

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

S1. TABLE OF SYMBOLS

Symbol	Description	Units
$\theta$	Sensor width	rad
$\alpha$	Animal call/beam width	rad
$x_i$	Focal angle, $i \in \{1, 2, 3, 4\}$	rad
$r$	Detection distance	m
$\bar{p}$	Average profile width	m
$p$	A specific profile width	m
$v$	Velocity	$\text{m s}^{-1}$
$t$	Time	s
$z$	Number of detections	-
$D$	Animal density	$\text{m}^{-2}$
$T$	Step length	s
$N$	Number of steps per simulation	-
$d$	Distance moved in a time step	m
$S$	Probability of remaining stationary	-
$A$	Maximum turning angle	rad

TABLE S1. List of symbols used to describe the gREM and simulations

## S2. SUPPLEMENTARY METHODS

**S2.1. Introduction.** These 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 calculation of all integrals is included in the Python script S3.

**S2.2. Gas model.** Following Yapp (1956), we derive the gas model where sensors can capture animals in any direction and animal's signal is detectable from any direction ( $\theta = 2\pi$  and  $\alpha = 2\pi$ ). We assume that animals are in a homogeneous environment, and move in straight lines of random direction with velocity  $v$ . We allow that our stationary sensor can capture animals at a detection distance  $r$  and that if an animal moves within this detection zone they are captured with a probability of one, while animals outside the zone are never captured.

**S2.3. Model SE1.** In order to derive animal density, we need to consider relative velocity from the reference frame of the animals. Conceptually, this requires us to imagine that 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 survey period we can estimate the number of animals the sensor should capture. As a circle moving across a plane, the area covered by the sensor per unit time is  $2rv$ . The number of expected captures,  $z$ , for a survey period of  $t$ , with an animal density of  $D$  is  $z = 2rvtD$ . To estimate the density, we rearrange to get  $D = z/2rvt$ .

**S2.3.1. gREM derivations for different detection and signal widths.** Different combinations of  $\theta$  and  $\alpha$  would be expected to occur (e.g., sensors have different detection widths and animals have different signal widths). For different combinations  $\theta$  and  $\alpha$ , the area covered per unit time is no longer given by  $2rv$ . Instead of the size of the sensor detection zone having a diameter of  $2r$ , the size changes with the approach angle between the sensor and the animal. For any given signal width and detector width and depending on the angle that the animal approaches the sensor, the width of the area within which an animal can be detected is called the profile,  $p$ . The size of the profile (averaged across all approach angles) is defined as the average profile  $\bar{p}$ . However, different combinations of  $\theta$  and  $\alpha$  need different equations to calculate  $\bar{p}$ .

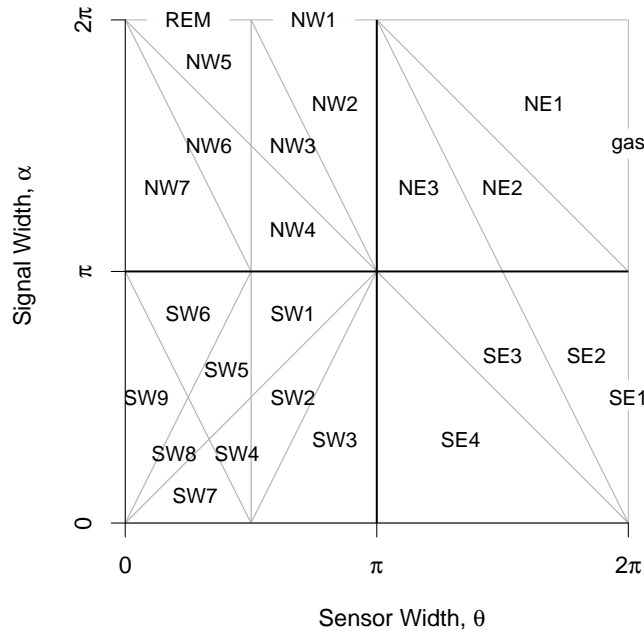


FIGURE S1. The location of each model in parameter space. Each named model must be derived separately. However, the results of the different models are often the same; areas coloured the same have the same result. Other than the gas model and the REM model, individual models are named after the compass 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  $\alpha = 2\pi$ ).

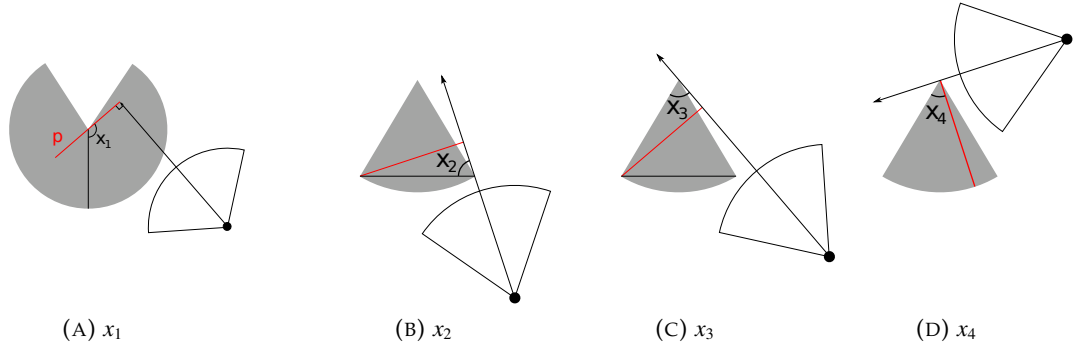


FIGURE S2. The location of the focal angles  $x_{i \in [1, 4]}$ . In these figures, the sector shaped detection region is shown in grey. Animals are filled black circles and the animal signal is an unfilled sector. The animals direction of movement is indicated with an arrow. The profile  $p$  is shown with a red line.

We have identified the parameter space for the combinations of  $\theta$  and  $\alpha$  for which the derivation of the equations are the same (defined as sub-models in the gREM) (Fig. S1). For example, the gas model becomes the simplest gREM sub-model (upper right in (Fig. S1) and the REM from (Rowcliffe *et al.*, 2008) is another gREM sub-model where  $\theta < \pi/2$  and  $\alpha = 2\pi$ .

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 Fig. S1.

SE1 is very similar to the gas model except that because  $\alpha \leq \pi$  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.

$$\bar{p}_{SE1} = \frac{1}{\pi} \int_{\frac{\pi}{2}}^{\frac{3\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_1 \quad \text{eqn S1}$$

$$\bar{p}_{SE1} = 2r \sin\left(\frac{\alpha}{2}\right) \quad \text{eqn S2}$$

This profile is integrated over the interval  $[\frac{\pi}{2}, \frac{3\pi}{2}]$  which is  $\pi$  radians of rotation starting with the animal moving directly towards the sensor (see Fig. S2).

**S2.4. Model NE.** When the detection zone is not a circle, we have more complex profiles and 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  $\bar{p}$  for all approach angles by integrating across all  $2\pi$  angles of approach and dividing by  $2\pi$ .

There are three submodels within quadrant 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 profiles.

- (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' limits its size to being  $r \cos(x_1 - \theta/2)$  wide (see Fig. S3a).
- (3) The third profile is only found in NE3. If  $\alpha < 4\pi - 2\theta$ , then at  $x_1 = \theta/2 + \pi/2$ , 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. S3b). This gives a profile size of just  $r$ .

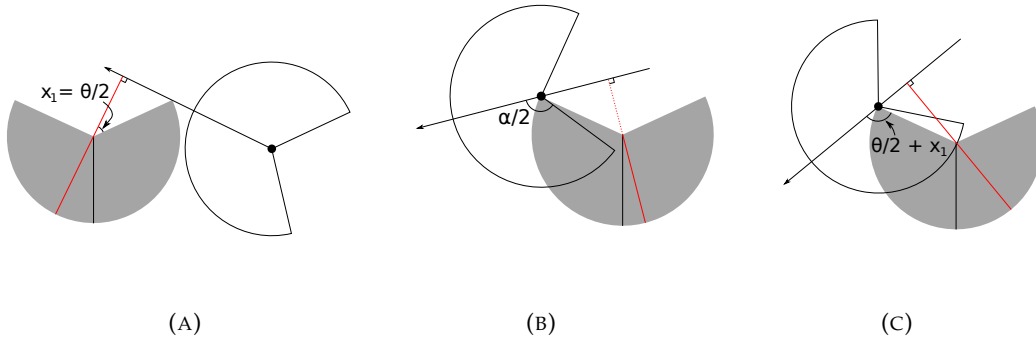


FIGURE S3. A) The second integral in NE with width  $r + r \cos(x_1 - \theta/2)$  B) The third integral in NE3.  $\alpha/2$  is labelled. As it is small, animals to the right of the detector cannot be detected (shown by a dashed red line.) C) After further rotation,  $\alpha/2$  is now bigger than the angle shown and animals to the right of the detector can again be sensed.

