

1 **Component processes of detection probability in camera-trap studies: understanding**  
2 **the occurrence of false-negatives**

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12 **Abstract:** Camera-trap studies in the wild record true-positive data, but data loss from false-negatives (i.e. an  
13 animal is present but not recorded) is likely to vary and widely impact data quality. Detection probability is  
14 defined as the probability of recording an animal if present in the study area. We propose a framework of  
15 sequential processes within detection - a pass, trigger, image registration, and images being of sufficient  
16 quality. Using Closed Circuit TV (CCTV) combined with camera-trap arrays we quantified variation in, and  
17 drivers of, these processes for three medium sized mammal species. We also compared trigger success of wet  
18 and dry otter *Lutra lutra*, as an example of a semi-aquatic species. Data loss from failed trigger, failed  
19 registration and poor capture quality varied between species, camera-trap model and settings, and were  
20 affected by different environmental and animal variables. Distance had a negative effect on trigger probability  
21 and a positive effect on registration probability. Faster animals had both reduced trigger and registration  
22 probabilities. Close passes (1m) frequently did not generate triggers, resulting in over 20% data loss for all  
23 species. Our results, linked to the framework describing processes, can inform study design to minimise, or  
24 account for data loss during analysis and interpretation.

25 **Keywords:** camera-trap; data quality; detection; false-negatives.

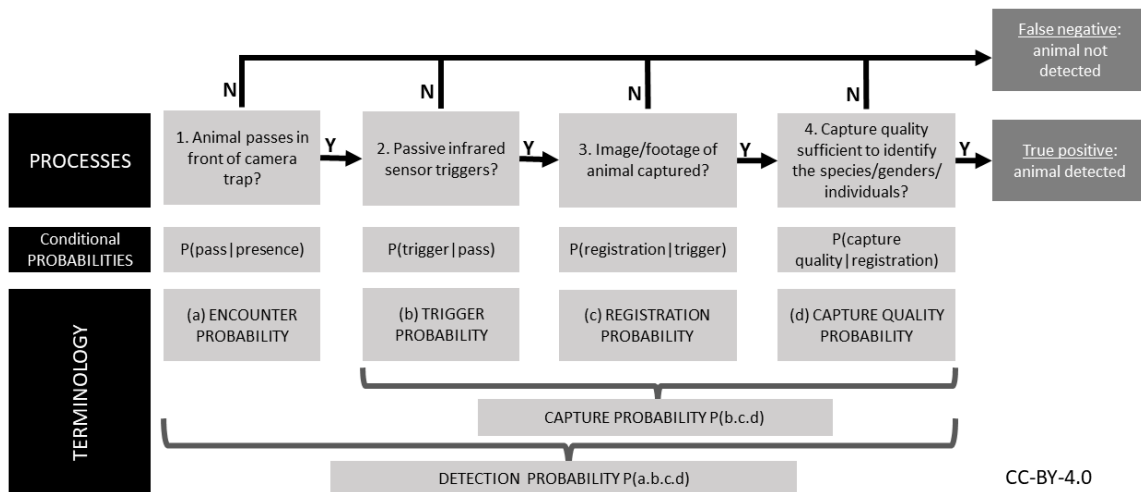
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## 27 Introduction

28 Camera-traps (CTs) are used for a range of ecological studies from determining presence or occupancy  
29 (Mugerwa et al. 2013; Tobler et al. 2015) to activity (Lim and Ng 2008). Studies using CTs have proliferated,  
30 however, it is not considered “fully mature as a methodological discipline” (Rowcliffe 2017). The technical  
31 aspects of how CTs using passive infrared (PIR) motion detectors function, and clarification of associated  
32 terminology have been described (Welbourne et al. 2016). In short, a specialised ‘Fresnel’ lens focuses  
33 background infrared radiation (IR), filtered to 8–14  $\mu\text{m}$  onto a pyroelectric sensor. This sensor detects rapid  
34 changes in background IR which triggers the camera to record. As with more traditional census techniques, it  
35 is recognised that PIR CTs are prone to false-negatives, i.e. fail to detect a species which is present (Gužvica et  
36 al. 2014). Detection probability is a fundamental issue in CT studies of occupation and population density,  
37 particularly in studies using Random Encounter Modelling (REM) of animals that lack easily distinguishable  
38 individual markings (Rowcliffe et al. 2008).

39 Field data from CTs can only include true-positives: when an animal pass elicits a trigger which results in  
40 registration of the animal as recorded footage. In order to achieve a true-positive, a number of sequential  
41 processes have to occur, all of which must have a successful outcome (Figure 1), and these sequential processes  
42 underlie a series of measurable conditional probabilities. False positives, such as misidentification of species,  
43 sex or individual, are errors by the observer of the footage, and not the CT itself. Some species may be more  
44 prone to being incorrectly identified, such as Scottish wildcat *Felis silvestris silvestris*, where the phenotype of  
45 the “pure” species and the hybrid are very similar. True negatives are the result of an absence of footage in an  
46 area where a species is absent. False-negatives can arise from failure of any processes in Figure 1. True and  
47 false-negatives cannot be distinguished from each other which is why it is important to try to understand and  
48 account for the latter.

49 **Fig. 1** The sequential processes required to detect an animal on a camera-trap given that it is present. Failure of  
50 any of these processes leads to a false-negative therefore detection success requires a positive outcome from all  
51 the component processes. Specific terminology we use in this study to quantify these processes is also shown.  
52 ‘Detection probability’ can thus be considered the product of a series of conditional probabilities representing  
53 each of these processes.



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55 Process 1: Encounter probability  $P(\text{pass}|\text{presence})$ . This is the probability an animal will pass through the  
 56 putative “detection zone” of a CT given that it is present in the study area. This has been demonstrated to be  
 57 affected by aspects of survey design such as the density and placement of CTs in relation to the species rarity  
 58 and home-range size (O’Connor et al. 2017), sampling effort, specifically number of CT days and number of  
 59 CTs deployed (Tobler et al. 2008), use of attractants such as bait (Hamel et al. 2013) and animal reaction to CT  
 60 presence (Larrucea et al. 2007). Inappropriate sampling design could affect the probability of a pass, for instance  
 61 setting the CT at ground level for arboreal species.

62 Process 2: Trigger probability  $P(\text{trigger}|\text{pass})$ . This is the probability that the CT’s PIR sensor senses a change  
 63 in infrared from the pass of an animal which causes the CT to trigger. It has been suggested that mammals with  
 64 aquatic lifestyles result in low trigger probability as their thermal footprint can be compromised by wet fur after  
 65 exiting water (Lerone et al. 2015).

66 Process 3: Registration probability  $P(\text{registration}|\text{trigger})$ . A CT trigger is not sufficient alone to record an  
 67 animal – the animal must also be visible on the CT image or video. Trigger latency or trigger speed is the  
 68 interval of time between PIR trigger and initiation of the camera (Rovero et al. 2013) which can vary widely  
 69 between CT models (Randler and Kalb 2018). A slow trigger speed coupled with fast moving animals means  
 70 that not all triggers lead to registration as the animal has passed through the field-of-view before the camera has  
 71 been activated (Rovero et al. 2013). The field-of-view of the camera is not necessarily the same width as the  
 72 detection zone monitored by the PIR motion detector (Rovero *et al.* 2013; Trolliet *et al.* 2014; Rovero and  
 73 Zimmermann 2016), thus affecting registration probability. Previous studies, without use of a control (to  
 74 identify scenarios where an animal triggers the camera but is not recorded) have only been able to measure the  
 75 combined detection of processes 2 and 3 (Rowcliffe et al. 2011; Hofmeester et al. 2017). So while body mass,  
 76 season and relative position of an animal with respect to the camera are likely to influence across processes 2  
 77 and 3 (Rowcliffe et al. 2011), these may operate on trigger probability, registration probability, or both.

