_{\frac{\pi}{2}}^{\frac{\theta}{2}} 2r \, dx_1 + \int_{\frac{\theta}{2}}^{\frac{\pi}{2} + \frac{\theta}{2}} r + r \cos\left(-x_1 + \frac{\theta}{2}\right) dx_1 \right. \\ & \left. + \int_{\frac{\pi}{2} + \frac{\theta}{2}}^{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}} r \, dx_1 + \int_{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}}^{2\pi - \frac{\theta}{2}} r + r \cos\left(x_1 + \frac{\theta}{2}\right) dx_1 + \int_{2\pi - \frac{\theta}{2}}^{\frac{3\pi}{2}} 2r \, dx_1 \right) \end{aligned} \quad \text{eqn S11}$$

$$\text{pNE3} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S12}$$

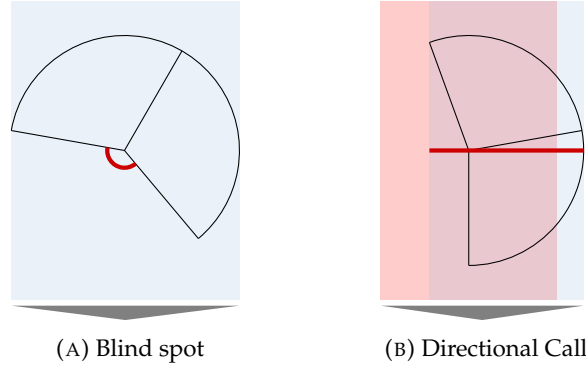


FIGURE S3. A) Shows the area referred to as the ‘blind spot’. B) For directional calls, with  $\alpha < \pi$ , the width of the profile can be limited by the call angle or by the detector region. The detector width is shown in blue, while the call width is shown as a red rectangle. Only where the two overlap, giving a purple area, can an animal be detected. Here we would say the right side of the profile is limited by the sensor, while the left side of the profile is limited by the call angle. The terms in equations would reflect this by containing  $\alpha$  if call limited and containing  $\theta$  if detector limited.

**S2.5. Model p32.** Cell p32 contains three regions that differ in ways reminiscent of the models in NE. There are four possible profile widths. 1) As  $\alpha$  is less than  $\pi$  the profile is smaller than  $2r$ , even when the sensor width is a full diameter. When this is the case, the profile width is instead  $2r \sin(\alpha/2)$ . 2) Similar to NE, at a certain point the blind spot of the sensor area limits the profile width (see Fig. S5a). This gives a profile width of  $r \sin(\alpha/2) + r \cos(x_1 - \theta/2)$ . 3) Also similar to NE, there can be a point where the right side of the profile is 0 giving a profile width of  $r \sin(\alpha/2)$ . 4) If  $\alpha \leq 2\pi - \theta$ , then at  $\theta/2 + \pi/2 + \alpha/2$  the profile width become 0 (see Fig. S5b). This inequality distinguishes between SE3 and SE4. The profile  $r \sin(\alpha/2)$  starts at  $\theta/2 + \pi/2$  while at  $5\pi/2 - \alpha/2 - \theta/2$  the profile returns to size  $2r \sin(\alpha/2)$ . If  $\theta/2 + \pi/2 \geq 5\pi/2 - \alpha/2 - \theta/2$  we go straight into the  $2r \sin(\alpha/2)$  profile and miss the  $r \sin(\alpha/2)$  profile. SE2 and SE3 are separated by this inequality which simplifies to  $\alpha \leq 4\pi - 2\theta$ .

**S2.5.1. Model SE2.** SE2 is bounded by  $\alpha \geq 4\pi - 2\theta$ ,  $\alpha \leq \pi$  and  $\theta \leq 2\pi$ . As  $\alpha \geq 4\pi - 2\theta$ , there is no  $r \sin(\alpha/2)$  profile. As  $\alpha \leq 4\pi - 2\theta$ , the profile returns to  $2r \sin(\alpha/2)$  rather than going to 0.

$$p_{SE2} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_1 + \int_{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}} r \cos\left(-x_1 + \frac{\theta}{2}\right) + r \sin\left(\frac{\alpha}{2}\right) dx_1 + \int_{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{3\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_1 \right) \quad \text{eqn S13}$$

$$p_{SE2} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + \cos\left(\frac{\alpha}{2} + \theta\right) \right) \quad \text{eqn S14}$$

**S2.5.2. Model SE3.** SE3 is bounded by  $4\pi - 2\theta \leq \alpha \leq 4\pi - 2\theta$  and  $\alpha \leq \pi$ . Therefore there is a  $r \sin(\alpha/2)$  profile but no 0r profile.

$$p_{SE3} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_1 + \int_{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{\pi}{2} + \frac{\theta}{2}} r \cos\left(-x_1 + \frac{\theta}{2}\right) + r \sin\left(\frac{\alpha}{2}\right) dx_1 + \int_{\frac{\pi}{2} + \frac{\theta}{2}}^{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_1 + \int_{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{3\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_1 \right) \quad \text{eqn S15}$$

$$p_{SE3} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S16}$$

**S2.5.3. Model SE4.** Finally SE4 is bounded by  $\alpha \leq 4\pi - 2\theta$ ,  $\alpha \leq \pi$  and  $\theta \leq \pi$ . It is the same as SE3 except that the profile becomes  $2r$  rather than returning to  $2r \sin(\alpha/2)$ .

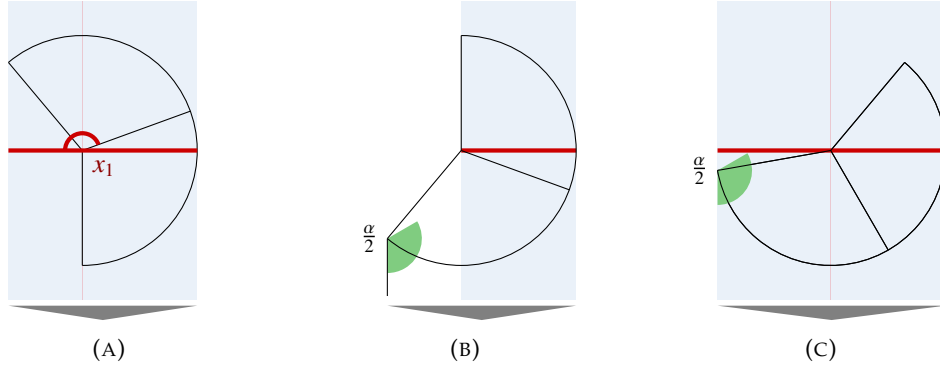


FIGURE S4. A) The second integral in NE with width  $r + r \cos(x_1 - \theta/2)$  B) The third integral in NE3. The angle shown in red is  $\alpha/2$ . As it is small, animals to the right of the detector cannot be detected. C) After further rotation,  $\alpha/2$  is now bigger than the angle shown and animals to the right of the detector can again be sensed.

$$pSE4 = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_1 + \int_{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{\pi}{2} + \frac{\theta}{2}} r \cos\left(-x_1 + \frac{\theta}{2}\right) + r \sin\left(\frac{\alpha}{2}\right) dx_1 + \int_{\frac{\pi}{2} + \frac{\theta}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} + \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_1 \right) \quad \text{eqn S17}$$

$$pSE4 = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S18}$$

**S2.6. Model NW1.** NW1 is the first model with  $\theta < \pi$ . Whereas previously the focal angle has always been  $x_1$ , we now use different focal angles.  $x_2$  and  $x_3$  correspond to  $\gamma_1$  and  $\gamma_2$  in Rowcliffe *et al.* (2008) while  $x_4$  is new. They are described in Fig. S2.

There are five different profiles in NW1. 1)  $x_2$  has an interval of  $[\pi/2, \theta/2]$  which is from the angle of approach being directly towards the sensor until the profile is parallel to the left hand radius of the sensor segment. During this region the profile width is  $2r \sin(\theta/2) \sin(x_2)$  which is calculated using the equation for the length of a chord (see Fig. S2b). Note that while rotating anti-clockwise (as usual)  $x_2$  decreases in size. 2) From here, we examine focal angle  $x_4$  (note that  $x_3$  is used in later models, but is not relevant here.) The left side of the profile is a full radius while the right side is limited to  $-r \cos(x_4 - \theta)$  (see Fig. S6a). 3) At  $x_4 = \theta - \pi/2$ , the profile is perpendicular to the edge of the sensor area. Here, the right side of the profile is  $0r$ . 4) When  $x_4 = \pi/2$  the angle of approach is from behind the sensor, but we can once again be detected on the right side of the sensor (see Fig. S6b). Therefore the width of the profile is  $r - r \cos(x_4)$ . 5) Finally, we enter the  $x_2$  region, but from behind.

$$pNW1 = \frac{1}{\pi} \left( \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_0^{-\frac{\pi}{2} + \theta} r - r \cos(-x_4 + \theta) dx_4 + \int_{-\frac{\pi}{2} + \theta}^{\frac{\pi}{2}} r dx_4 + \int_{\frac{\pi}{2}}^{\theta} r - r \cos(x_4) dx_4 + \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 \right) \quad \text{eqn S19}$$

$$pNW1 = \frac{r}{\pi} (\theta + 2) \quad \text{eqn S20}$$

**S2.7. Model NW2–4.** The models in cell NW2–4 have the five potential profiles in NW1 but not all profiles occur in each model, and the angle at which transitions occur are different. Furthermore, there is one extra profile possible. When approaching the sensor from behind, there is a period where the profile is  $r$  wide as in NW1. At some point the right side of the profile becomes viable again. If this occurs in the  $x_4$  region, the profile width becomes  $r - r \cos(x_4)$  as in NW1. However, as  $\alpha$  is now less than  $2\pi$ , the right side of the profile might not be viable until we are in the second  $x_2$  region. In this case, when we first enter the second  $x_2$  region, the profile has a width of  $r \cos(x_2 - \theta/2)$ . This occurs only if  $\alpha \leq 3\pi - 2\theta$ . This inequality is found by noting that the right side of the profile become viable at  $x_4 = 3\pi/2 - \alpha$  but the  $x_2$  region starts at  $x_4 = \theta$ . The new profile in  $x_2$  will only

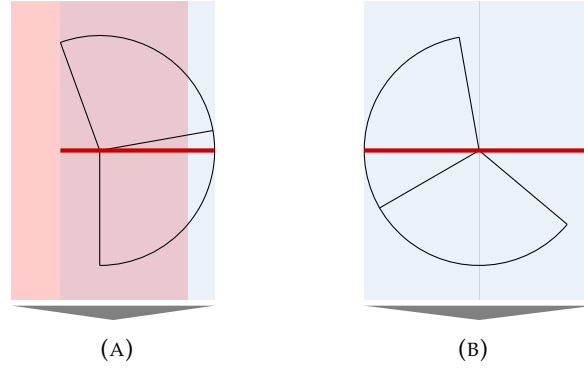


FIGURE S5. A) The third integral in p32. The right side of the profile is limited by the size of the sensor region (blue region) while the left side of the profile is limited by the size of the call angle (red region). The profile width is the purple region where these two overlap. B)

occur if  $\theta < 3\pi/2 - \alpha/2$  which is rearranged to find the inequality above. This defines the boundary between NW2 and NW3.