- (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 immediately 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  $5\pi/2 - \theta/2 - \alpha/2$ .
- (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.* Submodel NE1 exists within the area bounded by  $\alpha \leq 2\pi$ ,  $\theta \leq 2\pi$  and  $\alpha \geq 3\pi - \theta$ . It has four profiles; it does not include the  $r$  profile at  $x_1 = \pi$  (profile 3 above). Furthermore,  $\theta$  is wide enough that the  $r + r \cos(x_1 + \theta/2)$  profile starts at  $\pi$ . This then gives us

$$\bar{p}_{NE1} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}}^{\frac{\theta}{2}} 2r \, dx_1 + \int_{\frac{\theta}{2}}^{\pi} r \cos\left(\frac{\theta}{2} - x_1\right) + r \, dx_1 + \int_{\pi}^{2\pi - \frac{\theta}{2}} r \cos\left(\frac{\theta}{2} + x_1\right) + r \, dx_1 + \int_{2\pi - \frac{\theta}{2}}^{\frac{3\pi}{2}} 2r \, dx_1 \right) \quad \text{eqn S3}$$

$$\bar{p}_{NE1} = \frac{r}{\pi} \left( \theta + 2 \sin\left(\frac{\theta}{2}\right) \right) \quad \text{eqn S4}$$

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.

$$\bar{p}_{NE2} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}}^{\frac{\theta}{2}} 2r \, dx_1 + \int_{\frac{\theta}{2}}^{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}} r \cos\left(\frac{\theta}{2} - x_1\right) + r \, dx_1 + \int_{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}}^{2\pi - \frac{\theta}{2}} r \cos\left(\frac{\theta}{2} + x_1\right) + r \, dx_1 + \int_{2\pi - \frac{\theta}{2}}^{\frac{3\pi}{2}} 2r \, dx_1 \right) \quad \text{eqn S5}$$

$$\bar{p}_{NE2} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + \cos\left(\frac{\alpha}{2} + \theta\right) \right) \quad \text{eqn S6}$$

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).

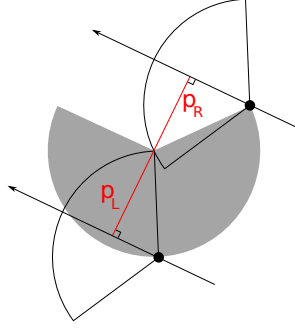


FIGURE S4. A) The second integral in SE. The right side of the profile ( $p_R$ ) is limited by the size of the sensor region while the left side of the profile ( $p_L$ ) is limited by the size of the call angle. The full profile has width  $p = r \sin(\alpha/2) + r \cos(\theta/2 - x_1)$ .

$$\bar{p}_{NE3} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}}^{\frac{\theta}{2}} 2r \, dx_1 + \int_{\frac{\theta}{2}}^{\frac{\theta}{2} + \frac{\pi}{2}} r \cos\left(\frac{\theta}{2} - x_1\right) + r \, dx_1 + \int_{\frac{\theta}{2} + \frac{\pi}{2}}^{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}} r \, dx_1 + \int_{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}}^{2\pi - \frac{\theta}{2}} r \cos\left(\frac{\theta}{2} + x_1\right) + r \, dx_1 + \int_{2\pi - \frac{\theta}{2}}^{\frac{3\pi}{2}} 2r \, dx_1 \right) \quad \text{eqn S7}$$

$$\bar{p}_{NE3} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S8}$$

**S2.5. Models SE2–4.** Quadrant SE contains three submodels (excluding SE1) that differ in ways reminiscent of the models in NE. There are four possible profiles.

- (1) As  $\alpha$  is less than  $\pi$  the profile is smaller than  $2r$ , even when the sensor width is a full diameter. The profile width starts as  $2r \sin(\alpha/2)$ .
- (2) Similar to NE, at a certain point the blind spot of the sensor area limits the profile width on one side. This gives a profile width of  $r \sin(\alpha/2) + r \cos(x_1 - \theta/2)$  (see Fig. S4).
- (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  $x_1 = \theta/2 + \pi/2 + \alpha/2$  the profile width becomes 0. This inequality distinguishes between SE3 and SE4.
- (5) The third 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. These integrals relate to profiles (1), (2) and (5) above.

$$\bar{p}_{SE2} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}} 2r \sin\left(\frac{\alpha}{2}\right) \, dx_1 + \int_{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) + r \cos\left(\frac{\theta}{2} - x_1\right) \, dx_1 + \int_{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{3\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) \, dx_1 \right) \quad \text{eqn S9}$$

$$\bar{p}_{SE2} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + \cos\left(\frac{\alpha}{2} + \theta\right) \right) \quad \text{eqn S10}$$

**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. This relates to profiles (1), (2), (3) and (5) above.

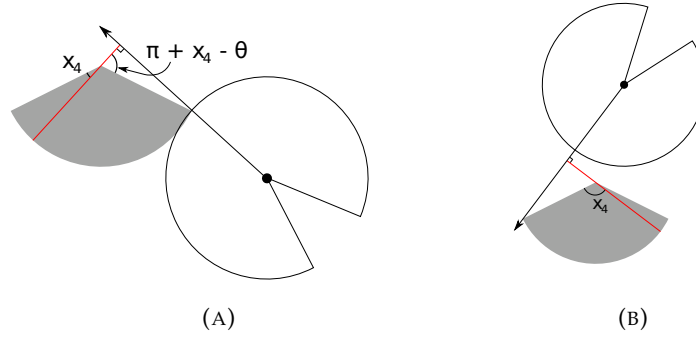


FIGURE S5. A) and B) The second and fourth profiles of NW1. The left side of both profiles is of width  $r$  while the right side is  $r \cos(\pi + x_4 - \theta) = -r \cos(\theta - x_4)$  and  $r \cos(\pi - x_4) = -r \cos x_4$  respectively.

$$\bar{p}_{SE3} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_1 + \int_{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{\theta}{2} + \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) + r \cos\left(\frac{\theta}{2} - x_1\right) dx_1 \right. \\ \left. + \int_{\frac{\theta}{2} + \frac{\pi}{2}}^{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_1 + \int_{\frac{5\pi}{2} - \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{3\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_1 \right) \quad \text{eqn S11}$$

$$\bar{p}_{SE3} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S12}$$

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 0 rather than returning to  $2r \sin(\alpha/2)$ . This relates to profiles (1), (2), (3) and (4) above though profile (4) with width 0 is not shown.

$$\bar{p}_{SE4} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_1 + \int_{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{\theta}{2} + \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) + r \cos\left(\frac{\theta}{2} - x_1\right) dx_1 + \int_{\frac{\theta}{2} + \frac{\pi}{2}}^{\frac{\alpha}{2} + \frac{\theta}{2} + \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_1 \right) \quad \text{eqn S13}$$

$$\bar{p}_{SE4} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S14}$$

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 sector (see Fig. S2b). During this interval the profile width is  $2r \sin(\theta/2) \sin(x_2)$  which is calculated using the equation for the length of a chord. 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. S5a).
- (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  $0r$  giving a profile size of  $r$ .
- (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. S5b). Therefore the width of the profile is  $r - r \cos(x_4)$ .
- (5) Finally, we have the  $x_2$  profile, but from behind.

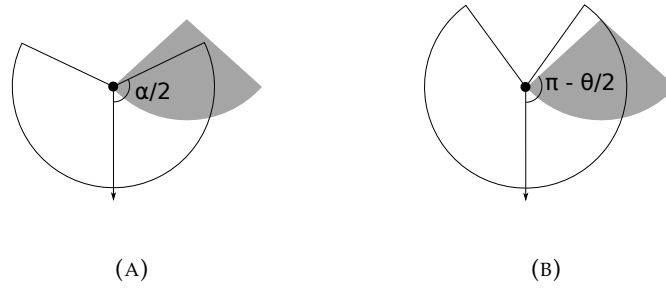


FIGURE S6. A) If  $\alpha/2$  is less than  $\pi - \theta/2$ , as is the case here, then the width of the profile when an animal approaches directly from behind is zero. B) If  $\alpha/2 > \pi - \theta/2$  the profile width from behind is  $2r \sin\left(\frac{\theta}{2}\right) \sin(x_2)$ .

$$\bar{p}_{NW1} = \frac{1}{\pi} \left( \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_0^{\theta - \frac{\pi}{2}} r - r \cos(-x_4 + \theta) dx_4 \right. \\ \left. + \int_{\theta - \frac{\pi}{2}}^{\frac{\pi}{2}} r dx_4 + \int_{\frac{\pi}{2}}^{\theta} r - r \cos(x_4) dx_4 + \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 \right) \quad \text{eqn S15}$$

$$\bar{p}_{NW1} = \frac{r}{\pi} (\theta + 2) \quad \text{eqn S16}$$

**S2.7. Models NW2–4.** The models 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.

- (1) When approaching the sensor from behind, there is a period where the profile is  $r$  wide as in NW1 profile (3).
- (2) At some point after profile (1) animals to the right of the sensor can be detected again. If this occurs in the  $x_4$  region, the profile width becomes  $r - r \cos(x_4)$  as in NW1.
- (3) However, as  $\alpha$  is now less than  $2\pi$ , animals to the right of the sensor may be undetectable 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 animals to the right of the sensor can be detected again 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 occur if  $\theta < 3\pi/2 - \alpha/2$  which is rearranged to find the inequality above. This defines the boundary between NW2 and NW3.
- (4) 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. S6. This inequality (simplified as  $\alpha \leq 2\pi - \theta$ ) 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  $x_4 = \theta$ .