78 Process 4: Capture quality probability  $P(\text{capture quality}|\text{registration})$ . Not all footage/images of a study species  
 79 are of equal value, as images of a given quality may be required depending on a study’s objectives. ‘Quality’  
 80 here refers to the contents of the footage/images rather than image resolution per se. For example, if aiming

81 to identify individuals, reliable unique markers need to be visible, so a given angle of view or fully body image  
82 may be required (Foster and Harmsen 2012). Similarly, in species where it is possible to determine sex, and the  
83 study aims require this, footage containing sufficient views of an animal in terms of primary and/or secondary  
84 sexual characteristics may be required (Findlay et al. 2017), and whilst video may be better than stills, sexing  
85 animals may not be possible for every registration.

86 Hofmeester *et al.*(2019) developed a conceptual framework for detectability in CT studies which considers  
87 animal characteristics, CT specifications, CT set-up protocols and environmental variables in context with a  
88 hierarchy of different spatial scales and six orders of habitat selection. Our framework broadly converges with  
89 this. In practice, most CT studies can't quantify trigger probability in isolation from registration probability and  
90 often trigger probability is misrepresented as a combination of trigger and registration together. Using Closed  
91 Circuit TV (CCTV), we look specifically at Processes 2–3 (Figure 1), which equate to the 5<sup>th</sup> and 6<sup>th</sup> scale  
92 described by Hofmeester *et al.* (2019), i.e. what happens when an animal passes in front of a CT, and we also  
93 present capture quality probability as a separate process.

94 We hypothesise that different environmental and animal-based factors will bias/influence each process as they  
95 result from different functional components of the CT (the PIR sensor and the camera). For example, trigger  
96 probability will relate to changes in IR received by the PIR sensor and the PIR sensitivity setting. This received  
97 IR will in turn will be governed by the spatial relationship between the animal and the PIR sensor as the animal  
98 enters the putative zone of detection, as well as the thermal properties of the animal's surface in relation to the  
99 background, CT height and vegetation density (see Hofmeester et al. 2019). Registration probability only  
100 applies when the PIR sensor has triggered and will be governed by the spatio-temporal relationship between the  
101 animal and the camera's field-of-view in the time between the trigger and camera initiation (i.e. the trigger  
102 speed), and may also be affected by variables such as the speed of the passing animal, and variables with  
103 potential to completely obscure the image such as dense vegetation and fog. Capture quality probability may be  
104 affected by the proportion, and which portion, of the animal that is within the image, in addition to factors that  
105 may affect the quality of the image e.g. the speed of the passing animal (blurring), vegetation density (obscuring  
106 view), weather (mist and rain) and time of day (glare from sun).

107 We used CCTV as a control to record all passes of each of our target species through the putative detection  
108 zones of arrays of CTs in order to observe at which process CTs produced false negatives. CCTV explicitly  
109 allowed us to observe all passes, even when these did not elicit a trigger, or did elicit a trigger but not a  
110 registration. Using CCTV enables distinction between the latter and genuine "false triggers" (i.e. triggers caused  
111 by extraneous stimuli which also result in footage not containing the target species). Such a distinction cannot  
112 be made without a control (e.g. CCTV or direct observation). Two CT models were chosen to contrast field-of-  
113 view and detection zone differences, one with a more standard detection zone and field-of-view (Bushnell) and  
114 one with wide detection and field-of-view (Acorn). We were able to separately investigate variation in trigger  
115 probability, registration probability and elements of capture quality probability for one semi-aquatic (Eurasian  
116 otter *Lutra lutra*), and two terrestrial (red fox *Vulpes vulpes* and Eurasian badger *Meles meles*) mammal species  
117 of a similar size (hereafter 'otter', 'fox' and 'badger'). We hypothesised that the variables driving success in  
118 processes 2, 3 and 4 would be different, for example we would expect trigger probability to be influenced  
119 primarily by distance, whilst registration probability would be most influenced by movement patterns, such as

120 speed. Furthermore, we hypothesised that trigger probability of wet otters would be lower than that of dry otters  
121 (Lerone et al. 2015). We use our findings to suggest key considerations of study design and potential sources  
122 of bias in CT studies.

## 123 **Materials and Methods**

### 124 *Data collection*

125 We used two study sites. The first was a wild area in SE Scotland (55.9°N, 3.2°W). We targeted a mammal  
126 run in woodland known to be used by both badger and fox. The second was a captive otter enclosure (50.6°N,  
127 4.2°W) in SW England. The enclosure was approximately 700m<sup>2</sup>, with a pond accounting for approximately a  
128 third of the area. The enclosure included two wooden hutches for denning, termed ‘holts’. A male and a female  
129 otter lived in the enclosure; they were not intended for release and were habituated to humans. In both study  
130 areas we set up two CCTV cameras (Swann SRPRO-842) at approximately 2m above ground to continuously  
131 record to a CCTV recorder (M2/UTC-FDVR-4). The CCTV used IR illumination at night and was able to  
132 observe 24h per day. Both sites had flat topography and work was undertaken in winter when vegetation would  
133 be at minimum density and height (otter: 14 Nov–5 Dec 2017, fox & badger: 21 Feb–14 April 2017). At both  
134 sites, we set up four CT stations, subsequently referred to as CT ‘positions’, within the CCTV field-of-view  
135 with the PIR at 27cm above the ground approximating average shoulder height of the three species studied. CTs  
136 were aimed parallel to the ground and placed in security boxes so that they could be replaced at the same height  
137 and angle.

138 For both trials we used Bushnell Aggressor (model 119776) CTs programmed to record 5s video with an  
139 interval of 5s between recordings. Video potentially captures more data than still images and use of video is  
140 likely to increase due to technological advances (Swinnen et al. 2014). In the otter enclosure, at each recording  
141 station, we also set a Bushnell CT to record a burst of 3 still images with a 5s interval between bursts and a  
142 Little Acorn (model 5310 WA) CT to record 5s video with a 5s interval, see Figure 2. We set Bushnell CTs to  
143 ‘auto’ sensitivity as recommended by the manufacturer. The Acorn was set to medium sensitivity. The Acorn  
144 was used as a contrast to the Bushnell as its PIR sensor has an advertised 100° detection angle and 100° camera  
145 field-of-view, compared to an advertised 55° detection angle and 40° field-of-view for the Bushnell. At both  
146 sites, we fixed a data logger (Onset Hobo) 1.5m above the ground to record hourly air temperature, and in the  
147 otter enclosure pond we secured a data logger at 30cm depth to record hourly water temperature.

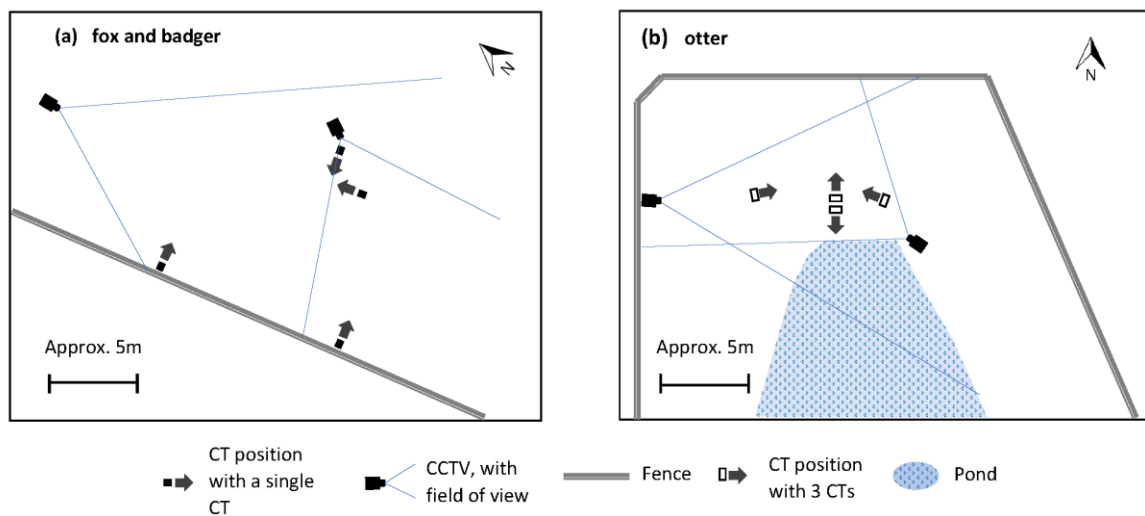
148 At both sites, we determined distances between each CT and features visible on the CCTV such as habitually  
149 used trails and trees in each CTs’ field-of-view. CCTV footage was reviewed to identify passes of a single  
150 animal and we created a chronological list of passes. We defined a ‘pass’ as a single animal moving across the  
151 central line of the CT’s field-of-view, (see Hofmeester et al. 2017). As CTs targeted mammal runs, virtually  
152 all animals passed the central line. We included passes where the target species was considered the only  
153 potential stimulus for the CT PIR sensor, so we excluded passes where extraneous stimuli were present, such  
154 as birds and rodents. Waving vegetation and direct sunlight would also have been seen as an extraneous  
155 stimuli, but these were not an issue during our study period because vegetation was sparse at the time of year  
156 of the study, and it was overcast and not windy. We also excluded passes where the animal was less than 1m  
157 from the CT, as the animals could potentially pass beneath the PIR sensor and/or field-of-view (Rowcliffe et  
158 al. 2011).