As  $\alpha \leq 2\pi$  it is possible that when the angle of approach is from directly behind the sensor the animal will not be detected at all. This is the case if  $\alpha/2 \leq \pi - \theta/2$  as shown in Fig. S7a. This inequality defines the boundary between NW3 and NW4.

S2.7.1. *Model NW2.* NW2 is bounded by  $\alpha \geq 3\pi - 2\theta$ ,  $\alpha \leq 2\pi$  and  $\theta \leq \pi$ .

NW2 has all five profiles as found in NW1. However, the change from the  $r$  profile (third integral) to the  $r - r \cos(x_4)$  profile (fourth integral) occurs at  $x_4 = 3\pi/2 - \alpha/2$  instead of at  $x_4 = \theta$ .

$$\text{pNW2} = \frac{1}{\pi} \left( \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_0^{-\frac{\pi}{2}+\theta} r - r \cos(-x_4 + \theta) dx_4 \right. \\ \left. + \int_{-\frac{\pi}{2}+\theta}^{\frac{3\pi}{2}-\frac{\alpha}{2}} r dx_4 + \int_{\frac{3\pi}{2}-\frac{\alpha}{2}}^{\theta} r - r \cos(x_4) dx_4 + \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 \right) \quad \text{eqn S21}$$

$$\text{pNW2} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S22}$$

S2.7.2. *Model NW3.* NW3 is bounded by  $\alpha \leq 3\pi - 2\theta$ ,  $\alpha \geq 2\pi - \theta$  and  $\theta \leq \pi$ .

NW3 does not have the fourth integral from NW2 as the right side of the profile does not become viable until after the  $x_4$  region has ended and the  $x_2$  region has begun. Therefore the second  $x_4$  integral has an upper limit of  $\theta$  and the integral after has a width of  $r \cos(x_2 - \theta/2)$  and is integrated with respect to  $x_2$ . The final integral starts at  $x_4 = 3\pi/2 - \alpha/2 - \theta/2$  and has the full width of  $2r \sin(x_2) \sin(\theta/2)$ .

$$\text{pNW3} = \frac{1}{\pi} \left( \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_0^{-\frac{\pi}{2}+\theta} r - r \cos(-x_4 + \theta) dx_4 \right. \\ \left. + \int_{-\frac{\pi}{2}+\theta}^{\theta} r dx_4 + \int_{\frac{\theta}{2}}^{\frac{3\pi}{2}-\frac{\theta}{2}-\frac{\alpha}{2}} r \cos\left(-x_2 + \frac{\theta}{2}\right) dx_2 + \int_{\frac{3\pi}{2}-\frac{\theta}{2}-\frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 \right) \quad \text{eqn S23}$$

$$\text{pNW3} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S24}$$

S2.7.3. *Model NW4.* Finally, NW4 is bounded by  $\alpha \leq \pi$ ,  $\theta \geq \pi/2$  and  $\alpha \leq 3\pi - 2\theta$ . NW4 is the same as NW3 except that the final profile width is zero and this profile is reached at  $\alpha/2 + \theta/2 - \pi/2$ .

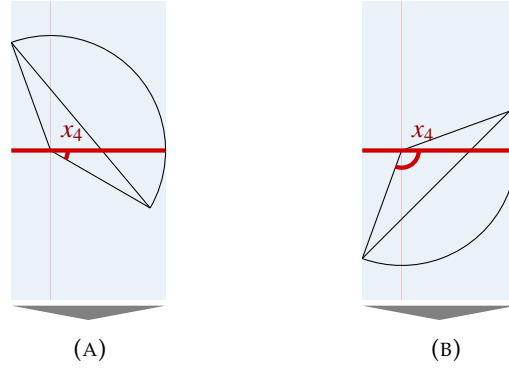


FIGURE S6. A) and B) The third and fourth profiles of NW1. The left side of both profiles is of width  $r$  while the right side is  $-r \cos(x_4 - \theta)$  and  $-r \cos(x_4)$  respectively.

$$\begin{aligned} \text{pNW4} = \frac{1}{\pi} & \left( \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_0^{-\frac{\pi}{2}+\theta} r - r \cos(-x_4 + \theta) dx_4 \right. \\ & \left. + \int_{-\frac{\pi}{2}+\theta}^{\theta} r dx_4 + \int_{\frac{\theta}{2}}^{-\frac{\pi}{2}+\frac{\theta}{2}+\frac{\alpha}{2}} r \cos\left(-x_2 + \frac{\theta}{2}\right) dx_2 \right) \end{aligned} \quad \text{eqn S25}$$

$$\text{pNW4} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S26}$$

**S2.8. Model p33.** The models in p33 are described with the two focal angles used in models NW2–4,  $x_2$  and  $x_4$ . As  $\alpha \leq \pi$  an animal can never be detected if it is approaching the detector from behind. This makes these models simpler in that they go through the  $x_2$  and  $x_4$  eons only once each.

There are five potential profile sizes. At the beginning of  $x_2$ , with an approach direction directly towards the sensor, the factor that limits the width of the profile can either be 1) the sensor width, in which case the profile width is  $2r \sin(\theta/2) \sin(x_2)$ , or 2) the call width, in which case the profile width is instead  $2r \sin(\alpha/2)$  (see Figure S8)

3) The next potential profile in  $x_2$  has a width of  $r \sin(\alpha/2) - r \cos(x_2 + \theta/2)$  as the right side of the profile is limited by the width of the sensor region while the left side is limited by the call width. However, the angle at which the profile starts depends on whether the first profile was 1) or 2) above. If the first profile is profile 1) then the profile is limited on both sides by the sensor region and then the left side of the profile becomes limited by the call width. This happens at  $x_2 = \pi/2 - \alpha/2 + \theta/2$ . If however the first profile was 2) then the first profile is limited by the call width. We move into the new profile when the right side of the profile becomes limited by the sensor region. This occurs at  $x_2 = \pi/2 + \alpha/2 - \theta/2$ .

In the  $x_4$  region the left side of the profile is always  $r \sin(\alpha/2)$  while the right side is either 4) 0, giving a profile of  $r \sin(\alpha/2)$ , or 5) limited by the sensor giving a profile of size  $r \sin(\alpha/2) - r \cos(x_4 - \theta)$ .

**S2.8.1. Model SW1.** SW1 is bounded by  $\alpha \geq \theta$ ,  $\alpha \leq \pi$  and  $\theta \leq \pi$ .

As  $\alpha$  is large the first profile is limited by the size of the sensor region giving it a width of  $2r \sin(\theta/2) \sin(x_2)$ . It is the only one of the three p33 models to start in this way. Later on, still with  $x_2$  as the focal angle the left side of the profile does become limited by the call width. So at  $x_2 = \pi/2 - \alpha/2 + \theta/2$  the profile width becomes  $r \sin(\alpha/2) - r \cos(x_2 + \theta/2)$ .

As we enter the  $x_4$  region, the profile remains limited by the call on the left and by the sensor on the right, giving a profile width of  $r \sin(\alpha/2) - r \cos(x_4 - \theta)$ . Finally, at  $x_4 = \theta - \pi/2$  the right side of the profile becomes zero and the profile is width is  $r \sin(\alpha/2)$ .



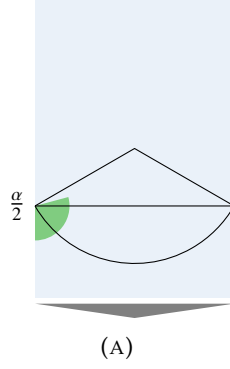


FIGURE S7. A) If  $\alpha/2$ , shown in green, is less than  $\pi - \theta/2$ , as is the case here, then the width of the profile when an animal approaches directly from behind is zero.

$$\begin{aligned} \text{pSW1} = \frac{1}{\pi} & \left( \int_{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\frac{\theta}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}} -r \cos\left(x_2 + \frac{\theta}{2}\right) + r \sin\left(\frac{\alpha}{2}\right) dx_2 \right. \\ & \left. + \int_0^{-\frac{\pi}{2} + \theta} -r \cos(-x_4 + \theta) + r \sin\left(\frac{\alpha}{2}\right) dx_4 + \int_{-\frac{\pi}{2} + \theta}^{-\frac{\pi}{2} + \theta + \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \end{aligned} \quad \text{eqn S27}$$

$$\text{pSW1} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S28}$$

S2.8.2. *Model SW2.* SW2 is bounded by  $\theta \geq \pi/2$ ,  $\alpha \leq \theta$  and  $\alpha \geq 2\theta - \pi$ .