$$\bar{p}_{NW2} = \frac{1}{\pi} \left( \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_0^{\theta - \frac{\pi}{2}} r - r \cos(-x_4 + \theta) dx_4 \right. \\ \left. + \int_{\theta - \frac{\pi}{2}}^{\frac{3\pi}{2} - \frac{\alpha}{2}} r dx_4 + \int_{\frac{3\pi}{2} - \frac{\alpha}{2}}^{\theta} r - r \cos(x_4) dx_4 + \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 \right) \quad \text{eqn S17}$$

$$\bar{p}_{NW2} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S18}$$

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

NW3 does not have the fourth integral from NW2 as animals are not detectable to the right of the sensor 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 profile 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  $2r \sin(x_2) \sin(\theta/2)$ .

$$\bar{p}_{NW3} = \frac{1}{\pi} \left( \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_0^{\theta - \frac{\pi}{2}} r - r \cos(-x_4 + \theta) dx_4 \right. \\ \left. + \int_{\theta - \frac{\pi}{2}}^{\theta} r dx_4 + \int_{\frac{3\pi}{2} - \frac{\alpha}{2} - \frac{\theta}{2}}^{\frac{3\pi}{2} - \frac{\alpha}{2}} r \cos\left(\frac{\theta}{2} - x_2\right) dx_2 + \int_{\frac{3\pi}{2} - \frac{\alpha}{2} - \frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 \right) \quad \text{eqn S19}$$

$$\bar{p}_{NW3} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S20}$$

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

$$\bar{p}_{NW4} = \frac{1}{\pi} \left( \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_0^{\theta - \frac{\pi}{2}} r - r \cos(-x_4 + \theta) dx_4 \right. \\ \left. + \int_{\theta - \frac{\pi}{2}}^{\theta} r dx_4 + \int_{\frac{\alpha}{2} + \frac{\theta}{2} - \frac{\pi}{2}}^{\frac{\alpha}{2} + \frac{\theta}{2} - \frac{\pi}{2}} r \cos\left(\frac{\theta}{2} - x_2\right) dx_2 \right) \quad \text{eqn S21}$$

$$\bar{p}_{NW4} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S22}$$

S2.8. **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 in front of the sensor and once as the animal approaches from behind the sensor.

- (1) Starting with an approach direction of directly towards the sensor, and examining focal angle  $x_2$ , the profile width is  $2r \sin(x_2) \sin(\theta/2)$ .
- (2) When the profile is perpendicular to the radius on the right hand of the sector sensor region, we instead examine  $x_3$  where the profile width is  $r \sin(x_3)$ .
- (3) At  $x_3 = \pi/2$  the profile becomes simply  $r$  and this continues for  $\theta$  radians of  $x_4$ .
- (4) The  $x_3$  profile is then repeated with an approach direction from behind the sensor.
- (5) Finally the  $x_2$  profile is repeated, again with an approach direction from behind the sensor.



$$\bar{p}_{\text{REM}} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) dx_3 + \int_0^{\theta} r dx_4 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) dx_3 + \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 \right) \quad \text{eqn S23}$$

$$\bar{p}_{\text{REM}} = \frac{r}{\pi} (\theta + 2) \quad \text{eqn S24}$$

**S2.9. Model NW5–7.** In the models NW5–7, the sensor has  $\theta \leq \pi/2$  as in the REM. As  $\alpha \geq \pi$  a lot of the profiles are similar to the REM. Specifically, the first three profiles are always the same as the first three profiles of the 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 the signal width is large enough that it can be detected once it has passed the sensor.

- (1) Starting with an approach direction of directly towards the sensor, and examining focal angle  $x_2$ , the profile width is  $2r \sin(x_2) \sin(\theta/2)$ .
- (2) When the profile is perpendicular to the radius edge of the sector sensor region, we instead examine  $x_3$  where the profile width is  $r \sin(x_3)$ .
- (3) At  $x_3 = \pi/2$  the profile becomes simply  $r$  and this continues for  $\theta$  radians of  $x_4$ .
- (4) 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.
- (5) If instead  $\alpha \geq 2\pi + 2\theta$  then the animal does not become undetectable during the  $x_3$  focal angle. Instead the profile has width greater than zero for the whole of the  $x_3$  angle. The  $x_2$  profile starts with width  $r \cos(x_2 - \theta/2)$  as only animals approaching to the left of the sensor are detectable.
- (6) 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)
- (7) or the right becomes detectable (if  $\alpha \geq 2\pi - \theta$  as in NW5), making both sides detectable and giving a profile width of  $2r \sin(x_2) \sin(\theta/2)$ .

**S2.9.1. 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.

$$\bar{p}_{\text{NW5}} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) dx_3 + \int_0^{\theta} r dx_4 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) dx_3 + \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{\pi}{2}} r \cos\left(\frac{\theta}{2} - x_2\right) dx_2 + \int_{\frac{3\pi}{2}-\frac{\theta}{2}-\frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 \right) \quad \text{eqn S25}$$

$$\bar{p}_{\text{NW5}} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S26}$$

**S2.9.2. 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.

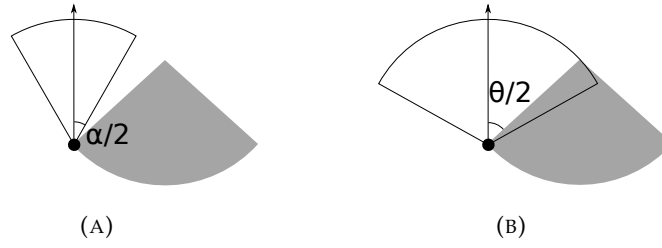


FIGURE S7. A) As  $\alpha/2 < \theta/2$  the profile width is limited by the call angle rather than the sensor region. The profile width is  $2r \sin(\frac{\alpha}{2})$  B) As  $\alpha/2 > \theta/2$  the profile width is limited by the sensor region, not the call angle. The profile width is  $2r \sin(\frac{\theta}{2}) \sin(x_2)$ .

$$\bar{p}_{NW6} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) dx_3 \right. \\ \left. + \int_0^{\theta} r dx_4 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) dx_3 + \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\alpha}{2} + \frac{\theta}{2} - \frac{\pi}{2}} r \cos\left(\frac{\theta}{2} - x_2\right) dx_2 \right) \quad \text{eqn S27}$$

$$\bar{p}_{NW6} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S28}$$

S2.9.3. *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.

$$\bar{p}_{NW7} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\theta}^{\frac{\pi}{2}} r \sin(x_3) dx_3 \right. \\ \left. + \int_0^{\theta} r dx_4 + \int_{\pi - \frac{\theta}{2}}^{\frac{\pi}{2}} r \sin(x_3) dx_3 \right) \quad \text{eqn S29}$$

$$\bar{p}_{NW7} = \frac{r}{\pi} \left( \theta - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S30}$$

S2.10. **Model SW1–3**. The models in SW1–3 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  $x_4$  profiles only once each.

There are five potential profile sizes.

- (1) At the beginning of  $x_2$ , with an approach direction directly towards the sensor, the parameter that limits the width of the profile can either be the sensor width, in which case the profile width is  $2r \sin(\theta/2) \sin(x_2)$ .
- (2) Or the call width can be the limiting parameter, in which case the profile width is instead  $2r \sin(\alpha/2)$  (see Fig. S7)
- (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 (see Fig. S8b). 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  $x_2 = \pi/2 + \alpha/2 - \theta/2$ .

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

S2.10.1. *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 SW 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  $r \sin(\alpha/2)$ .

$$\bar{p}_{SW1} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\frac{\theta}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) - r \cos\left(\frac{\theta}{2} + x_2\right) dx_2 \right. \\ \left. + \int_0^{\theta - \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) - r \cos(\theta - x_4) dx_4 + \int_{\theta - \frac{\pi}{2}}^{\frac{\alpha}{2} + \theta - \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \quad \text{eqn S31}$$

$$\bar{p}_{SW1} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S32}$$

S2.10.2. *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  $x_2 = \pi/2 - \alpha/2 + \theta/2$ .

$$\bar{p}_{SW2} = \frac{1}{\pi} \left( \int_{\frac{\alpha}{2} - \frac{\theta}{2} + \frac{\pi}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_2 + \int_{\frac{\theta}{2}}^{\frac{\alpha}{2} - \frac{\theta}{2} + \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) - r \cos\left(\frac{\theta}{2} + x_2\right) dx_2 \right. \\ \left. + \int_0^{\theta - \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) - r \cos(\theta - x_4) dx_4 + \int_{\theta - \frac{\pi}{2}}^{\frac{\alpha}{2} + \theta - \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \quad \text{eqn S33}$$

$$\bar{p}_{SW2} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S34}$$

S2.10.3. *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.

$$\bar{p}_{SW3} = \frac{1}{\pi} \left( \int_{\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_2 + \int_0^{-\frac{\pi}{2} + \theta - \frac{\alpha}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_4 \right. \\ \left. + \int_{-\frac{\pi}{2} + \theta - \frac{\alpha}{2}}^{\theta - \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) - r \cos(\theta - x_4) dx_4 + \int_{\theta - \frac{\pi}{2}}^{\frac{\alpha}{2} + \theta - \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \quad \text{eqn S35}$$

$$\bar{p}_{SW3} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S36}$$

S2.11. **Model SW4–9.** 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.