159 We cross-referenced passes on the CCTV footage against the CT footage using their respective time-  
 160 stamps. This enabled us to separately quantify Processes 2 and 3 (Figure 1), i.e. distinguishing an animal passing  
 161 but not triggering the CT from an animal triggering the CT but not registering in its footage. This process  
 162 eliminated any false triggers (i.e. where a CT triggered but no otter had passed).

163

164 **Fig. 2** Schematic maps showing the positions of the camera-trap (CT) arrays and closed-circuit television  
 165 (CCTV) at the study sites for (a) badger and fox, and (b) otter. Scales and relative positions are approximate  
 166 and CTs and CCTVs are oversized. Arrows indicate direction CT stations faced

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170 *Variables recorded*

171 We quantified trigger probability  $P(\text{trigger}|\text{pass})$  with a binary variable of passes which either triggered  
 172 the camera (1) or did not (0), regardless of whether its footage registered the animal. We also quantified  
 173 registration probability  $P(\text{registration}|\text{trigger})$  with a binary variable of passes which either triggered the camera  
 174 and registered the animal (1), or triggered the camera but failed to register the animal (0).

175 As discussed, capture quality probability  $P(\text{capture quality}|\text{registration})$  depends on a study's objectives.  
 176 In many studies of mammals, identifying presence of the species is not necessarily sufficient, but rather a good  
 177 view of the head and body is needed to identify the age category/sex/breeding status of the individual (for  
 178 instance, lactating females) (Sollmann and Kelly 2013; Findlay et al. 2017), or to observe individual natural  
 179 markings (Karanth 1995; Silver et al. 2004). We used capture of the head of the animal in the first video frame  
 180 or image as an indication of minimum capture quality as more of the animal would normally be captured in the  
 181 following video footage or images. We quantified capture quality probability with a binary variable categorising  
 182 good capture quality probability as capture of head only, head and body, or head body and tail (1), or poor  
 183 capture quality probability when the head had already passed through the field-of-view (0).

184 From the CCTV footage and data loggers, a suite of animal and environmental variables were recorded  
 185 for each pass (Table 1). The orientation of the animal pass to the CT was recorded, using three categories. A  
 186 lateral pass was when the animal passed exposing a complete side view, an anterior pass was when the animal  
 187 approached the camera-trap presenting the head, shoulders and front legs and a posterior pass when the animal

188 approached the CT from behind and walked away exposing its hind-quarters. We chose to record an animal's  
 189 gait (i.e. walk, trot, run) to represent speed as gait was quickly identifiable whilst estimating ms-1 over such  
 190 short distances would be prone to inaccuracies from perspective using CCTV footage and inconsistencies due  
 191 to instances of the animal pausing. Running animals were subsequently combined with trotting animals as  
 192 running animals were too infrequent to analyse separately, our variable GAIT therefore had two categories  
 193 (walk/trot or run). We recorded whether there was any delay in the animal passing through the field-of-view as  
 194 a result of the animal pausing to sniff, or scent mark (i.e. loitering). This was recorded as a binary variable  
 195 LOIT. For otter, we also recorded whether the animal was dry after being in the holt and prior to immersion in  
 196 water (from holt) or whether the animal had been immersed in water since leaving the holt (not from holt). This  
 197 enabled us to subset the data to include passes where the otter was fully dry, or not fully dry. For fox and badger,  
 198 we only used Bushnell CTs on video setting. For otter, we had stations of three CTs (Busnell video, Bushnell  
 199 still images, Acorn video) together, to maximise data acquisition from each pass. We analysed data for each of  
 200 the three CT models/settings separately so we could compare Bushnell video between fox/badger and otter, and  
 201 because aspects of the three CT models/setting differ substantially in key elements such as detection zone, field-  
 202 of-view etc., for otter.

203

204 Table 1. Data collected for each animal pass identified on CCTV. Response variables were recorded against the  
 205 first frame of the CT video or the first still image from the burst of three. Explanatory variables described  
 206 parameters of the pass as observed on CCTV prior to viewing passes on the CTs.

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<b>Response variables from CT recordings</b>	<b>Badger/Fox</b>	<b>Otter</b>
TRIGGER: binary (1 = trigger / 0 = no trigger)	✓	✓
REGISTRATION: when trigger = 1. Binary (1 = animal registered / 0 = no animal registered)	✓	✓
CAPTURE QUALITY: when trigger = 1 and registration = 1. Binary (1 = good / 0 = poor)	✓	✓
<b>Explanatory variables from CCTV footage</b>		
DIST: perpendicular distance (m) between CT and animal, continuous	✓	✓
GAIT: binary (walk/trot or run)	✓	✓
ORIENT: orientation of animal pass to CT, factor with 3 levels (anterior/lateral/posterior)	✓	✓
LOIT: any pauses in animal's progress when passes the CT such as sniffing or scent marking. Binary (LOIT/NO LOIT)	✓	✓
TFW: Time From Water (s), continuous		✓
WET.DRY: binary, DRY i.e. from holt, and WET (passes where $TFW \leq 10s$ )		✓
<b>Explanatory variables from data loggers</b>		
AIR: air temperature (°C), continuous	✓	✓
WATER: water temperature (°C), continuous		✓

ABSDIFF: the absolute difference between air and water temperatures (°C),  
 continuous ✓

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**Random variable**

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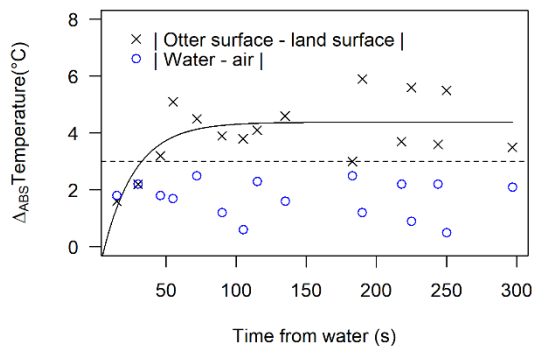
CAM.POS: The location of the CT within the study area, categorical ✓ ✓

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To understand how the otters' IR footprint develops after exiting from water, we used a thermal imager (FLIR PAL65) to take thermal-images of otter on dry ground from the point of exiting water to 300s post-immersion. Seventeen images were taken, the land temperature ranged between 6-10°C and water 9.5 C. Mean temperature of the otter trunk and an equivalent area of ground adjacent to the otter were measured using FLIR Tools software (v5.13.17214.2001). The absolute difference in temperature was plotted against time from water (Figure 3) and an exponential model was fitted to the data. Approximately a 2.7 °C difference between an animals emitted IR and the background IR is needed for a PIR sensor to initiate a trigger (Meek et al. 2012), although this will depend on the CT model and PIR sensitivity setting. Under these conditions, the fitted model predicts 32s to have elapsed before the temperature difference reaches a conservative 3°C.