SW2 is largely similar to SW1. However, as  $\alpha \leq \theta$  the first profile is limited by  $\alpha$  and not by the detection region. Therefore the first profile has width  $2r \sin(\alpha/2)$ . This also means the transition to the second profile occurs at  $x_2 = \pi/2 + \alpha/2 - \theta/2$  instead of  $x_2 = \pi/2 - \alpha/2 + \theta/2$ .

$$\begin{aligned} \text{pSW2} = \frac{1}{\pi} & \left( \int_{\frac{\pi}{2} - \frac{\theta}{2} + \frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_2 + \int_{\frac{\theta}{2}}^{\frac{\pi}{2} - \frac{\theta}{2} + \frac{\alpha}{2}} -r \cos\left(x_2 + \frac{\theta}{2}\right) + r \sin\left(\frac{\alpha}{2}\right) dx_2 \right. \\ & \left. + \int_0^{-\frac{\pi}{2} + \theta} -r \cos(-x_4 + \theta) + r \sin\left(\frac{\alpha}{2}\right) dx_4 + \int_{-\frac{\pi}{2} + \theta}^{-\frac{\pi}{2} + \theta + \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \end{aligned} \quad \text{eqn S29}$$

$$\text{pSW2} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S30}$$

S2.8.3. *Model SW3.* SW3 is bounded by  $\alpha \leq 2\theta - \pi$  and  $\theta \leq \pi$ .

SW3 is similar to SW2 except that the profile does not become limited by sensor at all during the  $x_4$  regions. Therefore, at  $x_4 = 0$  the profile is still of width  $2r \sin(\alpha/2)$ . Only at  $x_4 = \theta - \pi/2 - \alpha/2$  does the profile become limited on the right by the sensor region.

$$\begin{aligned} \text{pSW3} = \frac{1}{\pi} & \left( \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_2 + \int_0^{-\frac{\pi}{2} + \theta - \frac{\alpha}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_4 \right. \\ & \left. + \int_{-\frac{\pi}{2} + \theta - \frac{\alpha}{2}}^{-\frac{\pi}{2} + \theta} -r \cos(-x_4 + \theta) + r \sin\left(\frac{\alpha}{2}\right) dx_4 + \int_{-\frac{\pi}{2} + \theta}^{-\frac{\pi}{2} + \theta + \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \end{aligned} \quad \text{eqn S31}$$

$$\text{pSW3} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S32}$$

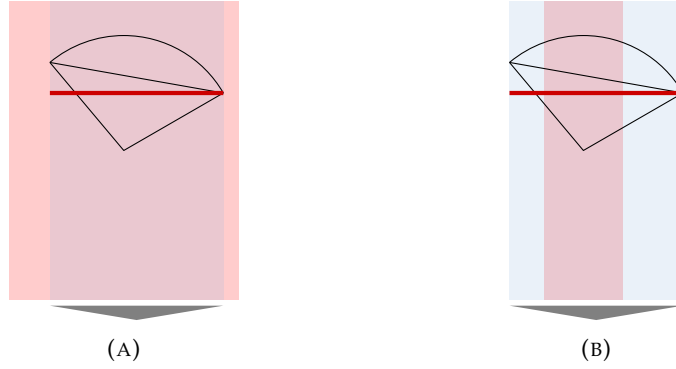


FIGURE S8. A) As  $\alpha > \theta$  the profile width (purple) is limited by the sensor region, not the call angle (red). The profile width is  $2r \sin\left(\frac{\theta}{2}\right) \sin(x_2)$ . B) As  $\alpha < \theta$  the profile width is limited by the call angle rather than the sensor region (blue). The profile width is  $2r \sin\left(\frac{\alpha}{2}\right)$

**S2.9. Model REM.** REM is the model from (Rowcliffe *et al.*, 2008). It has  $\alpha = 2\pi$  and  $\theta \leq \pi/2$ . It has three profile widths, two of which are repeated, once as the animal approaches from on front of the sensor and once as the animal approaches from behind the sensor.

Starting with an approach direction of directly towards the sensor, and examining focal angle  $x_2$ , the profile width is  $2r \sin(x_2) \sin(\theta/2)$ . When the profile is perpendicular to the radius edge of the segment sensor region, we instead examine  $x_3$  where the profile width is  $r \sin(x_3)$ . At  $x_3 = \pi/2$  the profile becomes simply  $r$  and this continues for  $\theta$  radians of  $x_4$ . Finally the  $x_3$  and  $x_2$  are repeated with an approach direction from behind the sensor.

$$\text{pREM} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) dx_3 + \int_0^{\theta} r dx_4 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) dx_3 + \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 \right) \quad \text{eqn S33}$$

$$\text{pREM} = \frac{r}{\pi} (\theta + 2) \quad \text{eqn S34}$$

**S2.10. Model NW5–7.** In the models in NW5–7, the sensor has  $\theta \leq \pi/2$  as in REM. As  $\alpha \geq \pi/2$  a lot of the profiles are similar to REM. Specifically, the first three profiles are always the same as the first three profiles of REM. This is because when an animal is moving towards the sensor, the  $\alpha \geq \pi$  call is no different to a  $2\pi$  call. However, when approaching the sensor from behind, things are slightly different. The animal can only be detected by the sensor if it's call is wide enough that it can be detected once it has passed the sensor.

The second  $x_3$  profile is always the same width as in REM. This is because there is no detection region to one side of the sensor so this side is unaffected by call width, while the width of the other side of the profile is unaffected by  $\alpha$  as when  $\alpha > \pi$  the profile width will never be limited by  $\alpha$ . If  $\alpha \leq 2\pi + 2\theta$ , the animal becomes undetectable during this profile when  $x_3$  has decreased in size to  $\pi - \alpha/2$ . This inequality marks the boundary between NW7 and NW6.

As the focal angle moves from  $x_3$  to  $x_2$  at  $x_3 = \theta$ , we can see that if  $\alpha \geq 2\pi + 2\theta$ , then the  $x_2$  region is reached before the animal become undetectable. When this second  $x_2$  region is reached, the profile starts with width  $r \cos(x_2 - \theta/2)$  as at the beginning of the  $x_2$  profile as only animals approaching to the left of the sensor are detectable. The sensor is directly behind the right side of the profile.

During this second  $x_2$  profile the call angle needed for animals to be detected to the left of the detector is increasing while the angle needed for animals to be detected to the right of the detector is decreasing. Therefore, either the left side becomes undetectable, making both sides undetectable (this occurs if  $\alpha \leq 2\pi - \theta$  as in NW6) or the right becomes detectable (if  $\alpha \geq 2\pi - \theta$  as in NW5), making both sides detectable and giving a profile width of  $2r \sin(x_2) \sin(\theta/2)$ .

**S2.10.1. Model NW5.** NW5 is bounded by  $\alpha \geq 2\pi - \theta$ ,  $\alpha \leq 2\pi$  and  $\theta \leq \pi/2$ .

It is the same as REM except that it includes the extra profile in  $x_2$  (the fifth integral) where only animals approaching to the left of the profile are detected.

$$\begin{aligned} \text{pNW5} = \frac{1}{\pi} & \left( \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) \, dx_2 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) \, dx_3 + \int_0^{\theta} r \, dx_4 \right. \\ & \left. + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) \, dx_3 + \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{3\pi}{2}-\frac{\theta}{2}-\frac{\alpha}{2}} r \cos\left(-x_2 + \frac{\theta}{2}\right) \, dx_2 + \int_{\frac{3\pi}{2}-\frac{\theta}{2}-\frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) \, dx_2 \right) \end{aligned} \quad \text{eqn S35}$$

$$\text{pNW5} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S36}$$

S2.10.2. *Model NW6.* NW6 is bounded by  $\alpha \leq 2\pi - \theta$ ,  $\alpha \geq 2\pi + 2\theta$  and  $\theta \leq \pi/2$

NW6 is the same NW5 except that as  $\alpha \leq 2\pi - \theta$ , animals that approach from directly behind the detector are not detected. Therefore at  $x_2 = \alpha/2 + \theta/2 - \pi/2$  the profile width goes to zero and therefore the last integral in NW5 is not included.

$$\begin{aligned} \text{pNW6} = \frac{1}{\pi} & \left( \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) \, dx_2 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) \, dx_3 \right. \\ & \left. + \int_0^{\theta} r \, dx_4 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) \, dx_3 + \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{-\frac{\pi}{2}+\frac{\theta}{2}+\frac{\alpha}{2}} r \cos\left(-x_2 + \frac{\theta}{2}\right) \, dx_2 \right) \end{aligned} \quad \text{eqn S37}$$

$$\text{pNW6} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S38}$$

S2.10.3. *Model NW7.* NW7 is bounded by  $\alpha \geq 2\pi + 2\theta$ ,  $\alpha \geq \pi$  and  $\theta \geq 0$ .

It is similar to NW6 but does not include the last integral as during the  $x_3$  profile, at  $x_3 = \pi - \alpha/2$  the call width is too small for any animals to be detected, so the profile width goes to zero.

$$\begin{aligned} \text{pNW7} = \frac{1}{\pi} & \left( \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) \, dx_2 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) \, dx_3 \right. \\ & \left. + \int_0^{\theta} r \, dx_4 + \int_{\pi-\frac{\alpha}{2}}^{\frac{\pi}{2}} r \sin(x_3) \, dx_3 \right) \end{aligned} \quad \text{eqn S39}$$

$$\text{pNW7} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S40}$$

S2.11. **Model SW4–9.** Cell SW4–9 is split into six models rather than three like most of the other cells. As  $\alpha < \pi$ , animals approaching the sensor from behind can never be detected, so unlike REM, the second  $x_2$  and  $x_3$  profiles are always zero. The six models are split by three inequalities that relate to the models as follows.

Models with  $\alpha \leq \pi - 2\theta$  have no  $x_4$  profile. This is because at  $x_4 = 0$ , the call angle is already too small to be detected as can be seen in Figure S9a where  $\alpha/2 < \pi/2 - \theta$  which simplifies to give the previous inequality.