- (1) 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 Fig. S8a where  $\alpha/2 < \pi/2 - \theta$  which simplifies to give the previous inequality.

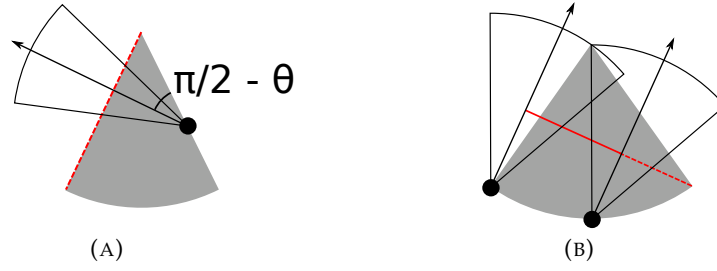


FIGURE S8. A) At  $x_4 = 0$ , if  $\alpha/2 < \pi/2 - \theta$  then  $\alpha/2$  is too small for an animal to be detected at all during the  $x_4$  profile (shown with dashed red.) This inequality simplifies to  $\alpha < \pi - 2\theta$ . B) The right of the profile is limited by the call width, not the sensor. On the left, the profile is limited by the sensor and not the call. Overall the profile width is  $r \sin(\alpha/2) - r \cos(x_2 + \theta/2)$ .

- (2) Models with  $\alpha \leq \theta$  are limited by  $\alpha$  in the first,  $x_2$  region (see Fig. S7), rather than being limited by  $\theta$ . Therefore this first profile is of width  $2r \sin(\alpha/2)$  rather than  $2r \sin(\theta/2) \sin(x_2)$ .
- (3) 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 Fig. S8b). This gives a width of  $r \sin(\alpha/2) - r \cos(x_2 + \theta/2)$ . This profile does not occur in models with  $\alpha \geq 2\theta$ .

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  $x_2$ .

$$\bar{p}_{SW4} = \frac{1}{\pi} \left( \int_{\frac{\alpha}{2} - \frac{\theta}{2} + \frac{\pi}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_2 + \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\alpha}{2} - \frac{\theta}{2} + \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) - r \cos\left(\frac{\theta}{2} + x_2\right) dx_2 \right. \\ \left. + \int_{\theta}^{\frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_3 + \int_0^{\frac{\alpha}{2} + \theta - \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \quad \text{eqn S37}$$

$$\bar{p}_{SW4} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S38}$$

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  $x_2$ .

$$\bar{p}_{SW5} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\frac{\pi}{2} - \frac{\theta}{2}}^{\frac{\pi}{2} + \frac{\theta}{2} - \frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) - r \cos\left(\frac{\theta}{2} + x_2\right) dx_2 \right. \\ \left. + \int_{\theta}^{\frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_3 + \int_0^{\frac{\alpha}{2} + \theta - \frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \quad \text{eqn S39}$$

$$\bar{p}_{SW5} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S40}$$

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.

$$\bar{p}_{\text{SW6}} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\theta}^{\frac{\alpha}{2}} r \sin(x_3) dx_3 \right. \\ \left. + \int_{\frac{\alpha}{2}}^{\frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_3 + \int_0^{\frac{\alpha}{2}+\theta-\frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) dx_4 \right) \quad \text{eqn S41}$$

$$\bar{p}_{\text{SW6}} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S42}$$

S2.11.4. *Model SW7.* SW7 is bounded by  $\alpha \leq \pi - 2\theta$ ,  $\alpha \geq \theta$  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  $x_2$ .

$$\bar{p}_{\text{SW7}} = \frac{1}{\pi} \left( \int_{\frac{\alpha}{2}-\frac{\theta}{2}+\frac{\pi}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\alpha}{2}\right) dx_2 + \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{\alpha}{2}-\frac{\theta}{2}+\frac{\pi}{2}} r \sin\left(\frac{\alpha}{2}\right) - r \cos\left(\frac{\theta}{2} + x_2\right) dx_2 + \int_{\theta}^{\frac{\alpha}{2}+\theta} r \sin\left(\frac{\alpha}{2}\right) dx_3 \right) \quad \text{eqn S43}$$

$$\bar{p}_{\text{SW7}} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S44}$$

S2.11.5. *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.

$$\bar{p}_{\text{SW8}} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}+\frac{\theta}{2}-\frac{\alpha}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{\pi}{2}+\frac{\theta}{2}-\frac{\alpha}{2}} r \sin\left(\frac{\alpha}{2}\right) - r \cos\left(\frac{\theta}{2} + x_2\right) dx_2 + \int_{\theta}^{\frac{\alpha}{2}+\theta} r \sin\left(\frac{\alpha}{2}\right) dx_3 \right) \quad \text{eqn S45}$$

$$\bar{p}_{\text{SW8}} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S46}$$

S2.11.6. *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 does not contain the extra  $x_2$  profile nor a  $x_4$  profile.

$$\bar{p}_{\text{SW9}} = \frac{1}{\pi} \left( \int_{\frac{\pi}{2}-\frac{\theta}{2}}^{\frac{\pi}{2}} 2r \sin\left(\frac{\theta}{2}\right) \sin(x_2) dx_2 + \int_{\theta}^{\frac{\alpha}{2}} r \sin(x_3) dx_3 + \int_{\frac{\alpha}{2}}^{\frac{\alpha}{2}+\theta} r \sin\left(\frac{\alpha}{2}\right) dx_3 \right) \quad \text{eqn S47}$$

$$\bar{p}_{\text{SW9}} = \frac{r}{\pi} \left( \theta \sin\left(\frac{\alpha}{2}\right) - \cos\left(\frac{\alpha}{2}\right) + 1 \right) \quad \text{eqn S48}$$

## 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 pl
11 from datetime import datetime
12 import os as os
13
14
15 os.chdir('/home/tim/Dropbox/liz-paper/lucasMoorcroftManuscript/supplementary-material')
16
17 # Use LaTeX printing
18 from sympy import init_printing ;
19 init_printing()
20 # Make LaTeX output white. Because I use a dark theme
21 init_printing(forecolor="White")
22
23
24 # Load symbols used for symbolic maths
25 t, a, r, x2, x3, x4, x1 = symbols('theta alpha r x_2 x_3 x_4 x_1', positive=True)
26 r1 = {r:1} # useful for lots of checks
27
28
29
30 # Define functions
31 # Calculate the final profile averaged over pi.
32 def calcModel(model):
33     x = pi*-1 * sum( [integrate(m[0], m[1:]) for m in model] ).simplify().trigsimp()
34     return x
35
36 # Do the replacements fit within the area defined by the conditions?
37 def confirmReplacements(conds, reps):
38     if not all([c.subs(reps) for c in eval(conds)]):
39         print('reps' + conds[4:] + ' incorrect')
40
41 # is average profile in range 0r-2r?
42 def profileRange(prof, reps):
43     if not 0 <= eval(prof).subs(dict(reps, **r1)) <= 2:
44         print('Total ' + prof + ' not in 0, 2r')
45
46 # Are the individuals integrals >0r
47 def intsPositive(model, reps):
48     m = eval(model)
49     for i in range(len(m)):
50         if not integrate(m[i][0], m[i][1:]).subs(dict(reps, **r1)) > 0:
51             print('Integral ' + str(i+1) + ' in ' + model + ' is negative')
52
53 # Are the individual averaged integrals between 0 and 2r
54 def intsRange(model, reps):
55     m = eval(model)
56     for i in range(len(m)):
57         if not 0 <= (integrate(m[i][0], m[i][1:])/(m[i][3]-m[i][2])).subs(dict(reps, **r1)) <=
58             2:
59             print('Integral ' + str(i+1) + ' in ' + model + ' has averaged integral outside
60                 0<p<2r')
61
62 # Are the bounds the correct way around
63 def checkBounds(model, reps):
64     m = eval(model)
65     for i in range(len(m)):
66         if not (m[i][3]-m[i][2]).subs(reps) > 0:
67             print('Bounds ' + str(i+1) + ' in ' + model + ' has lower bounds bigger than
68                 upper bounds')
69
70 # create latex strings with the 1) the integral equation that defines it and 2) the final calculated
71 model.
72 # There's some if statements to split longer equations on two lines and get +s in the right place.
73 def parseLaTeX(prof):
74     m = eval('m' + prof[1:] )
75
76     f = open('/latexFiles/'+prof+'.tex', 'w')
77     f.write('\begin{align}\n \quad \bar{p}_{\text{\tiny' + prof[1:] + '}} = &\frac{1}{\pi} \left(\right.\n
78         (\backslash;')
79     for i in range(len(m)):
80         # Roughly try and prevent expressions beginning with minus signs.
81         if latex(m[i][2])[0]=='-':
82             o1 = 'rev-lex'

```