**Fig. 3** Absolute difference ( $\Delta_{ABS}$ ) in temperature (°C) between an otter's trunk and surrounding land against time after being immersed in water illustrating how long since immersion it takes for the otter to emit enough heat (c. 3°C) for a passive infrared sensor to theoretically detect the otter. To describe the asymptotic relationship, we fitted an exponential model in the form  $y = a(1 - e^{-bx}) + c$  where  $y$  is the temperature difference,  $x$  is the time since exiting water, and  $a$ ,  $b$  and  $c$  are parameters estimated by the model. The absolute difference between air and water temperatures is also plotted, using temperature from data loggers.



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229 *Modelling trigger and registration probabilities*

230 We carried out modelling in R version 3.2.2 (RCore Team 2015) within R Studio (RStudioTeam 2015),  
 231 fitting generalised linear mixed models (GLMMs) using lme4 (Bates et al. 2015) and generating model  
 232 comparison tables using MuMIn (Barton 2016). We used the package manipulate (Allaire 2014) to fit the  
 233 exponential model in Figure 3.



234 We used GLMMs with a binomial distribution to investigate variation in the response variables  
235  $P(\text{trigger}|\text{pass})$  and  $P(\text{registration}|\text{trigger})$  for each species and CT model. The CTs positions potentially had  
236 different local conditions. Therefore, we set CT position as a categorical random effect, and built a list of  
237 candidate models (online resource 1) containing combinations of appropriate variables in Table 1, including a  
238 null model in each.

239 Distance to CT and orientation of animal could not be investigated in the same model sets, as the trigger  
240 distance could not be measured for anterior passes, i.e. when the animal approaches the CT at  $180^\circ$ , while for  
241 most posterior passes when the animal walks away at  $180^\circ$  the animal would have to enter the detection zone  
242 close to the CT. Distance was prioritised as a variable, and lateral passes approximating  $90^\circ$  were selected for  
243 analysis unless otherwise stated.

244 We investigated whether immersion in water negatively affected trigger probability for otter, as suggested  
245 by (Lerone et al. 2015). First we modelled trigger probability for dry otters after they had emerged from their  
246 holts and prior to entering water. This allowed us to compare dry otter to fox and badger. Then, we repeated the  
247 model comparison including a generated binary variable WET.DRY, to distinguish passes where the otter was  
248 fully ‘wet’ ( $\leq 10$  s since exiting water) and passes where the otter was fully ‘dry’ (passes where FROM.HOLT  
249 = 1). Finally, using all passes where FROM.HOLT=0, we repeated the model comparison including TFW  
250 to test whether it was a significant variable, but it was not well supported. We tested all GLMMs for over  
251 dispersion, and used a threshold of  $\Delta\text{AIC} \leq 2$  to indicate models with “substantial support” (Burnham and  
252 Anderson 2004). For brevity we only include plots for the best supported model ( $\Delta\text{AIC} = 0$ ) in the main text,  
253 but other plots of all models with  $\Delta\text{AIC} \leq 2$  and parameter estimates for all models are provided in the online  
254 supplement.

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#### 256 *Quantifying detection in a ‘worst-case scenario’*

257 Poor triggering of CTs by otters after emergence from water (Lerone et al. 2015) implies that studies on  
258 semi-aquatic mammals could carry large bias, particularly if some CTs are closer to water than others. We  
259 hypothesised that a ‘worst-case scenario’ would be an otter emerging directly from water into the detection  
260 zone, with an anterior or posterior orientation i.e. travelling towards or away from the CT. An otter after  
261 immersion may emit less IR radiation relative to the background (Kuhn and Meyer 2009). Anterior and posterior  
262 passes presents a smaller surface area to the PIR sensor and are less likely to create enough movement across  
263 the PIR which is required for a trigger (see Rovero and Zimmermann 2016 for further details). One of our CT  
264 stations in the otter enclosure faced the pond at a distance of 2.5m. Thus we quantified trigger and registration  
265 percentages for any anterior passes of otter following immersion, although the sample size ( $n = 28$ ) was too  
266 small for further analyses.

#### 267 *Latency between trigger and registration*

268 Trigger speeds of the CT models were tested by placing a digital clock within the field-of-view of a CT  
269 and simultaneously triggering the CT with a moving hand whilst starting the clock, thus the trigger speed was  
270 displayed on the clock in the first frame of the video or still. Across 40 repeats per camera, trigger speeds were:  
271 Bushnell video 2.4s ( $\pm 0.1$  SD), Bushnell still 0.5s ( $\pm 0.1$  SD); Acorn video 2.3s ( $\pm 0.1$  SD); Acorn 0.7s still ( $\pm$   
272 0.1 SD).

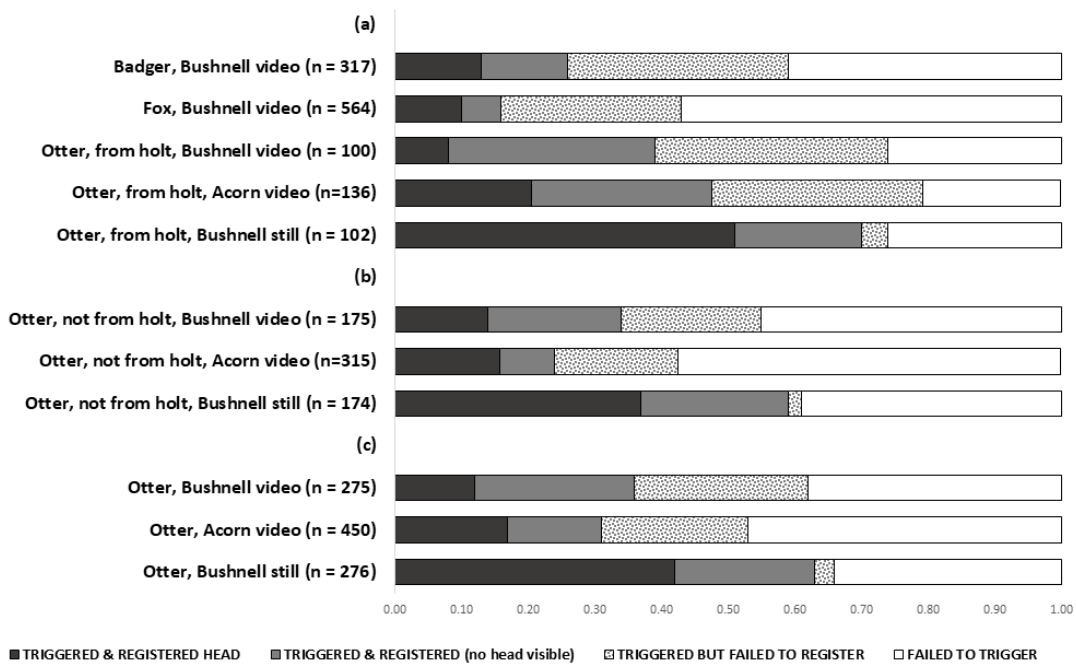
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274 **Results**

275 False-negatives were recorded at each stage of detection we studied (triggering, registering, capture  
 276 quality), but the extent of false-negatives from each process varied between species, within species (e.g. wet vs  
 277 dry otters), with CT mode (still vs video) and CT model (Acorn vs Bushnell) (Figure 4). For all scenarios, at  
 278 least 20% of passes did not elicit a trigger despite the animal entering the putative detection area (Figure 4,  
 279 white bars). For otters, badgers and foxes on videos, a substantial component of false-negatives occurred when  
 280 the CT triggered but did not register the animal, while for stills (otters only) this occurred very infrequently  
 281 (stippled bars). Based on our specific criteria of recording the animal’s head, substantial data loss occurred due  
 282 to poor capture quality regardless of whether stills or videos were used, although this varied widely between  
 283 scenarios (light grey bars). There was substantial variation in the proportion of passes that registered images  
 284 (combined dark and light grey bars) or images of sufficient quality (dark grey bars).