Models with  $\alpha \leq \theta$  are limited by  $\alpha$  in the first,  $x_2$  region (see Figure S8), rather than being limited by  $\theta$ . Therefore this first profile is of width  $2r \sin(\alpha/2)$  rather than  $2r \sin(\theta/2) \sin(x_2)$ .

Finally, models with  $\alpha \leq 2\theta$  have a second profile in  $x_2$  where to one side of the sensor  $\alpha$  is the limiting factor of profile width, while on the other side  $\theta$  is (see Figure S9b). This gives a width of  $r \sin(\alpha/2) - r \cos(x_2 + \theta/2)$ . This profile does not occur in models with  $\alpha \geq 2\theta$ .

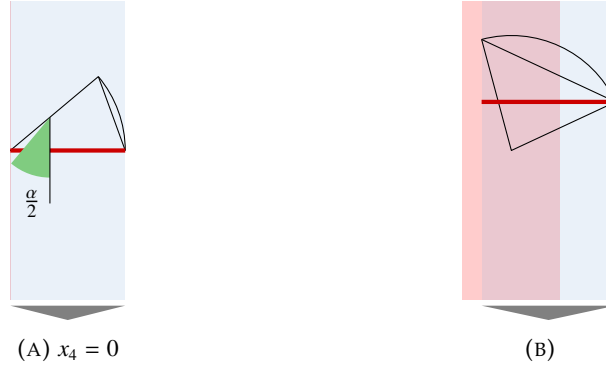


FIGURE S9. A) At  $x_4 = 0$ , if  $\alpha < \pi - 2\theta$  then  $\alpha/2$  is too small for an animal to be detected at all during the  $x_4$  profile. B) The left of the profile is limited by the call width, not the sensor (blue). On the right, the profile is limited by the sensor and not the call (red). Overall the profile width is  $r \sin(\alpha/2) - r \cos(x_2 + \theta/2)$ .

S2.11.1. *Model SW4*. SW4 is bounded by  $\alpha \leq \theta$ ,  $\alpha \geq \pi - 2\theta$  and  $\theta \leq \pi/2$ . Therefore it does contain a  $x_4$  profile, starts with an  $\alpha$  limited profile and does contain the  $r \sin(\alpha/2) - r \cos(x_2 + \theta/2)$  profile in  $x_2$ .

$$\begin{aligned} \text{pSW4} = \frac{1}{\pi} & \left( \int_{\frac{\pi}{2} - \frac{\theta}{2} + \frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_2 + \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\pi}{2} - \frac{\theta}{2} + \frac{\alpha}{2}} -r \cos\left(x_2 + \frac{\theta}{2}\right) + r \sin\left(\frac{\alpha}{2}\right) dx_2 \right. \\ & \left. + \int_{\theta}^{\frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_3 + \int_0^{-\frac{\pi}{2} + \theta + \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \end{aligned} \quad \text{eqn S41}$$

$$\text{pSW4} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S42}$$

S2.11.2. *Model SW5*. SW5 is the only model with a tetrahedral bounding region. It is bounded by  $\alpha \geq \theta$ ,  $\alpha \geq \pi - 2\theta$ ,  $\alpha \leq 2\theta$  and  $\theta \leq \pi/2$ . Therefore it does contain a  $x_4$  profile, but starts with a  $\theta$  limited profile. It does contain the  $r \sin(\alpha/2) - r \cos(x_2 + \theta/2)$  profile in  $x_2$ .

$$\begin{aligned} \text{pSW5} = \frac{1}{\pi} & \left( \int_{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}} -r \cos\left(x_2 + \frac{\theta}{2}\right) + r \sin\left(\frac{\alpha}{2}\right) dx_2 \right. \\ & \left. + \int_{\theta}^{\frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_3 + \int_0^{-\frac{\pi}{2} + \theta + \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \end{aligned} \quad \text{eqn S43}$$

$$\text{pSW5} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S44}$$

S2.11.3. *Model SW6*. SW6 is bounded by  $\alpha \geq \pi - 2\theta$ ,  $\alpha \geq 2\theta$  and  $\alpha \leq \pi$ . It starts with a  $\theta$  limited profile and has a  $x_4$  profile. However, it does not contain the  $r \sin(\alpha/2) - r \cos(x_2 + \theta/2)$  profile.

$$\begin{aligned} \text{pSW6} = \frac{1}{\pi} & \left( \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) dx_3 \right. \\ & \left. + \int_{\frac{\alpha}{2}}^{\frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_3 + \int_0^{-\frac{\pi}{2} + \theta + \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \end{aligned} \quad \text{eqn S45}$$

$$\text{pSW6} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S46}$$

S2.11.4. *Model SW7.* SW7 is bounded by  $\alpha \leq \pi - 2\theta$ ,  $\alpha \leq \theta$  and  $\alpha < 0$ . Therefore it does not contain a  $x_4$  profile. It starts with an  $\alpha$  limited profile and contains the  $r \sin(\alpha/2) - r \cos(x_2 + \theta/2)$  profile in  $x_2$ .

$$pSW7 = \frac{1}{\pi} \left( \int_{\frac{\pi}{2} - \frac{\theta}{2} + \frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_2 + \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\pi}{2} - \frac{\theta}{2} + \frac{\alpha}{2}} -r \cos\left(x_2 + \frac{\theta}{2}\right) + r \sin\left(\frac{\alpha}{2}\right) dx_2 + \int_{\theta}^{\theta + \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_3 \right) \quad \text{eqn S47}$$

$$pSW7 = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S48}$$

S2.11.5. *Model SW8.* SW8 is bounded by  $\alpha \leq \pi - 2\theta$ ,  $\alpha \geq \theta$  and  $\alpha \leq 2\theta$ . It starts with a  $\theta$  limited profile. It does contain the  $r \sin(\alpha/2) - r \cos(x_2 + \theta/2)$  profile in  $x_2$  but does not have a  $x_4$  profile.

$$pSW8 = \frac{1}{\pi} \left( \int_{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}} -r \cos\left(x_2 + \frac{\theta}{2}\right) + r \sin\left(\frac{\alpha}{2}\right) dx_2 + \int_{\theta}^{\theta + \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_3 \right) \quad \text{eqn S49}$$

$$pSW8 = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S50}$$

S2.11.6. *Model SW9.* Finally, SW9, the last model, is bounded by  $\alpha \leq \pi - 2\theta$ ,  $\alpha \geq 2\theta$  and  $\theta \geq 0$ . Therefore it starts with a  $\theta$  limited profile. However it doesn't contain the extra  $x_2$  profile nor a  $x_4$  profile.

$$pSW9 = \frac{1}{\pi} \left( \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\theta}^{\frac{\alpha}{2}} r \sin(x_3) dx_3 + \int_{\frac{\alpha}{2}}^{\theta + \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_3 \right) \quad \text{eqn S51}$$

$$pSW9 = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S52}$$

## S3. SUPPLEMENTARY SCRIPT: SYMBOLIC ALGEBRA PYTHON SCRIPT

This script uses the SymPy package SymPy Development Team (2014), a computer algebra system to calculate the equations for  $p$  in the various models and to perform unit checks on the results.

```

1  """
2  Systematic analysis of REM models
3  Tim Lucas
4  01/10/13
5  """
6
7
8  from sympy import *
9  import numpy as np
10 import matplotlib.pyplot as plt
11 from datetime import datetime
12
13
14 # Use LaTeX printing
15 from sympy import init_printing ;
16 init_printing()
17 # Make LaTeX output white. Because I use a dark theme
18 # init_printing(forecolor="White")
19
20
21 # Load symbols used for symbolic maths
22 t, a, r, x2, x3, x4, x1 = symbols('theta alpha r x_2 x_3 x_4 x_1', positive=True)
23 r1 = {r:1} # useful for lots of checks
24
25
26 # Define functions
27 # Calculate the final profile averaged over pi.
28 def calcModel(model):
29     x = pi**1 * sum( [integrate(m[0], m[1:]) for m in model] ).simplify().trigsimp()
30     return x
31
32 # Do the replacements fit within the area defined by the conditions?
33 def confirmReplacements(conds, reps):
34     if not all([c.subs(reps) for c in eval(conds)]):
35         print('reps' + conds[4:] + ' incorrect')
36
37 # is average profile in range 0r-2r?
38 def profileRange(prof, reps):
39     if not 0 <= eval(prof).subs(dict(reps, **r1)) <= 2:
40         print('Total ' + prof + ' not in 0, 2r')
41
42 # Are the individuals integrals >0r
43 def intsPositive(model, reps):
44     m = eval(model)
45     for i in range(len(m)):
46         if not integrate(m[i][0], m[i][1:]).subs(dict(reps, **r1)) > 0:
47             print('Integral ' + str(i+1) + ' in ' + model + ' is negative')
48
49 # Are the individual averaged integrals between 0 and 2r
50 def intsRange(model, reps):
51     m = eval(model)
52     for i in range(len(m)):
53         if not 0 <= (integrate(m[i][0], m[i][1:])/(m[i][3]-m[i][2])).subs(dict(reps, **r1)) <=
54             2:
55             print('Integral ' + str(i+1) + ' in ' + model + ' has averaged integral outside
56                 0<p<2r')
57
58 # Are the bounds the correct way around
59 def checkBounds(model, reps):
60     m = eval(model)
61     for i in range(len(m)):
62         if not (m[i][3]-m[i][2]).subs(reps) > 0:
63             print('Bounds ' + str(i+1) + ' in ' + model + ' has lower bounds bigger than
64                 upper bounds')
65
66 # create latex strings with the 1) the integral equation that defines it and 2) the final calculated
67 model.
68 # There's some if statements to split longer equations on two lines and get +s in the right place.
69 def parseLaTeX(prof):
70     m = eval('m' + prof[1:] )
71     f = open('/home/tim/Dropbox/liz-paper/lucasMoorcroftManuscript/supplementary-material/latexFiles
72         /'+prof+'.tex', 'w')
73     f.write('\begin{align}\n \quad \mathrm{'} + prof + ' = &\frac{1}{\pi} \left(\frac{1}{\pi} \right)')
74     for i in range(len(m)):
75         f.write('\int\limits_{'+latex(m[i][2], order='rev-lex')+'}^{'+latex(m[i][3], order='rev-
76             lex')+'}'+latex(m[i][0], order='rev-lex')+'}\mathrm{d}' + latex(m[i][1]))
77         if len(m)>3 and i==(len(m)/2)-1:
78             f.write(' \\\right.\notag\\\\\n &\left.' )
79         if i<len(m)-1:
80             f.write(' + ')
81     f.write('\right)\label{' + prof + 'Def}\\\\\n ')