```

78     else:
79         o1 = 'lex'
80
81     if latex(m[i][3])[0]=='-':
82         o2 = 'rev-lex'
83     else:
84         o2 = 'lex'
85
86     if latex(m[i][0])[0]=='-':
87         o3 = 'rev-lex'
88     else:
89         o3 = 'lex'
90
91     if latex(m[i][1])[0]=='-':
92         o4 = 'rev-lex'
93     else:
94         o4 = 'lex'
95
96         f.write('\int\limits_{'+latex(m[i][2], order=o1)+'}^'+latex(m[i][3], order=o2)+''+
97             latex(m[i][0], order=o3)+';\mathrm{d}'+latex(m[i][1], order=o4))
98         if len(m)>3 and i==(len(m)/2)-1:
99             f.write( '\right.\notag\\\n &\left.' )
100             if i<len(m)-1:
101                 f.write('+' )
102             f.write('\right)\label{' + prof + 'Def}\n')
103             f.write('\bar{p}_{\text{\tiny{' + prof[1:] + '}}} =&' + latex(eval(prof)) + '\label{' +
104                 prof + 'Sln}\n\end{align}')
105             f.close()
106
107 # Apply all checks.
108 def allChecks(prof):
109     model = 'm' + prof[1:]
110     reps = eval('rep' + prof[1:])
111     conds = 'cond' + prof[1:]
112     confirmReplacements(conds, reps)
113     profileRange(prof, reps)
114     intsPositive(model, reps)
115     intsRange(model, reps)
116     checkBounds(model, reps)
117
118 #####
119 ### Define and solve all models ###
120 #####
121 # NE1 animal: a = 2*pi. sensor: t > pi, a > 3pi - t #
122
123 mNE1 = [ [2*r, x1, pi/2, t/2 ],
124          [r + r*cos(x1 - t/2), x1, t/2, pi ],
125          [r + r*cos(x1 + t/2), x1, pi, 2*pi-t/2 ],
126          [2*r, x1, 2*pi-t/2, 3*pi/2 ] ]
127
128 # Replacement values in range
129 repNE1 = {t:3*pi/2, a:2*pi}
130
131 # Define conditions for model
132 condNE1 = [pi <= t, a >= 3*pi - t]
133
134 # Calculate model, run checks, write output.
135 pNE1 = calcModel(mNE1)
136 allChecks('pNE1')
137 parseLaTeX('pNE1')
138
139
140 # NE2 animal: a > pi. sensor: t > pi Condition: a < 3pi - t, a > 4pi - 2t #
141
142 mNE2 = [ [2*r, x1, pi/2, t/2 ],
143          [r + r*cos(x1 - t/2), x1, t/2, 5*pi/2 - t/2 - a/2 ],
144          [r + r*cos(x1 + t/2), x1, 5*pi/2 - t/2 - a/2, 2*pi-t/2 ],
145          [2*r, x1, 2*pi-t/2, 3*pi/2 ] ]
146
147 # Replacement values in range
148 repNE2 = {t:5*pi/3, a:4*pi/3-0.1}
149
150 # Define conditions for model
151 condNE2 = [pi <= t, a >= pi, a <= 3*pi - t, a >= 4*pi - 2*t]
152
153 # Calculate model, run checks, write output.
154 pNE2 = calcModel(mNE2)
155 allChecks('pNE2')
156 parseLaTeX('pNE2')
157
158
159 # NE3 animal: a > pi. sensor: t > pi Condition: a < 4pi - 2t #
160
161 mNE3 = [ [2*r, x1, pi/2, t/2 ],
162          [r + r*cos(x1 - t/2), x1, t/2, t/2 + pi/2 ],

```

```

163      [r, x1, t/2 + pi/2, 5*pi/2 - t/2 - a/2 ],
164      [r + r*cos(x1 + t/2), x1, 5*pi/2 - t/2 - a/2, 2*pi-t/2 ],
165      [2*r, x1, 2*pi-t/2, 3*pi/2 ] ]
166
167 # Replacement values in range
168 repNE3 = {t:5*pi/4-0.1, a:3*pi/2}
169
170 # Define conditions for model
171 condNE3 = [pi <= t, a >= pi, a <= 4*pi - 2*t]
172
173 # Calculate model, run checks, write output.
174 pNE3 = calcModel(mNE3)
175 allChecks('pNE3')
176 parseLaTeX('pNE3')
177
178 # NW1 animal: a = 2*pi. sensor: pi/2 <= t <= pi #
179
180 mNW1 = [ [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2 ],
181          [r - r*cos(x4 - t), x4, 0, t - pi/2 ],
182          [r, x4, t - pi/2, pi/2 ],
183          [r - r*cos(x4), x4, pi/2, t ],
184          [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2 ] ]
185
186 # Replacement values in range
187 repNW1 = {t:3*pi/4}
188
189 # Define conditions for model
190 condNW1 = [pi/2 <= t, t <= pi]
191
192 # Calculate model, run checks, write output.
193 pNW1 = calcModel(mNW1)
194 allChecks('pNW1')
195 parseLaTeX('pNW1')
196
197
198
199
200 # NW2 animal: a > pi. Sensor: pi/2 <= t <= pi. Condition: a > 2pi - t #
201
202 mNW2 = [ [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2 ],
203          [r - r*cos(x4 - t), x4, 0, t - pi/2 ],
204          [r, x4, t - pi/2, 3*pi/2 - a/2],
205          [r - r*cos(x4), x4, 3*pi/2 - a/2, t ],
206          [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2 ] ]
207
208 repNW2 = {t:3*pi/4, a:15*pi/8} # Replacement values in range
209
210 # Define conditions for model
211 condNW2 = [a > pi, pi/2 <= t, t <= pi, a >= 3*pi - 2*t]
212
213 # Calculate model, run checks, write output.
214 pNW2 = calcModel(mNW2)
215 allChecks('pNW2')
216 parseLaTeX('pNW2')
217
218
219
220 # NW3 animal: a > pi. Sensor: pi/2 <= t <= pi. Cond: 2pi - t < a < 3pi - 2t #
221
222 mNW3 = [ [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2 ],
223          [r - r*cos(x4 - t), x4, 0, t - pi/2 ],
224          [r, x4, t - pi/2, t ],
225          [r*cos(x2 - t/2), x2, t/2, 3*pi/2 - a/2 - t/2],
226          [2*r*sin(t/2)*sin(x2), x2, 3*pi/2 - a/2 - t/2, pi/2 ] ]
227
228 repNW3 = {t:5*pi/8, a:6*pi/4} # Replacement values in range
229
230 # Define conditions for model
231 condNW3 = [a > pi, pi/2 <= t, t <= pi, 2*pi - t <= a, a <= 3*pi - 2*t]
232
233 # Calculate model, run checks, write output.
234 pNW3 = calcModel(mNW3)
235 allChecks('pNW3')
236 parseLaTeX('pNW3')
237
238
239
240 # NW4 animal: a > pi. Sensor: pi/2 <= t <= pi. Condition: a <= 2pi - t #
241
242 mNW4 = [ [2*r*sin(t/2)*sin(x2), x2, t/2, pi/2],
243          [r - r*cos(x4 - t), x4, 0, t - pi/2],
244          [r, x4, t - pi/2, t],
245          [r*cos(x2 - t/2), x2, t/2, a/2 + t/2 - pi/2] ]
246
247
248
249

```



```

250 repNW4 = {t:3*pi/4, a:9*pi/8} # Replacement values in range
251
252 # Define conditions for model
253 condNW4 = [a > pi, pi/2 <= t, t <= pi, a <= 2*pi - t]
254
255 # Calculate model, run checks, write output.
256 pNW4 = calcModel(mNW4)
257 allChecks('pNW4')
258 parseLaTeX('pNW4')
259
260
261 # REM animal: a=2pi. Sensor: t <= pi/2. #
262
263 mREM = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2],
264          [r*sin(x3), x3, t, pi/2],
265          [r, x4, 0*t, t],
266          [r*sin(x3), x3, t, pi/2],
267          [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2] ]
268
269
270 repREM = {t:3*pi/8, a:2*pi} # Replacement values in range
271
272 # Define conditions for model
273 condREM = [ t <= pi/2 ]
274
275 # Calculate model, run checks, write output.
276 pREM = calcModel(mREM)
277 allChecks('pREM')
278 parseLaTeX('pREM')
279
280
281
282 # NW5 animal: a>pi. Sensor: t <= pi/2. Condition: 2*pi - t < a #
283
284
285 mNW5 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2],
286          [r*sin(x3), x3, t, pi/2],
287          [r, x4, 0, t],
288          [r*sin(x3), x3, t, pi/2],
289          [r*cos(x2 - t/2), x2, pi/2 - t/2, 3*pi/2 - t/2 - a/2],
290          [2*r*sin(t/2)*sin(x2), x2, 3*pi/2 - t/2 - a/2, pi/2] ]
291
292
293 repNW5 = {t:3*pi/8, a:29*pi/16} # Replacement values in range
294
295 # Define conditions for model
296 condNW5 = [a >= pi, t <= pi/2, 2*pi - t <= a ]
297
298 # Calculate model, run checks, write output.
299 pNW5 = calcModel(mNW5)
300 allChecks('pNW5')
301 parseLaTeX('pNW5')
302
303
304 # NW6 animal: a>pi. Sensor: t <= pi/2. Condition: 2*pi - 2*t <= a <= 2*pi - t #
305
306
307 mNW6 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2],
308          [r*sin(x3), x3, t, pi/2],
309          [r, x4, 0, t],
310          [r*sin(x3), x3, t, pi/2],
311          [r*cos(x2 - t/2), x2, pi/2 - t/2, a/2 + t/2 - pi/2] ]
312
313 repNW6 = {t:3*pi/8, a:3*pi/2} # Replacement values in range
314
315 # Define conditions for model
316 condNW6 = [a >= pi, t <= pi/2, 2*pi - 2*t <= a, a <= 2*pi - t]
317
318 # Calculate model, run checks, write output.
319 pNW6 = calcModel(mNW6)
320 allChecks('pNW6')
321 parseLaTeX('pNW6')
322
323
324
325 # NW7 animal: a>pi. Sensor: t <= pi/2. Condition: a <= 2pi - 2t #
326
327
328 mNW7 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2],
329          [r*sin(x3), x3, t, pi/2],
330          [r, x4, 0, t],
331          [r*sin(x3), x3, pi - a/2, pi/2] ]
332
333
334 repNW7 = {t:pi/9, a:10*pi/9} # Replacement values in range
335
336 # Define conditions for model