286 **Fig.4** Success rate of Trigger, Trigger and Registration, and Trigger and Registration of head as a proportion  
 287 of the number of passes for (a) terrestrial mammals on video and dry otter on video and still images (b) otter  
 288 passes not from holt (c) all otter passes (passes from holt and not from holt)

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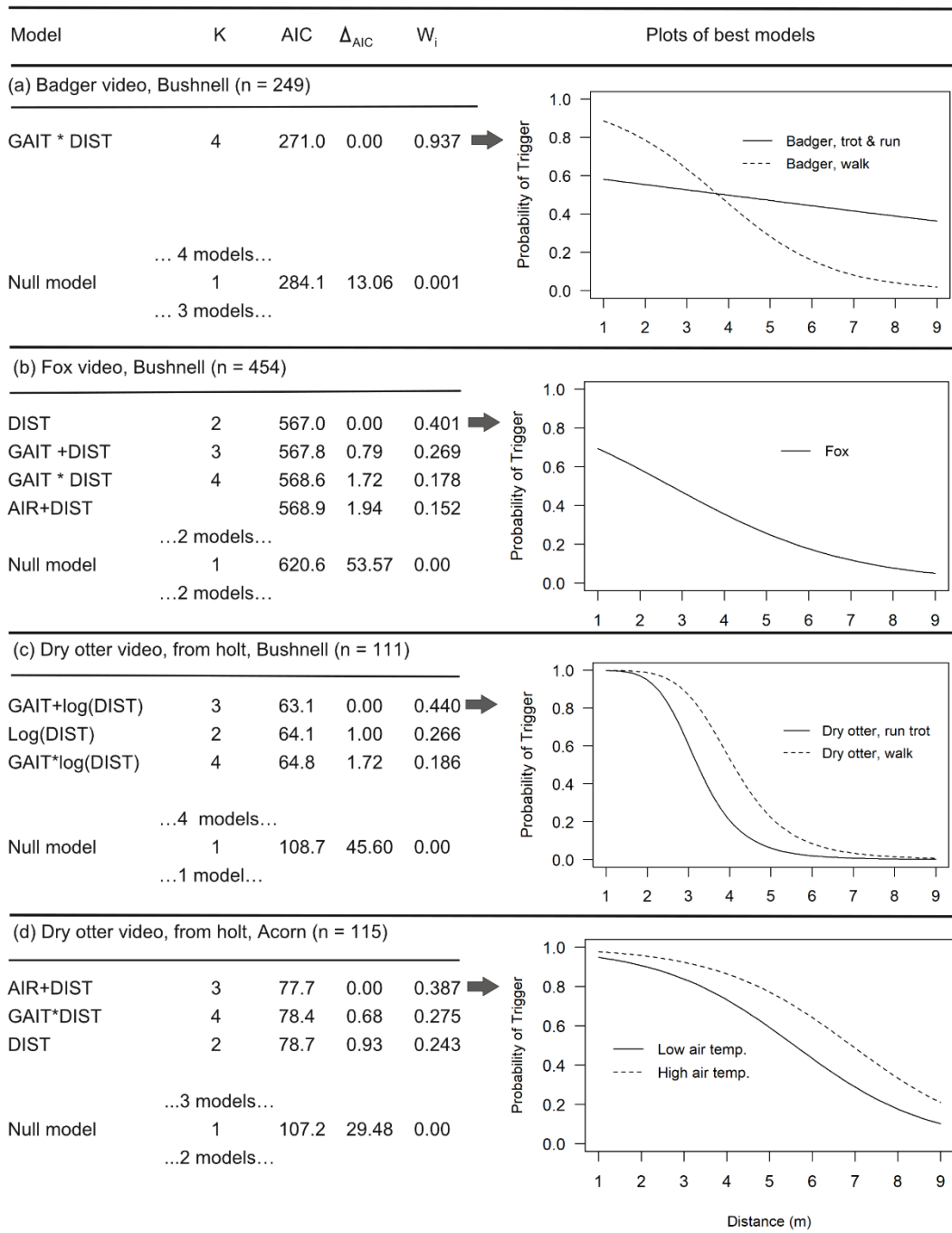
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291 *Trigger probability  $P(trigger/pass)$*

292 For the terrestrial mammals and fully dry otters, model comparison results and plots of lowest AIC models  
 293 are in Figure 5. DIST and GAIT influenced trigger probability for all species using the Bushnell CTs. DIST has  
 294 a negative effect in each scenario, with a slower GAIT having greater trigger probability except for the  
 295 interaction seen in badger where this was only true close to the CT. Trigger rate by the Acorn CT was influenced  
 296 by AIR and DIST with trigger probability being better at the higher air temperature, but again decreasing with  
 297 increased DIST.

298

299 **Fig. 5** Model selection tables, and plots of the best supported model for Trigger Probability,  $P(\text{trigger}|\text{pass})$ ,  
 300 for (a) badger with Bushnell camera-trap (CT) on video setting (b) fox with Bushnell CT on video and (c) dry  
 301 otter with Bushnell CT on video, and (d) dry otter with Acorn CT on video. Model variables are defined in  
 302 Table 1. For brevity, only models with  $\Delta\text{AIC} \leq 2$  and the null model are shown in the ranking tables. Full model  
 303 results are included in online resource 1  
 304

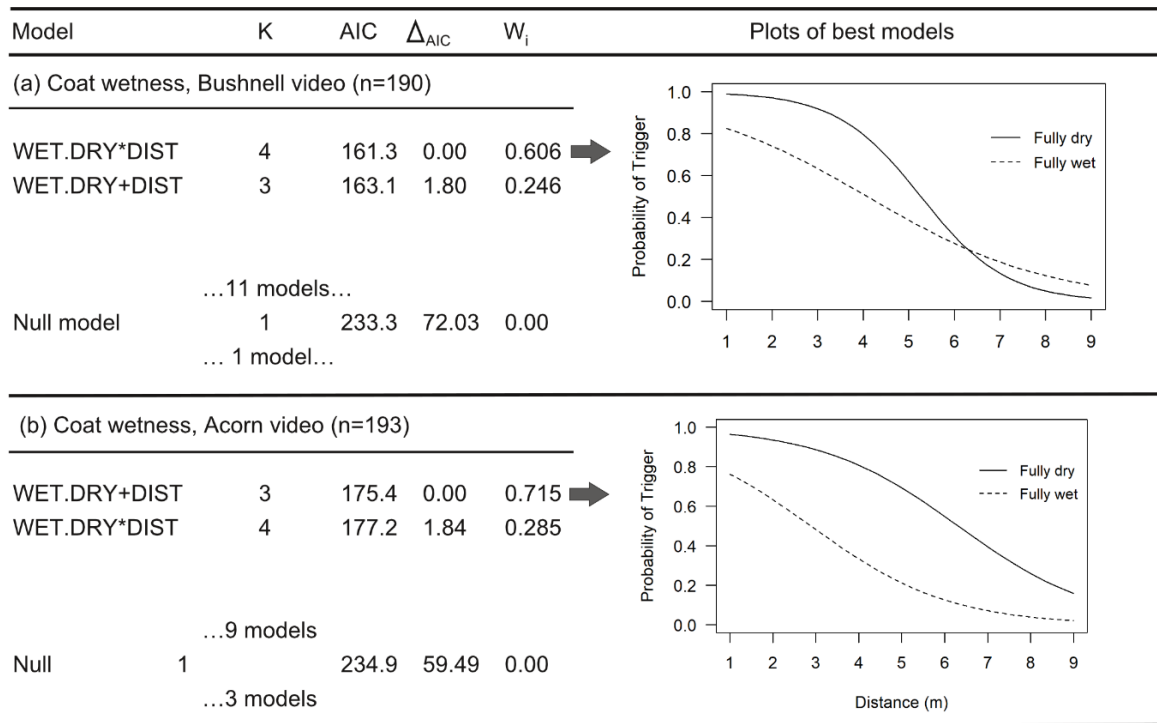


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Figure 6 shows model comparisons for trigger probability of the best supported models in which fully wet and fully dry otter were considered. With both CT models, DIST had a negative effect but the negative effect was reduced for dry otter compared to wet.