```

```

76         f.write('\mathrm{' + prof + '}' =& ' + latex(eval(prof)) + '\label{' + prof + 'Sln}\n\\end{align}
77         f.close()
78
79
80 # Apply all checks.
81 def allChecks(prof):
82     model = 'm' + prof[1:]
83     reps = eval('rep' + prof[1:])
84     conds = 'cond' + prof[1:]
85     confirmReplacements(conds, reps)
86     profileRange(prof, reps)
87     intsPositive(model, reps)
88     intsRange(model, reps)
89     checkBounds(model, reps)
90
91 #####
92 ### Define and solve all models ###
93 #####
94
95 # NE1 animal: a = 2*pi.  sensor: t > pi, a > 3pi - t #
96
97 mNE1 = [ [2*r, x1, pi/2, t/2 ],
98          [r + r*cos(x1 - t/2), x1, t/2, pi ],
99          [r + r*cos(x1 + t/2), x1, pi, 2*pi-t/2 ],
100          [2*r, x1, 2*pi-t/2, 3*pi/2 ] ]
101
102 # Replacement values in range
103 repNE1 = {t:3*pi/2, a:2*pi}
104
105 # Define conditions for model
106 condNE1 = [pi <= t, a >= 3*pi - t]
107
108 # Calculate model, run checks, write output.
109 pNE1 = calcModel(mNE1)
110 allChecks('pNE1')
111 parseLaTeX('pNE1')
112
113
114 # NE2 animal: a > pi.  sensor: t > pi Condition: a < 3pi - t, a > 4pi - 2t #
115
116 mNE2 = [ [2*r, x1, pi/2, t/2 ],
117          [r + r*cos(x1 - t/2), x1, t/2, 5*pi/2 - t/2 - a/2 ],
118          [r + r*cos(x1 + t/2), x1, 5*pi/2 - t/2 - a/2, 2*pi-t/2 ],
119          [2*r, x1, 2*pi-t/2, 3*pi/2 ] ]
120
121 # Replacement values in range
122 repNE2 = {t:5*pi/3, a:4*pi/3-0.1}
123
124 # Define conditions for model
125 condNE2 = [pi <= t, a >= pi, a <= 3*pi - t, a >= 4*pi - 2*t]
126
127 # Calculate model, run checks, write output.
128 pNE2 = calcModel(mNE2)
129 allChecks('pNE2')
130 parseLaTeX('pNE2')
131
132
133 # NE3 animal: a > pi.  sensor: t > pi Condition: a < 4pi - 2t #
134
135 mNE3 = [ [2*r, x1, pi/2, t/2 ],
136          [r + r*cos(x1 - t/2), x1, t/2 + pi/2, 5*pi/2 - t/2 - a/2 ],
137          [r, x1, t/2 + pi/2, 5*pi/2 - t/2 - a/2 ],
138          [r + r*cos(x1 + t/2), x1, 5*pi/2 - t/2 - a/2, 2*pi-t/2 ],
139          [2*r, x1, 2*pi-t/2, 3*pi/2 ] ]
140
141 # Replacement values in range
142 repNE3 = {t:5*pi/4-0.1, a:3*pi/2}
143
144 # Define conditions for model
145 condNE3 = [pi <= t, a >= pi, a <= 4*pi - 2*t]
146
147 # Calculate model, run checks, write output.
148 pNE3 = calcModel(mNE3)
149 allChecks('pNE3')
150 parseLaTeX('pNE3')
151
152
153 # NW1 animal: a = 2*pi.  sensor: pi/2 <= t <= pi #
154
155 mNW1 = [ [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2 ],
156          [r - r*cos(x4 - t), x4, 0, t - pi/2 ],
157          [r, x4, t - pi/2, pi/2 ],
158          [r - r*cos(x4), x4, pi/2, t ],
159          [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2 ] ]
160
161 # Replacement values in range

```

```

162 repNW1 = {t:3*pi/4}
163
164 # Define conditions for model
165 condNW1 = [pi/2 <= t, t <= pi]
166
167 # Calculate model, run checks, write output.
168 pNW1 = calcModel(mNW1)
169 allChecks('pNW1')
170 parseLaTeX('pNW1')
171
172
173
174
175 # NW2 animal: a > pi. Sensor: pi/2 <= t <= pi. Condition: a > 2pi - t #
176
177 mNW2 = [ [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2 ],
178          [r - r*cos(x4 - t), x4, 0, t - pi/2 ],
179          [r, x4, t - pi/2, 3*pi/2 - a/2],
180          [r - r*cos(x4), x4, 3*pi/2 - a/2, t ],
181          [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2 ] ]
182
183
184 repNW2 = {t:3*pi/4, a:15*pi/8} # Replacement values in range
185
186 # Define conditions for model
187 condNW2 = [a > pi, pi/2 <= t, t <= pi, a >= 3*pi - 2*t]
188
189 # Calculate model, run checks, write output.
190 pNW2 = calcModel(mNW2)
191 allChecks('pNW2')
192 parseLaTeX('pNW2')
193
194
195
196 # NW3 animal: a > pi. Sensor: pi/2 <= t <= pi. Cond: 2pi - t < a < 3pi - 2t #
197
198 mNW3 = [ [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2 ],
199          [r - r*cos(x4 - t), x4, 0, t - pi/2 ],
200          [r, x4, t - pi/2, t ],
201          [r*cos(x2 - t/2), x2, t/2, 3*pi/2 - a/2 - t/2],
202          [2*r*sin(t/2)*sin(x2), x2, 3*pi/2 - a/2 - t/2, pi/2 ] ]
203
204
205 repNW3 = {t:5*pi/8, a:6*pi/4} # Replacement values in range
206
207 # Define conditions for model
208 condNW3 = [a > pi, pi/2 <= t, t <= pi, 2*pi - t <= a, a <= 3*pi - 2*t]
209
210 # Calculate model, run checks, write output.
211 pNW3 = calcModel(mNW3)
212 allChecks('pNW3')
213 parseLaTeX('pNW3')
214
215
216
217 # NW4 animal: a > pi. Sensor: pi/2 <= t <= pi. Condition: a <= 2pi - t #
218
219 mNW4 = [ [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2],
220          [r - r*cos(x4 - t), x4, 0, t - pi/2],
221          [r, x4, t - pi/2, t],
222          [r*cos(x2 - t/2), x2, t/2, a/2 + t/2 - pi/2] ]
223
224 repNW4 = {t:3*pi/4, a:9*pi/8} # Replacement values in range
225
226 # Define conditions for model
227 condNW4 = [a > pi, pi/2 <= t, t <= pi, a <= 2*pi - t]
228
229 # Calculate model, run checks, write output.
230 pNW4 = calcModel(mNW4)
231 allChecks('pNW4')
232 parseLaTeX('pNW4')
233
234
235 # REM animal: a=2pi. Sensor: t <= pi/2. #
236
237 mREM = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2],
238          [r*sin(x3), x3, t, pi/2],
239          [r, x4, 0*t, t],
240          [r*sin(x3), x3, t, pi/2],
241          [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2] ]
242
243
244 repREM = {t:3*pi/8, a:2*pi} # Replacement values in range
245
246 # Define conditions for model
247 condREM = [ t <= pi/2 ]
248

```



```

249 # Calculate model, run checks, write output.
250 pREM = calcModel(mREM)
251 allChecks('pREM')
252 parseLaTeX('pREM')
253
254
255
256 # NW5 animal:  $a > \pi$ . Sensor:  $t \leq \pi/2$ . Condition:  $2\pi - t < a$  #
257
258
259 mNW5 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2],
260          [r*sin(x3), x3, t, pi/2],
261          [r, x4, 0, t],
262          [r*sin(x3), x3, t, pi/2],
263          [r*cos(x2 - t/2), x2, pi/2 - t/2, 3*pi/2 - t/2 - a/2],
264          [2*r*sin(t/2)*sin(x2), x2, 3*pi/2 - t/2 - a/2, pi/2] ]
265
266
267 repNW5 = {t:3*pi/8, a:29*pi/16} # Replacement values in range
268
269 # Define conditions for model
270 condNW5 = [a >= pi, t <= pi/2, 2*pi - t <= a ]
271
272 # Calculate model, run checks, write output.
273 pNW5 = calcModel(mNW5)
274 allChecks('pNW5')
275 parseLaTeX('pNW5')
276
277
278 # NW6 animal:  $a > \pi$ . Sensor:  $t \leq \pi/2$ . Condition:  $2\pi - 2t \leq a \leq 2\pi - t$  #
279
280
281 mNW6 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2],
282          [r*sin(x3), x3, t, pi/2],
283          [r, x4, 0, t],
284          [r*sin(x3), x3, t, pi/2],
285          [r*cos(x2 - t/2), x2, pi/2 - t/2, a/2 + t/2 - pi/2] ]
286
287 repNW6 = {t:3*pi/8, a:3*pi/2} # Replacement values in range
288
289 # Define conditions for model
290 condNW6 = [a >= pi, t <= pi/2, 2*pi - 2*t <= a, a <= 2*pi - t]
291
292 # Calculate model, run checks, write output.
293 pNW6 = calcModel(mNW6)
294 allChecks('pNW6')
295 parseLaTeX('pNW6')
296
297
298
299 # NW7 animal:  $a > \pi$ . Sensor:  $t \leq \pi/2$ . Condition:  $a \leq 2\pi - 2t$  #
300
301
302 mNW7 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2],
303          [r*sin(x3), x3, t, pi/2],
304          [r, x4, 0, t],
305          [r*sin(x3), x3, pi - a/2, pi/2] ]
306
307
308 repNW7 = {t:pi/9, a:10*pi/9} # Replacement values in range
309
310 # Define conditions for model
311 condNW7 = [t <= pi/2, a >= pi, a <= 2*pi - 2*t]
312
313 # Calculate model, run checks, write output.
314 pNW7 = calcModel(mNW7)
315 allChecks('pNW7')
316 parseLaTeX('pNW7')
317
318
319
320 # SE1 animal:  $a \leq \pi$ . Sensor:  $t = 2\pi$ . #
321
322 mSE1 = [ [ 2*r*sin(a/2), x1, pi/2, 3*pi/2 ],
323          ]
324
325
326 repSE1 = {a:pi/4} # Replacement values in range
327
328 # Define conditions for model
329 condSE1 = [a <= pi]
330
331 # Calculate model, run checks, write output.
332 pSE1 = calcModel(mSE1)
333 allChecks('pSE1')
334 parseLaTeX('pSE1')
335