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```

337 condNW7 = [t <= pi/2, a >= pi, a <= 2*pi - 2*t]
338
339 # Calculate model, run checks, write output.
340 pNW7 = calcModel(mNW7)
341 allChecks('pNW7')
342 parseLaTeX('pNW7')
343
344
345
346 # SE1 animal: a <= pi. Sensor: t = 2pi. #
347
348 mSE1 = [ [ 2*r*sin(a/2), x1, pi/2, 3*pi/2 ],
349          ]
350
351
352 repSE1 = {a:pi/4} # Replacement values in range
353
354 # Define conditions for model
355 condSE1 = [a <= pi]
356
357 # Calculate model, run checks, write output.
358 pSE1 = calcModel(mSE1)
359 allChecks('pSE1')
360 parseLaTeX('pSE1')
361
362
363
364
365 # SE2 animal: a <= pi. Sensor: t > pi. Condition: a > 2pi - t, a > 4pi - 2t #
366
367 mSE2 = [ [ 2*r*sin(a/2), x1, pi/2, t/2 + pi/2 - a/2 ],
368          [ r*sin(a/2) + r*cos(x1 - t/2), x1, t/2 + pi/2 - a/2, 5*pi/2 - a/2 - t/2 ],
369          [ 2*r*sin(a/2), x1, 5*pi/2 - a/2 - t/2, 3*pi/2 ] ]
370
371
372 repSE2 = {t:19*pi/10, a:pi/2} # Replacement values in range
373
374 # Define conditions for model
375 condSE2 = [a <= pi, t >= pi, a >= 4*pi - 2*t]
376
377 # Calculate model, run checks, write output.
378 pSE2 = calcModel(mSE2)
379 allChecks('pSE2')
380 parseLaTeX('pSE2')
381
382
383 # SE3 animal: a <= pi. Sensor: t > pi. Condition: 2pi - t < a < 4pi - 2t #
384
385 mSE3 = [ [ 2*r*sin(a/2), x1, pi/2, t/2 + pi/2 - a/2 ],
386          [ r*sin(a/2) + r*cos(x1 - t/2), x1, t/2 + pi/2 - a/2, t/2 + pi/2 ],
387          [ r*sin(a/2), x1, t/2 + pi/2, 5*pi/2 - a/2 - t/2 ],
388          [ 2*r*sin(a/2), x1, 5*pi/2 - a/2 - t/2, 3*pi/2 ] ]
389
390 repSE3 = {t:3*pi/2 + 0.1, a:pi/2} # Replacement values in range
391
392 # Define conditions for model
393 condSE3 = [a <= pi, t >= pi, a >= 2*pi - t, a <= 4*pi - 2*t]
394
395 # Calculate model, run checks, write output.
396 pSE3 = calcModel(mSE3)
397 allChecks('pSE3')
398 parseLaTeX('pSE3')
399
400
401 # SE4 animal: a <= pi. Sensor: t > pi. Condition: a <= 4*pi - 2*t and a < 2*pi - t #
402
403
404 mSE4 = [ [ 2*r*sin(a/2), x1, pi/2, t/2 + pi/2 - a/2 ],
405          [ r*sin(a/2) + r*cos(x1 - t/2), x1, t/2 + pi/2 - a/2, t/2 + pi/2 ],
406          [ r*sin(a/2), x1, t/2 + pi/2, t/2 + pi/2 + a/2 ] ]
407
408
409 repSE4 = {t:3*pi/2, a:pi/3} # Replacement values in range
410
411 # Define conditions for model
412 condSE4 = [a <= pi, t >= pi/2, a <= 4*pi - 2*t, a <= 2*pi - t]
413
414 # Calculate model, run checks, write output.
415 pSE4 = calcModel(mSE4)
416 allChecks('pSE4')
417 parseLaTeX('pSE4')
418
419
420
421 # SW1 animal: a <= pi. Sensor: pi/2 <= t <= pi. Condition: a >= t and a/2 >= t - pi/2 #
422
423 mSW1 = [ [ 2*r*sin(t/2)*sin(x2), x2, pi/2 - a/2 + t/2, pi/2 ],

```

```

424      [r*sin(a/2) - r*cos(x2 + t/2),      x2, t/2,      pi/2 - a/2 + t/2],
425      [r*sin(a/2) - r*cos(x4 - t),      x4, 0,      t - pi/2 ],
426      [r*sin(a/2),      x4, t-pi/2,      t - pi/2 + a/2 ] ]
427
428
429 repSW1 = {t:5*pi/8, a:6*pi/8} # Replacement values in range
430
431 # Define conditions for model
432 condSW1 = [a <= pi, pi/2 <= t, t <= pi, a >= t, a/2 >= t - pi/2]
433
434 # Calculate model, run checks, write output.
435 pSW1 = calcModel(mSW1)
436 allChecks('pSW1')
437 parseLaTeX('pSW1')
438
439
440 # SW2 animal: a <= pi. Sensor: pi/2 <= t <= pi. Condition: a <= t and a/2 >= t - pi/2 #
441
442 mSW2 = [ [2*r*sin(a/2),      x2, pi/2 + a/2 - t/2, pi/2 ],
443          [r*sin(a/2) - r*cos(x2 + t/2), x2, t/2,      pi/2 + a/2 - t/2],
444          [r*sin(a/2) - r*cos(x4 - t),   x4, 0*t,      t - pi/2 ],
445          [r*sin(a/2),      x4, t - pi/2,      t - pi/2 + a/2 ] ]
446
447
448 repSW2 = {t:7*pi/8, a:7*pi/8-0.1} # Replacement values in range
449
450 # Define conditions for model
451 condSW2 = [a <= pi, pi/2 <= t, t <= pi, a/2 <= t/2, a/2 >= t - pi/2]
452
453 # Calculate model, run checks, write output.
454 pSW2 = calcModel(mSW2)
455 allChecks('pSW2')
456 parseLaTeX('pSW2')
457
458
459 # SW3 animal: a <= pi. Sensor: pi/2 <= t <= pi. Condition: a <= t and a/2 <= t - pi/2 #
460
461 mSW3 = [ [2*r*sin(a/2),      x2, t/2,      pi/2 ],
462          [2*r*sin(a/2),      x4, 0,      t - pi/2 - a/2 ],
463          [r*sin(a/2) - r*cos(x4 - t), x4, t - pi/2 - a/2, t - pi/2 ],
464          [r*sin(a/2),      x4, t - pi/2,      t - pi/2 + a/2 ] ]
465
466
467 repSW3 = {t:7*pi/8, a:2*pi/8} # Replacement values in range
468
469 # Define conditions for model
470 condSW3 = [a <= pi, pi/2 <= t, t <= pi, a/2 <= t/2, a/2 <= t - pi/2]
471
472 # Calculate model, run checks, write output.
473 pSW3 = calcModel(mSW3)
474 allChecks('pSW3')
475 parseLaTeX('pSW3')
476
477
478 # SW4 animal: a <= pi. Sensor: t <= pi/2. Condition: a > pi - 2t & a <= t #
479
480 mSW4 = [ [2*r*sin(a/2),      x2, pi/2 - t/2 + a/2, pi/2 ],
481          [r*sin(a/2) - r*cos(x2 + t/2), x2, pi/2 - t/2,      pi/2 - t/2 + a/2],
482          [r*sin(a/2),      x3, t,      pi/2 ],
483          [r*sin(a/2),      x4, 0,      a/2 + t - pi/2 ] ]
484
485
486 repSW4 = {t:pi/2-0.1, a:pi/4} # Replacement values in range
487
488 # Define conditions for model
489 condSW4 = [a <= pi, t <= pi/2, a >= pi - 2*t, a <= t]
490
491 # Calculate model, run checks, write output.
492 pSW4 = calcModel(mSW4)
493 allChecks('pSW4')
494 parseLaTeX('pSW4')
495
496
497 # SW5 animal: a <= pi. Sensor: t <= pi/2. Condition: a > pi - 2t & t <= a <= 2t #
498
499 mSW5 = [ [2*r*sin(t/2)*sin(x2),      x2, pi/2 + t/2 - a/2, pi/2 ],
500          [r*sin(a/2) - r*cos(x2 + t/2), x2, pi/2 - t/2,      pi/2 + t/2 - a/2],
501          [r*sin(a/2),      x3, t,      pi/2 ],
502          [r*sin(a/2),      x4, 0,      a/2 + t - pi/2 ] ]
503
504
505 repSW5 = {t:pi/2-0.1, a:pi/2} # Replacement values in range
506
507 # define conditions for model
508 condSW5 = [a <= pi, t <= pi/2, a >= pi - 2*t, t <= a, a <= 2*t]
509
510

```