310  
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 317

**Fig. 6** Model selection tables, and plots of the best supported model for Trigger Probability for otter,  $P(\text{trigger}|\text{pass})$ , including the variable WET.DRY, using (a) Bushnell video and (b) Acorn video. Model variables are defined in Table 1. For brevity, only models with  $\Delta\text{AIC} \leq 2$  and the null model are shown in the ranking tables. Full model results are included in Supporting Information S1



318

319 *Registration probability  $P(\text{Registration}|\text{trigger})$*

320 Registration probabilities for the Bushnell still images of otter were almost perfect (i.e. only 2-4% data  
 321 was lost from cameras triggering but not registering), see Figure 4, so we did not model these. For videos,  
 322 registration probability model comparisons are in Figure 7. Because registration probability is conditional on  
 323 the camera having triggered, we did not expect the thermal properties of the animal relative to the background  
 324 to influence it, so we combined wet and dry otter passes for the analysis.

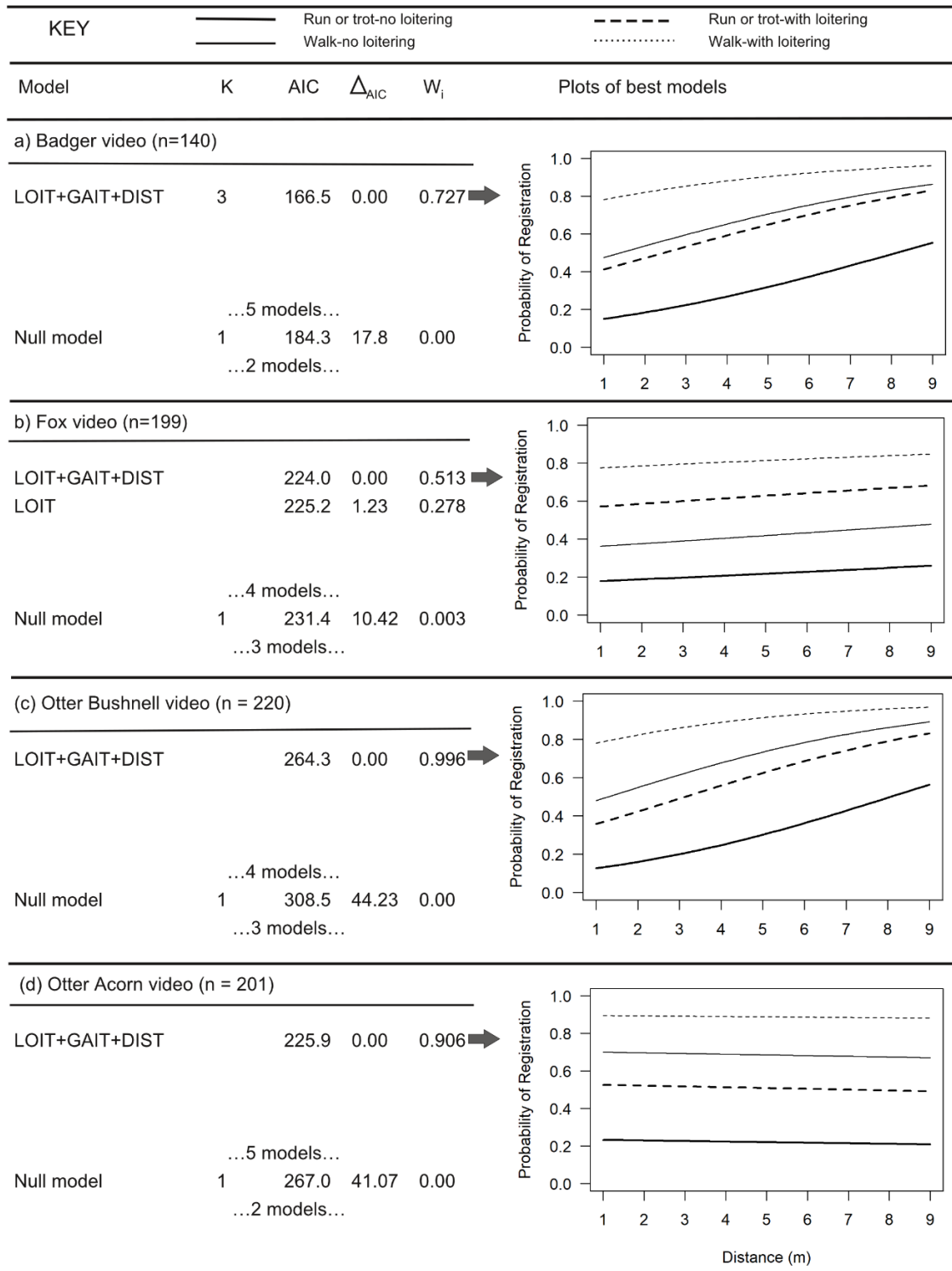
325 For video, in each species the model of LOIT+GAIT+DIST had strong support. Notably for registration,  
 326 the probability increased with distance in most cases, except for Acorn CTs where there was no relationship. In  
 327 all cases, the registration probability was substantially better when animals were walking and loitering than  
 328 when they were moving more rapidly.

329

330 **Fig. 7** Model selection tables, and plots of best models for registration probability  $P(\text{registration}|\text{trigger})$ , for  
 331 (a) badger, Bushnell video (b) fox, Bushnell video (c) otter (all passes), Bushnell video and, (d) otter (all passes),  
 332 Acorn video. Only lateral passes were included (see text). Model variables are defined in Table 1. For brevity,

333 only models with  $\Delta AIC \leq 2$  and the null model are shown in the ranking tables. Full model results are included  
 334 in online resource 1

335



336

337 *Capture quality probability*

338 GLMMs were not possible for capture quality probability as loss of data from the trigger and registration  
 339 stages reduced the number of captured images, furthermore the associated variables (GAIT, LOIT, DIST)  
 340 were too unevenly distributed. A summary table is provided, see Table 2.

341

342 Table 2. Percentages of the amount of mammal visible in the first frame of each capture for each species and  
 343 each camera-trap scenario, with capture of head only, head and body, head, body and tail representing ‘good’  
 344 capture quality by our standard (see text), and any capture not including head a ‘poor’ quality capture.

345

	‘Good’ capture quality			‘Poor’ capture quality	
	Head only	Head and body	Head, body and tail	Body and tail	Tail only
Badger -Bushnell video (n = 55)	4	4	60	27	5
Fox -Bushnell video (n = 72)	1	3	60	14	22
Otter- from holt, Bushnell video (n = 37)	0	11	27	11	51
Otter- from holt, Acorn video (n= 50)	2	0	54	20	24
Otter- from holt, Bushnell still (n = 65)	54	14	23	11	0
Otter-not from holt, Bushnell video (n = 68)	1	3	62	18	16
Otter- not from holt, Acorn video (n= 58)	0	3	76	16	5
Otter-not from holt, Bushnell still (n = 97)	26	18	38	9	9

346

347 *Detection in a ‘worst-case scenario’*

348 For 28 anterior passes of otters emerging from water at the CT station 2.5m from the pond, the percentage  
 349 of triggers, registrations and overall capture probabilities are in Table 3.

350

351 Table 3. Summary of trigger, registration and overall capture probabilities for otter representing “worst case  
 352 scenario”, from camera-trap position facing water’s edge at 2.5m recording anterior passes of otter emerging  
 353 directly from water (n = 28).