```

```

336
337
338
339 # SE2 animal: a <= pi. Sensor: t > pi. Condition: a > 2pi - t, a > 4pi - 2t #
340
341 mSE2 = [ [ 2*r*sin(a/2), x1, pi/2, t/2 + pi/2 - a/2 ],
342 [ r*sin(a/2) + r*cos(x1 - t/2), x1, t/2 + pi/2 - a/2, 5*pi/2 - a/2 - t/2 ],
343 [ 2*r*sin(a/2), x1, 5*pi/2 - a/2 - t/2, 3*pi/2 ] ]
344
345
346 repSE2 = {t:19*pi/10, a:pi/2} # Replacement values in range
347
348 # Define conditions for model
349 condSE2 = [a <= pi, t >= pi, a >= 4*pi - 2*t]
350
351 # Calculate model, run checks, write output.
352 pSE2 = calcModel(mSE2)
353 allChecks('pSE2')
354 parseLaTeX('pSE2')
355
356
357 # SE3 animal: a <= pi. Sensor: t > pi. Condition: 2pi - t < a < 4pi - 2t #
358
359 mSE3 = [ [ 2*r*sin(a/2), x1, pi/2, t/2 + pi/2 - a/2 ],
360 [ r*sin(a/2) + r*cos(x1 - t/2), x1, t/2 + pi/2 - a/2, t/2 + pi/2 ],
361 [ r*sin(a/2), x1, t/2 + pi/2, 5*pi/2 - a/2 - t/2 ],
362 [ 2*r*sin(a/2), x1, 5*pi/2 - a/2 - t/2, 3*pi/2 ] ]
363
364 repSE3 = {t:3*pi/2 + 0.1, a:pi/2} # Replacement values in range
365
366 # Define conditions for model
367 condSE3 = [a <= pi, t >= pi, a >= 2*pi - t, a <= 4*pi - 2*t]
368
369 # Calculate model, run checks, write output.
370 pSE3 = calcModel(mSE3)
371 allChecks('pSE3')
372 parseLaTeX('pSE3')
373
374
375 # SE4 animal: a <= pi. Sensor: t > pi. Condition: a <= 4*pi - 2*t and a < 2*pi - t #
376
377
378 mSE4 = [ [ 2*r*sin(a/2), x1, pi/2, t/2 + pi/2 - a/2 ],
379 [ r*sin(a/2) + r*cos(x1 - t/2), x1, t/2 + pi/2 - a/2, t/2 + pi/2 ],
380 [ r*sin(a/2), x1, t/2 + pi/2, t/2 + pi/2 + a/2 ] ]
381
382
383 repSE4 = {t:3*pi/2, a:pi/3} # Replacement values in range
384
385
386 # Define conditions for model
387 condSE4 = [a <= pi, t >= pi/2, a <= 4*pi - 2*t, a <= 2*pi - t]
388
389 # Calculate model, run checks, write output.
390 pSE4 = calcModel(mSE4)
391 allChecks('pSE4')
392 parseLaTeX('pSE4')
393
394
395 # SW1 animal: a <= pi. Sensor: pi/2 <= t <= pi. Condition: a >= t and a/2 >= t - pi/2 #
396
397 mSW1 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - a/2 + t/2, pi/2 ],
398 [r*sin(a/2) - r*cos(x2 + t/2), x2, t/2, pi/2 - a/2 + t/2],
399 [r*sin(a/2) - r*cos(x4 - t), x4, 0, t - pi/2 ],
400 [r*sin(a/2), x4, t-pi/2, t - pi/2 + a/2 ] ]
401
402
403 repSW1 = {t:5*pi/8, a:6*pi/8} # Replacement values in range
404
405 # Define conditions for model
406 condSW1 = [a <= pi, pi/2 <= t, t <= pi, a >= t, a/2 >= t - pi/2]
407
408 # Calculate model, run checks, write output.
409 pSW1 = calcModel(mSW1)
410 allChecks('pSW1')
411 parseLaTeX('pSW1')
412
413
414 # SW2 animal: a <= pi. Sensor: pi/2 <= t <= pi. Condition: a <= t and a/2 >= t - pi/2 #
415
416 mSW2 = [ [2*r*sin(a/2), x2, pi/2 + a/2 - t/2, pi/2 ],
417 [r*sin(a/2) - r*cos(x2 + t/2), x2, t/2, pi/2 + a/2 - t/2],
418 [r*sin(a/2) - r*cos(x4 - t), x4, 0*t, t - pi/2 ],
419 [r*sin(a/2), x4, t - pi/2, t - pi/2 + a/2 ] ]
420
421
422 repSW2 = {t:7*pi/8, a:7*pi/8-0.1} # Replacement values in range

```

```

423
424 # Define conditions for model
425 condSW2 = [a <= pi, pi/2 <= t, t <= pi, a/2 <= t/2, a/2 >= t - pi/2]
426
427 # Calculate model, run checks, write output.
428 pSW2 = calcModel(mSW2)
429 allChecks('pSW2')
430 parseLaTeX('pSW2')
431
432
433
434 # SW3 animal: a <= pi. Sensor: pi/2 <= t <= pi. Condition: a <= t and a/2 <= t - pi/2 #
435
436 mSW3 = [ [2*r*sin(a/2), x2, t/2, pi/2 ],
437          [2*r*sin(a/2), x4, 0, t - pi/2 - a/2 ],
438          [r*sin(a/2) - r*cos(x4 - t), x4, t - pi/2 - a/2, t - pi/2 ],
439          [r*sin(a/2), x4, t - pi/2, t - pi/2 + a/2 ] ]
440
441
442 repSW3 = {t:7*pi/8, a:2*pi/8} # Replacement values in range
443
444 # Define conditions for model
445 condSW3 = [a <= pi, pi/2 <= t, t <= pi, a/2 <= t/2, a/2 <= t - pi/2]
446
447 # Calculate model, run checks, write output.
448 pSW3 = calcModel(mSW3)
449 allChecks('pSW3')
450 parseLaTeX('pSW3')
451
452
453 # SW4 animal: a <= pi. Sensor: t <= pi/2. Condition: a > pi - 2t & a <= t #
454
455 mSW4 = [ [2*r*sin(a/2), x2, pi/2 - t/2 + a/2, pi/2 ],
456          [r*sin(a/2) - r*cos(x2 + t/2), x2, pi/2 - t/2, pi/2 - t/2 + a/2],
457          [r*sin(a/2), x3, t, pi/2 ],
458          [r*sin(a/2), x4, 0, a/2 + t - pi/2 ] ]
459
460 repSW4 = {t:pi/2-0.1, a:pi/4} # Replacement values in range
461
462 # Define conditions for model
463 condSW4 = [a <= pi, t <= pi/2, a >= pi - 2*t, a <= t]
464
465 # Calculate model, run checks, write output.
466 pSW4 = calcModel(mSW4)
467 allChecks('pSW4')
468 parseLaTeX('pSW4')
469
470
471 # SW5 animal: a <= pi. Sensor: t <= pi/2. Condition: a > pi - 2t & t <= a <= 2t #
472
473 mSW5 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 + t/2 - a/2, pi/2 ],
474          [r*sin(a/2) - r*cos(x2 + t/2), x2, pi/2 - t/2, pi/2 + t/2 - a/2],
475          [r*sin(a/2), x3, t, pi/2 ],
476          [r*sin(a/2), x4, 0, a/2 + t - pi/2 ] ]
477
478
479 repSW5 = {t:pi/2-0.1, a:pi/2} # Replacement values in range
480
481 # define conditions for model
482 condSW5 = [a <= pi, t <= pi/2, a >= pi - 2*t, t <= a, a <= 2*t]
483
484
485 # Calculate model, run checks, write output.
486 pSW5 = calcModel(mSW5)
487 allChecks('pSW5')
488 parseLaTeX('pSW5')
489
490
491 # SW6 animal: a <= pi. Sensor: t <= pi/2. Condition: a > pi - 2t & a > 2t #
492
493 mSW6 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2 ],
494          [r*sin(x3), x3, t, a/2 ],
495          [r*sin(a/2), x3, a/2, pi/2 ],
496          [r*sin(a/2), x4, 0, a/2 + t - pi/2 ] ]
497
498
499 repSW6 = {t:pi/4, a:3*pi/4} # Replacement values in range
500
501
502 # Define conditions for model
503 condSW6 = [a <= pi, t <= pi/2, a >= pi - 2*t, a > 2*t]
504
505 # Calculate model, run checks, write output.
506 pSW6 = calcModel(mSW6)
507 allChecks('pSW6')
508 parseLaTeX('pSW6')
509