```

511 # Calculate model, run checks, write output.
512 pSW5 = calcModel(mSW5)
513 allChecks('pSW5')
514 parseLaTeX('pSW5')
515
516
517 # SW6 animal: a <= pi. Sensor: t <= pi/2. Condition: a > pi - 2t & a > 2t #
518
519 mSW6 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2 ],
520          [r*sin(x3), x3, t, a/2 ],
521          [r*sin(a/2), x3, a/2, pi/2 ],
522          [r*sin(a/2), x4, 0, a/2 + t -pi/2 ] ]
523
524
525 repSW6 = {t:pi/4, a:3*pi/4} # Replacement values in range
526
527
528 # Define conditions for model
529 condSW6 = [a <= pi, t <= pi/2, a >= pi - 2*t, a > 2*t]
530
531 # Calculate model, run checks, write output.
532 pSW6 = calcModel(mSW6)
533 allChecks('pSW6')
534 parseLaTeX('pSW6')
535
536
537 # SW7 animal: a <= pi. Sensor: t <= pi/2. Condition: a <= pi - 2t & a <= t #
538
539 mSW7 = [ [2*r*sin(a/2), x2, pi/2 - t/2 + a/2, pi/2 ],
540          [r*sin(a/2) - r*cos(x2 + t/2), x2, pi/2 - t/2, pi/2 - t/2 + a/2],
541          [r*sin(a/2), x3, t, t + a/2 ] ]
542
543
544 repSW7 = {t:2*pi/8, a:pi/8} # Replacement values in range
545
546 # Define conditions for model
547 condSW7 = [a <= pi, t <= pi/2, a <= pi - 2*t, a <= t]
548
549 # Calculate model, run checks, write output.
550 pSW7 = calcModel(mSW7)
551 allChecks('pSW7')
552 parseLaTeX('pSW7')
553
554
555 # SW8 animal: a <= pi. Sensor: t <= pi/2. Condition: a <= pi - 2t & t <= a <= 2t #
556
557 mSW8 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 + t/2 - a/2, pi/2 ],
558          [r*sin(a/2) - r*cos(x2 + t/2), x2, pi/2 - t/2, pi/2 + t/2 - a/2],
559          [r*sin(a/2), x3, t, t + a/2 ] ]
560
561 repSW8 = {t:2*pi/8, a:pi/2-0.1} # Replacement values in range
562
563 # Define conditions for model
564 condSW8 = [a <= pi, t <= pi/2, a <= pi - 2*t, t <= a, a <= 2*t]
565
566 # Calculate model, run checks, write output.
567 pSW8 = calcModel(mSW8)
568 allChecks('pSW8')
569 parseLaTeX('pSW8')
570
571
572 # SW9 animal: a <= pi. Sensor: t <= pi/2. Condition: a <= pi - 2t & 2t <= a #
573
574 mSW9 = [ [2*r*sin(t/2)*sin(x2), x2, pi/2 - t/2, pi/2 ],
575          [r*sin(x3), x3, t, a/2 ],
576          [r*sin(a/2), x3, a/2, t + a/2 ] ]
577
578
579 repSW9 = {t:1*pi/8, a:pi/2} # Replacement values in range
580
581 # Define conditions for model
582 condSW9 = [a <= pi, t <= pi/2, a <= pi - 2*t, 2*t <= a]
583
584 # Calculate model, run checks, write output.
585 pSW9 = calcModel(mSW9)
586 allChecks('pSW9')
587 parseLaTeX('pSW9')
588
589
590 #####
591 ## Run tests ##
592 #####
593
594 # create gas model object
595 gas = 2*r
596
597

```

```

598 # for each model run through every adjacent model.
599 # Contains duplicates but better for avoiding missed comparisons.
600 # Also contains replacement t->a and a->t just in case.
601
602
603 allComps = [
604 ['gas', 'pNE1', {t:2*pi}], ['gas', 'pSE1', {a:pi}],
605
606 ['pNE1', 'gas', {t:2*pi}], ['pNE1', 'pNW1', {t:pi}],
607 ['pNE1', 'pNE2', {a:3*pi-t}], ['pNE1', 'pNE2', {t:3*pi-a}],
608
609 ['pNE2', 'pNE1', {a:3*pi-t}], ['pNE2', 'pNE1', {t:3*pi-a}],
610 ['pNE2', 'pNE3', {a:4*pi-2*t}], ['pNE2', 'pNE3', {t:2*pi-a/2}],
611 ['pNE2', 'pSE2', {a:pi}],
612
613 ['pNE3', 'pNE2', {a:4*pi-2*t}], ['pNE3', 'pNE2', {t:2*pi-a/2}],
614 ['pNE3', 'pSE3', {a:pi}], ['pNE3', 'pNW2', {t:pi}],
615
616 ['pNW1', 'pNE1', {t:pi}], ['pNW1', 'pNW2', {a:2*pi}],
617
618 ['pNW2', 'pNE3', {t:pi}], ['pNW2', 'pNW3', {a:3*pi-2*t}],
619 ['pNW2', 'pNW3', {t:3*pi/2-a/2}], ['pNW2', 'pNW1', {a:2*pi}],
620
621 ['pNW3', 'pNW5', {t:pi/2}], ['pNW3', 'pNW4', {a:2*pi-t}],
622 ['pNW3', 'pNW4', {t:2*pi-a}], ['pNW3', 'pNW2', {a:3*pi-2*t}],
623 ['pNW3', 'pNW2', {t:3*pi/2-a/2}],
624
625 ['pNW4', 'pNW6', {t:pi/2}], ['pNW4', 'pNW3', {t:2*pi-a}],
626 ['pNW4', 'pNW3', {a:2*pi-t}], ['pNW4', 'pSW1', {a:pi}],
627
628 ['pREM', 'pNW1', {t:pi/2}], ['pREM', 'pNW5', {a:2*pi}],
629
630 ['pNW5', 'pREM', {a:2*pi}], ['pNW5', 'pNW6', {a:2*pi-t}],
631 ['pNW5', 'pNW6', {t:2*pi-a}], ['pNW5', 'pNW3', {t:pi/2}],
632
633 ['pNW6', 'pNW5', {a:2*pi-t}], ['pNW6', 'pNW5', {t:2*pi-a}],
634 ['pNW6', 'pNW7', {t:pi-a/2}], ['pNW6', 'pNW7', {a:2*pi-2*t}],
635 ['pNW5', 'pNW4', {t:pi/2}],
636
637 ['pNW7', 'pNW6', {t:2*pi-2*a}], ['pNW7', 'pNW6', {a:2*pi-2*t}],
638 ['pNW7', 'pSW6', {a:pi}],
639
640 ['pSE1', 'pSE2', {t:2*pi}], ['pSE1', 'gas', {a:pi}],
641
642 ['pSE2', 'pSE3', {t:2*pi-a/2}], ['pSE2', 'pSE3', {a:4*pi-2*t}],
643 ['pSE2', 'pSE1', {t:2*pi}], ['pSE2', 'pNE2', {a:pi}],
644
645 ['pSE3', 'pSE2', {a:4*pi-2*t}], ['pSE3', 'pSE2', {t:2*pi-a/2}],
646 ['pSE3', 'pSE4', {a:2*pi-t}], ['pSE3', 'pSE4', {t:2*pi-a}],
647 ['pSE3', 'pNE3', {a:pi}],
648
649 ['pSE4', 'pSE3', {t:2*pi-a}], ['pSE4', 'pSE3', {a:2*pi-t}],
650 ['pSE4', 'pSW3', {t:pi}],
651
652 ['pSW1', 'pSW5', {t:pi/2}], ['pSW1', 'pSW2', {a:t}],
653 ['pSW1', 'pSW2', {t:a}], ['pSW1', 'pNW4', {a:pi}],
654
655 ['pSW2', 'pSW1', {a:t}], ['pSW2', 'pSW1', {t:a}],
656 ['pSW2', 'pSW4', {t:pi/2}], ['pSW2', 'pSW3', {a:2*t-pi}],
657 ['pSW2', 'pSW3', {t:a/2+pi/2}],
658
659 ['pSW3', 'pSW2', {t:a/2+pi/2}], ['pSW3', 'pSW2', {a:2*t-pi}],
660 ['pSW3', 'pSE4', {t:pi}],
661
662
663 ['pSW4', 'pSW7', {a:pi-2*t}], ['pSW4', 'pSW7', {t:pi/2-a/2}],
664 ['pSW4', 'pSW5', {t:a}], ['pSW4', 'pSW5', {a:t}],
665 ['pSW4', 'pSW2', {t:pi/2}],
666
667 ['pSW5', 'pSW4', {t:a}], ['pSW5', 'pSW4', {a:t}],
668 ['pSW5', 'pSW8', {t:pi/2-a/2}], ['pSW5', 'pSW8', {a:pi-2*t}],
669 ['pSW5', 'pSW6', {a:2*t}], ['pSW5', 'pSW6', {t:a/2}],
670 ['pSW5', 'pSW1', {t:pi/2}],
671
672 ['pSW6', 'pSW9', {t:pi/2-a/2}], ['pSW6', 'pSW9', {a:pi-2*t}],
673 ['pSW6', 'pSW5', {a:2*t}], ['pSW6', 'pSW5', {t:a/2}],
674 ['pSW6', 'pNW7', {a:pi}],
675
676
677 ['pSW7', 'pSW8', {t:a}], ['pSW7', 'pSW8', {a:t}],
678 ['pSW7', 'pSW4', {t:pi/2-a/2}], ['pSW7', 'pSW4', {a:pi-2*t}],
679
680 ['pSW8', 'pSW7', {a:t}], ['pSW8', 'pSW7', {t:a}],
681 ['pSW8', 'pSW9', {a:2*t}], ['pSW8', 'pSW9', {t:a/2}],
682 ['pSW8', 'pSW5', {a:pi-2*t}], ['pSW8', 'pSW5', {t:pi/2-a/2}],
683
684 ['pSW9', 'pSW8', {a:2*t}], ['pSW9', 'pSW8', {t:a/2}],

```