354

CT model & setting	Triggers as % of all otter passes (n)	Registrations as % of all triggers (n)	Overall trigger and registrations combined (i.e. ‘captures’) as % of all otter passes (n)
Little Acorn Video	36 (10)	40 (4)	14 (4)
Bushnell Video	39 (11)	63 (7)	25 (7)
Bushnell Still	43 (12)	100 (12)	43 (12)

355

356

## 357 **Discussion**

358 Consideration of the separate component processes of detectability, aligned with their measurable  
359 probabilities (Figure 1) facilitated a clearer understanding of false-negatives when camera-trapping our study  
360 species. We demonstrated that substantial data loss through false-negatives can occur at Processes 2-3 (Figure  
361 4), but that this varies with context (species, camera model, footage type). These false-negatives are driven by  
362 different variables as demonstrated by differences between drivers of trigger and registration probabilities.  
363 There are some clear methodological considerations that can be drawn from our findings.

364

### 365 *PIR sensitivity caused loss of data at close distances*

366 Decreased capture with increased distance is well documented (Rowcliffe 2017; Randler and Kalb 2018),  
367 but our data demonstrate this occurs primarily because of reduction in triggering, not a reduction in registering  
368 of animals on footage. The PIR sensor receives long-wave infrared (IR) through an 8-14  $\mu\text{m}$  filter. Atmospheric  
369 transmission of long-wave IR through air is good (Usamentiaga et al. 2014), therefore absorption (by  
370 atmospheric gases such as CO<sub>2</sub> and water vapour) of IR energy between the animal and PIR sensor is not thought  
371 to be of consequence (Welbourne et al. 2016). Other mechanisms are therefore needed to explain decreasing  
372 trigger probability with increased distance. We suggest that there are two ways that distance can affect the  
373 presentation of the animals IR footprint to the PIR sensor. The first relates to the loss of intensity of the animals  
374 emitted IR with increasing distance, as the energy per unit area from a point source decreases according to the  
375 inverse-square law (Papacosta and Linscheid 2014). The second is that the further away the animal is from the  
376 PIR, the more likely there are to be objects or vegetation between the animal and PIR sensor which could block  
377 the passage of IR and reduce capture rates (Hofmeester et al. 2017). Whilst distance will always have a  
378 predictable negative effect on trigger probability due to the loss of intensity of IR, this will be compounded by  
379 objects within the detection zone and lead to variation in the relationship between trigger probability and  
380 distance, depending on context, such as local vegetation density.

381 The negative effect of distance is critical in CT studies that adopt the Random Encounter Model (REM)  
382 to estimate population densities when individuals cannot be identified (Rowcliffe and Carbone 2008). This has  
383 been an important development in density estimation using camera-traps because capture-recapture methods  
384 cannot be applied to species that are not individually identifiable. The REM or similar could be used for all  
385 species, therefore removing any potential error from misidentification of individuals. REMs require knowledge  
386 of the size of the detection zone of CTs (Rowcliffe et al. 2008). However, because detection probability is  
387 variable within the detection zone, distance sampling has been integrated into REMs to estimate effective  
388 detection distances for species (i.e. the distance within which the number of animals not captured equals the  
389 number captured beyond) (Hofmeester et al. 2017). This relies upon “a shoulder of certain detectability up to a  
390 certain distance” from the camera-trap (Rowcliffe et al. 2011), i.e. there is an assumed zone close to the camera  
391 with a 100% capture probability for a passing animal. However, we found that at 1m there was a substantial  
392 predicted rate of false-negatives due to trigger failure. At 1m, trigger probability was already compromised,  
393 notably at faster gaits: fox 69%; badger run/trot 58% (walk 88%); dry otter from holt with Bushnell CTs run/trot  
394 74% (walk 93%). The REM approach is caveated with the assumption that PIR response must be reliable

395 (Rowcliffe et al. 2011). Our trials with two frequently used models of camera-trap demonstrate important  
396 limitations in PIR sensitivity. Similar poor capture at close distance (1m) has also been found in a study of birds  
397 (mean of 60% across six size classes of bird and six CT models), where CTs were programmed to capture still  
398 images and high sensitivity (Randler and Kalb 2018). We suggest that imperfect triggering at close distances  
399 for small to medium homiotherms may be ubiquitous in CT technology and thus needs to be evaluated prior to  
400 distance sampling and other quantitative studies, with a CCTV control being a useful method.

401

402 *Speed is important in registration probability*

403 Gait was an important variable affecting trigger probability for badger and dry otter, but less so for fox  
404 with a slower gait increasing trigger probability. We used gait to represent the relative speed of passes within  
405 each species, but in some species, there is also a difference in the vertical movement (i.e. bounce) as well as  
406 horizontal movement with different gaits. The bouncing gait of a trotting badger will interact with a larger  
407 proportion of its background, possibly creating a better signal to the PIR. This may lessen the effect of distance  
408 on trigger probability, as seen in the interaction of GAIT and DIST in Figure 5. There was a more consistent  
409 effect of gait on registration probability, in all cases slower passes are more likely to register in an image/video,  
410 see Figure 7. Observations of running animals were rare in our study, and this has been noted in other mammal  
411 groups such as the Felidae (Anile and Devillard 2016), so speed may cause greater bias in multi-species surveys  
412 where species move at different speeds affecting both trigger and registration probability (Hofmeester et al.  
413 2019).

414

415 *Distance drives trigger and registration probability in opposite directions*

416 In contrast to the strong negative effect of distance on trigger probability, there was a positive, though less  
417 marked, relationship between distance and registration probabilities when using Bushnell CTs on video setting.  
418 This is likely a function of the time interval between the PIR detecting the animal and the camera switching on,  
419 i.e. the trigger speed. Registration probability for CTs recording video was consistently affected by gait,  
420 loitering and distance across species and CT models, contrasting with the minimal data loss due to high  
421 registration probability on 'still' image setting. The longer trigger speed of videos (just over 2s) required slower  
422 passes and/or loitering (e.g. to scent mark or sniff) to achieve better registration probability. Also, the further  
423 the subject is from the CT, the greater the width of field-of-view of the camera and therefore it takes longer to  
424 pass through the field-of-view and is more likely to be within it when the camera starts recording.

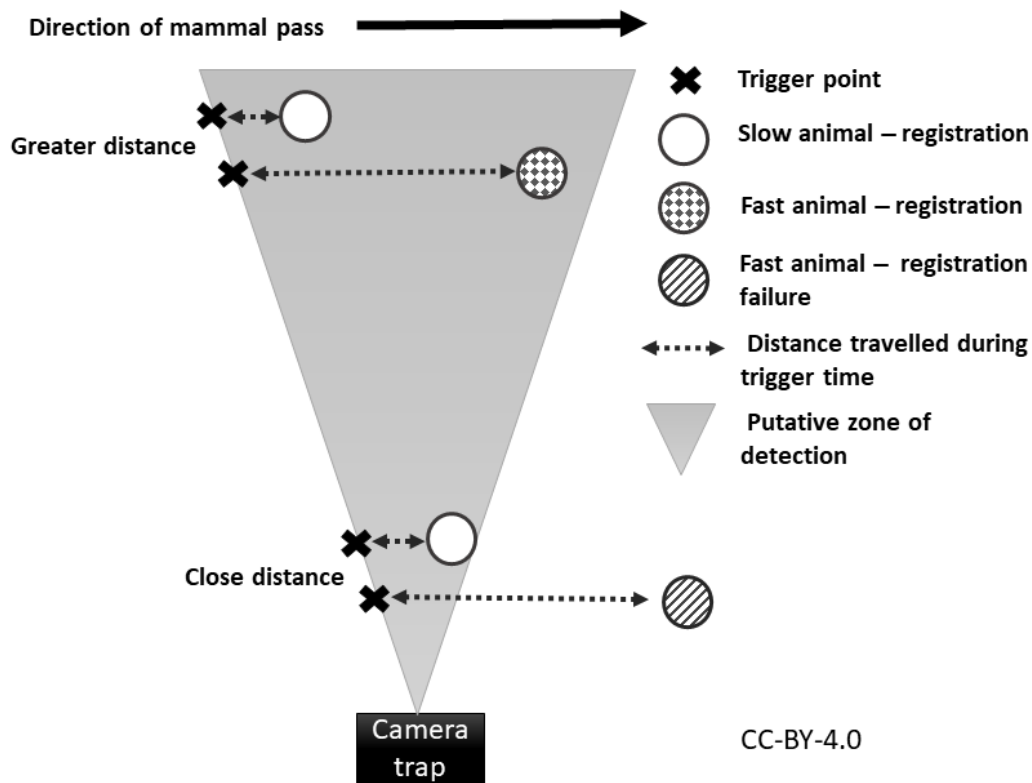
425 A hypothetical scenario, illustrating a mechanism by which registration probability for a lateral pass is  
426 likely to increase with distance, and how this is likely to interact with animal speed, is shown in Figure 8. This  
427 interpretation presents a hypothesis that could be tested in future experiments.