```

```

510
511 # SW7 animal: a <= pi. Sensor: t <= pi/2. Condition: a <= pi - 2t & a <= t #
512
513 mSW7 = [ [2*r*sin(a/2), x2, pi/2 - t/2 + a/2, pi/2 ],
514          [r*sin(a/2) - r*cos(x2 + t/2), x2, pi/2 - t/2, pi/2 - t/2 + a/2],
515          [r*sin(a/2), x3, t, t + a/2 ] ]
516
517
518 repSW7 = {t:2*pi/8, a:pi/8} # Replacement values in range
519
520 # Define conditions for model
521 condSW7 = [a <= pi, t <= pi/2, a <= pi - 2*t, a <= t]
522
523 # Calculate model, run checks, write output.
524 pSW7 = calcModel(mSW7)
525 allChecks('pSW7')
526 parseLaTeX('pSW7')
527
528
529 # SW8 animal: a <= pi. Sensor: t <= pi/2. Condition: a <= pi - 2t & t <= a <= 2t #
530
531 mSW8 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 + t/2 - a/2, pi/2 ],
532          [r*sin(a/2) - r*cos(x2 + t/2), x2, pi/2 - t/2, pi/2 + t/2 - a/2],
533          [r*sin(a/2), x3, t, t + a/2 ] ]
534
535 repSW8 = {t:2*pi/8, a:pi/2-0.1} # Replacement values in range
536
537 # Define conditions for model
538 condSW8 = [a <= pi, t <= pi/2, a <= pi - 2*t, t <= a, a <= 2*t]
539
540 # Calculate model, run checks, write output.
541 pSW8 = calcModel(mSW8)
542 allChecks('pSW8')
543 parseLaTeX('pSW8')
544
545
546 # SW9 animal: a <= pi. Sensor: t <= pi/2. Condition: a <= pi - 2t & 2t <= a #
547
548 mSW9 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2 ],
549          [r*sin(x3), x3, t, a/2 ],
550          [r*sin(a/2), x3, a/2, t + a/2 ] ]
551
552
553 repSW9 = {t:1*pi/8, a:pi/2} # Replacement values in range
554
555 # Define conditions for model
556 condSW9 = [a <= pi, t <= pi/2, a <= pi - 2*t, 2*t <= a]
557
558 # Calculate model, run checks, write output.
559 pSW9 = calcModel(mSW9)
560 allChecks('pSW9')
561 parseLaTeX('pSW9')
562
563
564 #####
565 ## Run tests ###
566 #####
567
568 # create gas model object
569 gas = 2*r
570
571
572 # for each model run through every adjacent model.
573 # Contains duplicatea but better for avoiding missed comparisons.
574 # Also contains replacement t->a and a->t just in case.
575
576
577 allComps = [
578 ['gas', 'pNE1', {t:2*pi}], ['gas', 'pSE1', {a:pi}],
579
580 ['pNE1', 'gas', {t:2*pi}], ['pNE1', 'pNW1', {t:pi}],
581 ['pNE1', 'pNE2', {a:3*pi-t}], ['pNE1', 'pNE2', {t:3*pi-a}],
582
583 ['pNE2', 'pNE1', {a:3*pi-t}], ['pNE2', 'pNE1', {t:3*pi-a}],
584 ['pNE2', 'pNE3', {a:4*pi-2*t}], ['pNE2', 'pNE3', {t:2*pi-a/2}],
585 ['pNE2', 'pSE2', {a:pi}],
586
587 ['pNE3', 'pNE2', {a:4*pi-2*t}], ['pNE3', 'pNE2', {t:2*pi-a/2}],
588 ['pNE3', 'pSE3', {a:pi}], ['pNE3', 'pNW2', {t:pi}],
589
590 ['pNW1', 'pNE1', {t:pi}], ['pNW1', 'pNW2', {a:2*pi}],
591
592 ['pNW2', 'pNE3', {t:pi}], ['pNW2', 'pNW3', {a:3*pi-2*t}],
593 ['pNW2', 'pNW3', {t:3*pi/2-a/2}], ['pNW2', 'pNW1', {a:2*pi}],
594
595 ['pNW3', 'pNW5', {t:pi/2}], ['pNW3', 'pNW4', {a:2*pi-t}],
596 ['pNW3', 'pNW4', {t:2*pi-a}], ['pNW3', 'pNW2', {a:3*pi-2*t}],

```

```

597 ['pNW3', 'pNW2', {t:3*pi/2-a/2}],
598
599 ['pNW4', 'pNW6', {t:pi/2}], ['pNW4', 'pNW3', {t:2*pi-a}],
600 ['pNW4', 'pNW3', {a:2*pi-t}], ['pNW4', 'pSW1', {a:pi}],
601
602 ['pREM', 'pNW1', {t:pi/2}], ['pREM', 'pNW5', {a:2*pi}],
603
604 ['pNW5', 'pREM', {a:2*pi}], ['pNW5', 'pNW6', {a:2*pi-t}],
605 ['pNW5', 'pNW6', {t:2*pi-a}], ['pNW5', 'pNW3', {t:pi/2}],
606
607 ['pNW6', 'pNW5', {a:2*pi-t}], ['pNW6', 'pNW5', {t:2*pi-a}],
608 ['pNW6', 'pNW7', {t:pi-a/2}], ['pNW6', 'pNW7', {a:2*pi-2*t}],
609 ['pNW5', 'pNW4', {t:pi/2}],
610
611 ['pNW7', 'pNW6', {t:2*pi-2*a}], ['pNW7', 'pNW6', {a:2*pi-2*t}],
612 ['pNW7', 'pSW6', {a:pi}],
613
614 ['pSE1', 'pSE2', {t:2*pi}], ['pSE1', 'gas', {a:pi}],
615
616 ['pSE2', 'pSE3', {t:2*pi-a/2}], ['pSE2', 'pSE3', {a:4*pi-2*t}],
617 ['pSE2', 'pSE1', {t:2*pi}], ['pSE2', 'pNE2', {a:pi}],
618
619 ['pSE3', 'pSE2', {a:4*pi-2*t}], ['pSE3', 'pSE2', {t:2*pi-a/2}],
620 ['pSE3', 'pSE4', {a:2*pi-t}], ['pSE3', 'pSE4', {t:2*pi-a}],
621 ['pSE3', 'pNE3', {a:pi}],
622
623 ['pSE4', 'pSE3', {t:2*pi-a}], ['pSE4', 'pSE3', {a:2*pi-t}],
624 ['pSE4', 'pSW3', {t:pi}],
625
626 ['pSW1', 'pSW5', {t:pi/2}], ['pSW1', 'pSW2', {a:t}],
627 ['pSW1', 'pSW2', {t:a}], ['pSW1', 'pNW4', {a:pi}],
628
629 ['pSW2', 'pSW1', {a:t}], ['pSW2', 'pSW1', {t:a}],
630 ['pSW2', 'pSW4', {t:pi/2}], ['pSW2', 'pSW3', {a:2*t-pi}],
631 ['pSW2', 'pSW3', {t:a/2+pi/2}],
632
633 ['pSW3', 'pSW2', {t:a/2+pi/2}], ['pSW3', 'pSW2', {a:2*t-pi}],
634 ['pSW3', 'pSE4', {t:pi}],
635
636
637 ['pSW4', 'pSW7', {a:pi-2*t}], ['pSW4', 'pSW7', {t:pi/2-a/2}],
638 ['pSW4', 'pSW5', {t:a}], ['pSW4', 'pSW5', {a:t}],
639 ['pSW4', 'pSW2', {t:pi/2}],
640
641 ['pSW5', 'pSW4', {t:a}], ['pSW5', 'pSW4', {a:t}],
642 ['pSW5', 'pSW8', {t:pi/2-a/2}], ['pSW5', 'pSW8', {a:pi-2*t}],
643 ['pSW5', 'pSW6', {a:2*t}], ['pSW5', 'pSW6', {t:a/2}],
644 ['pSW5', 'pSW1', {t:pi/2}],
645
646 ['pSW6', 'pSW9', {t:pi/2-a/2}], ['pSW6', 'pSW9', {a:pi-2*t}],
647 ['pSW6', 'pSW5', {a:2*t}], ['pSW6', 'pSW5', {t:a/2}],
648 ['pSW6', 'pNW7', {a:pi}],
649
650
651 ['pSW7', 'pSW8', {t:a}], ['pSW7', 'pSW8', {a:t}],
652 ['pSW7', 'pSW4', {t:pi/2-a/2}], ['pSW7', 'pSW4', {a:pi-2*t}],
653
654 ['pSW8', 'pSW7', {a:t}], ['pSW8', 'pSW7', {t:a}],
655 ['pSW8', 'pSW9', {a:2*t}], ['pSW8', 'pSW9', {t:a/2}],
656 ['pSW8', 'pSW5', {a:pi-2*t}], ['pSW8', 'pSW5', {t:pi/2-a/2}],
657
658 ['pSW9', 'pSW8', {a:2*t}], ['pSW9', 'pSW8', {t:a/2}],
659 ['pSW9', 'pSW6', {a:pi-2*t}], ['pSW9', 'pSW6', {t:pi/2-a/2}]
660 ]
661
662
663 # List of regions that touch a=0. Should equal 0 when a=0.
664 zeroRegions = ['pSW9', 'pSW8', 'pSW7', 'pSW4', 'pSW2', 'pSW3', 'pSE4', 'pSE3', 'pSE2', 'pSE1']
665
666 # Run through all the comparisons. Need simplify(). Even together() gives some false negatives.
667
668 checkFile = open('/home/tim/Dropbox/phd/Analysis/REM-chapter/checksFile.tex', 'w')
669
670 checkFile.write('All checks evaluated.\nTim Lucas - ' + str(datetime.now()) + '\n')
671 for i in range(len(allComps)):
672     if (eval(allComps[i][0]).subs(allComps[i][2]) - eval(allComps[i][1]).subs(allComps[i][2])):
673         simplify() == 0:
674             checkFile.write(str(i) + ': ' + allComps[i][0] + ' and ' + allComps[i][1] + ': OK\n')
675         else:
676             checkFile.write(str(i) + ': ' + allComps[i][0] + ' and ' + allComps[i][1] + ': Incorrect\n')
677
678 for i in range(len(zeroRegions)):
679     if eval(zeroRegions[i]).subs({a:0}).simplify() == 0:
680         checkFile.write(zeroRegions[i] + ' at a=0: OK\n')
681     else:
682         checkFile.write(zeroRegions[i] + ' at a=0: Incorrect\n')