```

685 ['pSW9', 'pSW6', {a:pi-2*t}], ['pSW9', 'pSW6', {t:pi/2-a/2}]
686 ]
687
688
689 # List of regions that touch a=0. Should equal 0 when a=0.
690 zeroRegions = ['pSW9', 'pSW8', 'pSW7', 'pSW4', 'pSW2', 'pSW3', 'pSE4', 'pSE3', 'pSE1']
691
692
693 # Run through all the comparisons. Need simplify(). Even together() gives some false negatives.
694
695 checkFile = open('checksFile.tex', 'w')
696
697 checkFile.write('All checks evaluated.\nTim Lucas - ' + str(datetime.now()) + '\n')
698 for i in range(len(allComps)):
699     if (eval(allComps[i][0]).subs(allComps[i][2]) - eval(allComps[i][1]).subs(allComps[i][2]))
       simplify() == 0:
700         checkFile.write(str(i) + ': ' + allComps[i][0] + ' and ' + allComps[i][1] + ': OK\n')
701     else:
702         checkFile.write(str(i) + ': ' + allComps[i][0] + ' and ' + allComps[i][1] + ': Incorrect\n')
703
704 for i in range(len(zeroRegions)):
705     if eval(zeroRegions[i]).subs({a:0}).simplify() == 0:
706         checkFile.write(zeroRegions[i] + ' at a = 0: OK\n')
707     else:
708         checkFile.write(zeroRegions[i] + ' at a = 0: Incorrect\n')
709
710 # pSE2 is slightly different. Only one corner touches a=0, so need theta value as well. I'm not sure why
       this isn't
711 # A problem for some other regions.
712 if pSE2.subs({a:0, t:2*pi}) == 0:
713     checkFile.write('pSE2 at a = 0, t = 2pi: OK\n')
714 else:
715     checkFile.write('pSE2 at a = 0, t = 2pi: Incorrect\n')
716 checkFile.close()
717
718
719 # And print to terminal
720 #for i in range(len(allComps)):
721     if not (eval(allComps[i][0]).subs(allComps[i][2]) - eval(allComps[i][1]).subs(allComps[i][2]))
       simplify() == 0:
722         print allComps[i][0] + ' and ' + allComps[i][1] + ': Incorrect\n'
723
724
725 #####
726 ### Define a function that calculates p bar answer. #####
727 #####
728
729 def calcP(A, T, R):
730     assert (A <= 2*pi and A >= 0), "a is out of bounds. Should be in 0<a<2*pi"
731     assert (T <= 2*pi and T >= 0), "s is out of bounds. Should be in 0<s<2*pi"
732
733     if A > pi:
734         if A < 4*pi - 2*T:
735             p = pNW7.subs({a:A, t:T, r:R}).n()
736         elif A <= 3*pi - T:
737             p = pNE2.subs({a:A, t:T, r:R}).n()
738         else:
739             p = pNE1.subs({a:A, t:T, r:R}).n()
740     else:
741         if A < 4*pi - 2*T:
742             p = pSE3.subs({a:A, t:T, r:R}).n()
743         else:
744             p = pSE2.subs({a:A, t:T, r:R}).n()
745     return p
746
747
748 #####
749 ## Apply to entire grid ##
750 #####
751
752 # How many values for each parameter
753 nParas = 100
754
755 # Make a vector for a and s. Make an empty nParas x nParas array.
756 # Calculated profile sizes will go in pArray
757 tVec = np.linspace(0, 2*pi, nParas)
758 aVec = np.linspace(0, 2*pi, nParas)
759 pArray = np.zeros((nParas, nParas))
760
761 # Calculate profile size for each combination of parameters
762 for i in range(nParas):
763     for j in range(nParas):
764         pArray[i][j] = calcP(aVec[i], tVec[j], 1)
765
766 # Turn the array upside down so origin is at bottom left.
767 pImage = np.flipud(pArray)
768

```

```

769 # Plot and save.
770 pl.imshow(pImage, interpolation='none', cmap=pl.get_cmap('Blues') )
771
772 # Show or save image.
773 # pl.show()
774 # pl.savefig('/imgs/profilesCalculated.png')
775
776
777
778 #####
779 ##### Output R function. #####
780 #####
781
782 # To reduce mistakes, output R function directly from python.
783 # However, the if statements, which correspond to the bounds of each model, are not automatic.
784
785 Rfunc = open('supplementaryRscript.R', 'w')
786
787 Rfunc.write("""
788 # Functions to calculate density.
789 #
790 # Tim C.D. Lucas, Elizabeth Moorcroft, Robin Freeman, Marcus J. Rowcliffe, Kate E. Jones.
791 #
792 # calcDensity is the main function to calculate density.
793 # It takes parameters z, alpha, theta, r, animalSpeed, t
794 # z - The number of camera/acoustic counts or captures.
795 # alpha - Call width in radians.
796 # theta - Sensor width in radians.
797 # r - Sensor range in metres.
798 # animalSpeed - Average animal speed in metres per second.
799 # t - Length of survey in sensor seconds i.e. number of sensors x survey duration.
800 #
801 # calcAbundance calculates abundance rather than density and requires an extra parameter
802 # area - In metres squared. The size of the region being examined.
803
804
805 # Internal function to calculate profile width as described in the text
806 calcProfileWidth <- function(alpha, theta, r){
807     if(alpha > 2*pi | alpha < 0)
808         stop('alpha is out of bounds. alpha should be in interval 0<a<2*pi')
809     if(theta > 2*pi | theta < 0)
810         stop('theta is out of bounds. theta should be in interval 0<a<2*pi')
811
812     if(alpha > pi){
813         if(alpha < 4*pi - 2*theta){
814             "" +
815             '      p <- ' + str(pNW7) +
816             '\n          } else if(alpha <= 3*pi - theta){'
817             '\n              p <- ' + str(pNE2) +
818             '\n          } else {'
819             '\n              p <- ' + str(pNE1) +
820             '\n          }'
821             '\n          } else {'
822             '\n              if(alpha < 4*pi - 2*theta){'
823             '\n                  p <- ' + str(pSE3) +
824             '\n              } else {'
825             '\n                  p <- ' + str(pSE2) +
826             '\n              }'
827             '\n          }'
828             '\n          return(p)'
829             '\n}' +
830             ""
831
832 # Calculate a population density. See above for units etc.
833 calcDensity <- function(z, alpha, theta, r, animalSpeed, t){
834     # Check the parameters are suitable.
835     if(z <= 0 | !is.numeric(z)) stop('Counts, z, must be a positive number.')
836     if(animalSpeed <= 0 | !is.numeric(animalSpeed)) stop('animalSpeed must be a positive number.')
837     if(t <= 0 | !is.numeric(t)) stop('Time, t, must be a positive number.')
838
839     # Calculate profile width, then density.
840     p <- calcProfileWidth(alpha, theta, r)
841     D <- z/(animalSpeed*t*p)
842     return(D)
843 }
844
845 # Calculate abundance rather than density.
846 calcAbundance <- function(z, alpha, theta, r, animalSpeed, t, area){
847     if(area <= 0 | !is.numeric(area)) stop('Area must be a positive number')
848     D <- calcDensity(z, alpha, theta, r, animalSpeed, t)
849     A <- D*area
850     return(A)
851 }
852 )
853
854 Rfunc.close()

```

---

REM-Analysis.py



## 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   D <- z/(animalSpeed*t*p)
54   return(D)
55 }
56
57 # Calculate abundance rather than density.
58 calcAbundance <- function(z, alpha, theta, r, animalSpeed, t, area){
59   if(area <= 0 | !is.numeric(area)) stop('Area must be a positive number')
60   D <- calcDensity(z, alpha, theta, r, animalSpeed, t)
61   A <- D*area
62   return(A)
63 }

```

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. 3, 6, 8
- SymPy Development Team (2014) *SymPy: Python library for symbolic mathematics*. 14
- Yapp, W. (1956) The theory of line transects. *Bird study*, **3**, 93–104. 2