```

```

683 checkFile.close()
684
685
686 # And print to terminal
687 #for i in range(len(allComps)):
688 #    if not (eval(allComps[i][0]).subs(allComps[i][2]) - eval(allComps[i][1]).subs(allComps[i][2])).
        simplify() == 0:
689 #        print allComps[i][0] + ' and ' + allComps[i][1]+' : Incorrect\n'
690
691
692 #####
693 ### Define a function that calculates p bar answer.      ###
694 #####
695
696 def calcP(A, T, R):
697     assert (A <= 2*pi and A >= 0), "a is out of bounds. Should be in 0<a<2*pi"
698     assert (T <= 2*pi and T >= 0), "s is out of bounds. Should be in 0<s<2*pi"
699
700     if A > pi:
701         if A < 4*pi - 2*T:
702             p = pNW7.subs({a:A, t:T, r:R}).n()
703         elif A <= 3*pi - T:
704             p = pNE2.subs({a:A, t:T, r:R}).n()
705         else:
706             p = pNE1.subs({a:A, t:T, r:R}).n()
707     else:
708         if A < 4*pi - 2*T:
709             p = pSE3.subs({a:A, t:T, r:R}).n()
710         else:
711             p = pSE2.subs({a:A, t:T, r:R}).n()
712     return p
713
714
715 #####
716 ## Apply to entire grid ##
717 #####
718
719 # How many values for each parameter
720 nParas = 100
721
722 # Make a vector for a and s. Make an empty nParas x nParas array.
723 # Calculated profile sizes will go in pArray
724 tVec = np.linspace(0, 2*pi, nParas)
725 aVec = np.linspace(0, 2*pi, nParas)
726 pArray = np.zeros((nParas,nParas))
727
728 # Calculate profile size for each combination of parameters
729 for i in range(nParas):
730     for j in range(nParas):
731         pArray[i][j] = calcP(aVec[i], tVec[j], 1)
732
733 # Turn the array upside down so origin is at bottom left.
734 pImage = np.flipud(pArray)
735
736 # Plot and save.
737 pl.imshow(pImage, interpolation='none', cmap=pl.get_cmap('Blues'))
738 #pl.show()
739
740 pl.savefig('/home/tim/Dropbox/phd/Analysis/REM-chapter/imgs/profilesCalculated.png')
741
742
743
744 #####
745 ### Output R function. ###
746 #####
747
748 # To reduce mistakes, output R function directly from python.
749 # However, the if statements, which correspond to the bounds of each model, are not automatic.
750
751 Rfunc = open('/home/tim/Dropbox/phd/Analysis/REM-chapter/supplementaryRscript.R', 'w')
752
753 Rfunc.write("""
754 # Functions to calculate density.
755 #
756 # Tim C.D. Lucas, Elizabeth Moorcroft, Robin Freeman, Marcus J. Rowcliffe, Kate E. Jones.
757 #
758 # calcDensity is the main function to calculate density.
759 # It takes parameters z, alpha, theta, r, animalSpeed, t
760 # z - The number of camera/acoustic counts or captures.
761 # alpha - Call width in radians.
762 # theta - Sensor width in radians.
763 # r - Sensor range in metres.
764 # animalSpeed - Average animal speed in metres per second.
765 # t - Length of survey in sensor seconds i.e. number of sensors x survey duration.
766 #
767 # calcAbundance calculates abundance rather than density and requires an extra parameter
768 # area - In metres squared. The size of the region being examined.

```

```

769
770
771 # Internal function to calculate profile width as described in the text
772 calcProfileWidth <- function(alpha, theta, r){
773   if(alpha > 2*pi | alpha < 0)
774     stop('alpha is out of bounds. alpha should be in interval 0<a<2*pi')
775   if(theta > 2*pi | theta < 0)
776     stop('theta is out of bounds. theta should be in interval 0<a<2*pi')
777
778   if(alpha > pi){
779     if(alpha < 4*pi - 2*theta){
780       "" +
781       '      p <- ' + str(pNW7) +
782       '\n      } else if(alpha <= 3*pi - theta){'
783       '\n      p <- ' + str(pNE2) +
784       '\n      } else {'
785       '\n      p <- ' + str(pNE1) +
786       '\n      }'
787       '\n      } else {'
788       '\n      if(alpha < 4*pi - 2*theta){'
789       '\n      p <- ' + str(pSE3) +
790       '\n      } else {'
791       '\n      p <- ' + str(pSE2) +
792       '\n      }'
793       '\n      }'
794       '\n      return(p)'
795       '\n}' +
796       ""
797 # Calculate a population density. See above for units etc.
798 calcDensity <- function(z, alpha, theta, r, animalSpeed, t){
799   # Check the parameters are suitable.
800   if(z <= 0 | !is.numeric(z)) stop('Counts, z, must be a positive number.')
801   if(animalSpeed <= 0 | !is.numeric(animalSpeed)) stop('animalSpeed must be a positive number.')
802   if(t <= 0 | !is.numeric(t)) stop('Time, t, must be a positive number.')
803
804   # Calculate profile width, then density.
805   p <- calcProfileWidth(alpha, theta, r)
806   D <- z/(animalSpeed*t*p)
807   return(D)
808 }
809
810 # Calculate abundance rather than density.
811 calcAbundance <- function(z, alpha, theta, r, animalSpeed, t, area){
812   if(area <= 0 | !is.numeric(area)) stop('Area must be a positive number')
813   D <- calcDensity(z, alpha, theta, r, animalSpeed, t)
814   A <- D*area
815   return(A)
816 }
817 ""
818 )
819
820 Rfunc.close()

```

## S4. SUPPLEMENTARY SCRIPT: R IMPLEMENTATION OF MODELS

This is a simple implementation of the models derived in the paper in R (R Development Core Team, 2010). Once given the parameters  $\theta$  and  $\alpha$  it automatically selects the correct model to apply.

```

1 # Functions to calculate density.
2 #
3 # Tim C.D. Lucas, Elizabeth Moorcroft, Robin Freeman, Marcus J. Rowcliffe, Kate E. Jones.
4 #
5 #
6 # calcDensity is the main function to calculate density.
7 # It takes parameters z, alpha, theta, r, animalSpeed, t
8 # z - The number of camera/acoustic counts or captures.
9 # alpha - Call width in radians.
10 # theta - Sensor width in radians.
11 # r - Sensor range in metres.
12 # animalSpeed - Average animal speed in metres per second.
13 # t - Length of survey in sensor seconds i.e. number of sensors x survey duration.
14 #
15 # calcAbundance calculates abundance rather than density and requires an extra parameter
16 # area - In metres squared. The size of the region being examined.
17
18
19 # Internal function to calculate profile width as described in the text
20 calcProfileWidth <- function(alpha, theta, r){
21   if(alpha > 2*pi | alpha < 0)
22     stop('alpha is out of bounds. alpha should be in interval 0<a<2*pi')
23   if(theta > 2*pi | theta < 0)
24     stop('theta is out of bounds. theta should be in interval 0<a<2*pi')
25
26   if(alpha > pi){
27     if(alpha < 4*pi - 2*theta){
28       p <- r*(theta - cos(alpha/2) + 1)/pi
29     } else if(alpha <= 3*pi - theta){
30       p <- r*(theta - cos(alpha/2) + cos(alpha/2 + theta))/pi
31     } else {
32       p <- r*(theta + 2*sin(theta/2))/pi
33     }
34   } else {
35     if(alpha < 4*pi - 2*theta){
36       p <- r*(theta*sin(alpha/2) - cos(alpha/2) + 1)/pi
37     } else {
38       p <- r*(theta*sin(alpha/2) - cos(alpha/2) + cos(alpha/2 + theta))/pi
39     }
40   }
41   return(p)
42 }
43
44 # Calculate a population density. See above for units etc.
45 calcDensity <- function(z, alpha, theta, r, animalSpeed, t){
46   # Check the parameters are suitable.
47   if(z <= 0 | !is.numeric(z)) stop('Counts, z, must be a positive number.')
48   if(animalSpeed <= 0 | !is.numeric(animalSpeed)) stop('animalSpeed must be a positive number.')
49   if(t <= 0 | !is.numeric(t)) stop('Time, t, must be a positive number.')
50
51   # Calculate profile width, then density.
52   p <- calcProfileWidth(alpha, theta, r)
53   if(p <= 0) stop('Calculated profile width is 0. We would therefore expect 0 captures. If z is
54     not zero, then the density is undefined.')
55   D <- z/(animalSpeed*t*p)
56   return(D)
57 }
58
59 # Calculate abundance rather than density.
60 calcAbundance <- function(z, alpha, theta, r, animalSpeed, t, area){
61   if(area <= 0 | !is.numeric(area)) stop('Area must be a positive number')
62   D <- calcDensity(z, alpha, theta, r, animalSpeed, t)
63   A <- D*area
64   return(A)
65 }

```

supplementaryRscript.R

## REFERENCES

- R Development Core Team (2010) *R: A Language And Environment For Statistical Computing*. R Foundation For Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. 25
- Rowcliffe, J., Field, J., Turvey, S. & Carbone, C. (2008) Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, **45**, 1228–1236. 6, 10
- SymPy Development Team (2014) *SymPy: Python library for symbolic mathematics*. 14