428

429 **Fig. 8** Hypothesised mechanism showing how distance to camera-trap (CT) can interact with animal speed to  
430 influence registration probability. Registration probability is positively affected by distance due to the larger  
431 area within the field of view at greater distances. Conversely, faster moving animals can completely pass  
432 through the small width of the field-of-view close to the CT before the camera takes an image

433





434

435

436

Given this reasoning, a stronger positive effect of distance on registration probability would have been expected with the Acorn CTs due to their wider field-of-view, but this was not observed. The Acorn's wide field-of-view led to difficulties identifying otter at greater distances as the otter had a smaller apparent size, thus reducing registration probability.

439

440  
441 *The choice between still image and video capture*

442

The fast trigger speed for Bushnell still images resulted in high registration probability, 96–98% of passes that triggered resulted in the otter being registered. This contrasts with the registration probability for Bushnell videos, where a lower 65–79% of passes that triggered resulted in registered otter. Survey design therefore needs to consider potential false-negatives due to longer trigger speeds of the video setting, which should influence the choice of CT make/model. Video capture, however, can facilitate behavioural observations which may be essential, but are not possible with still capture. For example, animal vocalisations can be recorded on video mode with CT models that have microphones.

448

449

Still capture is indicated for capture-recapture density studies where a key consideration is high quality images to distinguish pelage details (Trolliet et al. 2014); still capture also enables the use of Xenon white flash. It is also more efficient for faunal inventories and occupancy studies where data generated by videos is not usually required. Density studies using REM can use video, or a burst of still images to estimate average speed of an animal (Rowcliffe et al. 2016). Whilst there will be lost data from both settings due to imperfect trigger probability, the video setting is also likely to have reduced registration probability, unless the trigger speeds are comparable. Where data from video is required, for instance in behavioural studies, CTs should be aimed at areas with field signs indicating activity that delays the passage of a passing animal, such as at dens, bait stations or scent marking sites.

457

458

459 Although trigger speeds for video recording are generally slower than for still images, models are now  
460 available with a trigger speed of less than 1s (e.g. Bushnell Core DS), and these could be chosen if video is the  
461 preferred mode of study to increase registration probability. An additional constraint for video recording is that  
462 video data requires more storage capacity, and viewing video footage takes longer than still images. Whilst  
463 software to enable automated species identification is being developed and may be used in the future, this is  
464 directed at still images (Yu et al. 2013; Tabak et al. 2019).

465

466 *Effects of immersion of otter on detection are short-lived*

467 The trigger probability of dry otter passes on Bushnell videos broadly reflected those of the two terrestrial  
468 species, with distance and/or gait being important in all the best fitting models although the best supported  
469 model for the Acorn video CT included air temperature and distance. Our results corroborate observations that  
470 wet otters are poor in eliciting a PIR trigger (Lerone et al. 2015). However, time from exiting water was not an  
471 important variable in trigger success, indicating that other variables may impact on the rate of change in IR  
472 emitted after an otter has left water. Otter thermoregulation in cold water can result in reduced emission of  
473 infrared from an otter's body and tail, however the intensity and duration of swimming prior to exiting water  
474 can affect thermoregulation and hence the amount of IR emitted (Kuhn and Meyer 2009). These variables, and  
475 others, may confound any effect of time from exiting water on trigger success. When we set a CT facing water  
476 at 2.5m to record otter emerging from water, the trigger probabilities for Bushnell (video and still) and Acorn  
477 CTs were very poor (36–43%). The slower trigger speed for video led to poor registration probability of 40–  
478 63% (Table 2); the resulting capture of all passes on video setting (e.g. 14% for Acorn) is unlikely to be fit for  
479 any purpose. Within the limits of our study conditions and limited sample size, thermal imaging readings  
480 indicated that when an otter emerges from water, its surface temperature nearly matches water temperature (see  
481 Figure 3). It only takes a short period of time from immersion ( $\leq 1$  min) for an otter to develop a thermal footprint  
482 with a 3°C difference from the background, 3°C being an approximate difference that would trigger a camera-  
483 trap PIR (Meek et al. 2012). Although this is likely to be affected by background temperatures, and the otter's  
484 prior activity, it indicates such effects are potentially short-lived.

485

486 *Understanding the stages of detectability will improve study design*

487 CTs can be used for a range of study types, hence study design needs to consider CT model specifications,  
488 placement and settings (Rovero and Zimmermann 2016). Recognition of detection as a sequence of processes  
489 (Figure 1) enables each process to be considered independently when planning CT studies, as the mechanisms  
490 for success in each process are different. Understanding how the animal, environment and equipment interact  
491 is important for all CT studies and can help in considering potential bias, for example from detection  
492 heterogeneity between sites, or species in a study. We demonstrate the high level of data loss (on both video  
493 and still setting) on medium sized animals due to poor triggering, even at close distances. This would need to  
494 be accounted for within population density analyses such as the REM when distance-sampling is used to  
495 estimate effective detection distances. Using CCTV as a control, the influences of different seasons,  
496 temperatures, humidity and vegetation structure could also be quantified.

497

498

499 We found that trigger probability for otter was compromised after recent emergence from water, and it is  
500 anticipated that this would apply for other semi-aquatic species. In a pilot study, we also found very low trigger  
501 probabilities for European beaver *Castor fiber* in an enclosure where they spent a significant time in water  
502 (unpubl. data). Careful CT placement is therefore critical when studying semi-aquatic mammals and CTs set on  
503 in-stream features such as stones or on entry/exit points from water are likely to have poor trigger probability,  
504 as previously demonstrated (Lerone et al. 2015). Trigger probability would improve if CTs were set to anticipate  
505 semi-aquatic mammal passes where the animal has been out of water long enough to develop a better thermal  
506 footprint.

507 We would recommend that the trigger speed of the chosen CT model and mode of recording is established,  
508 either from the manufacturer's specification or via testing. Video trigger speeds are rarely specified by  
509 manufacturers, perhaps because they are usually significantly slower than those for still images.

510

## 511 **Conclusions**

512 Our approach has demonstrated where false-negatives potentially occur during the process of detection  
513 using camera-traps and what factors drive variation in trigger and registration probabilities, and this can help  
514 optimise camera-trap deployments to try to reduce false negatives given the study species, environmental  
515 context and study aims. Our findings could generalise to other species of medium-sized terrestrial and semi-  
516 aquatic mammals. Similarly, this approach, using CCTV as a control to separate component processes of  
517 detection (trigger, registration and capture quality), could be carried out as a precursor to CT studies in different  
518 contexts, such as with small or large mammals, or in different seasons and environmental conditions. Results  
519 could be used to inform modelling of detection functions for REM with distance sampling and would help to  
520 improve study design more widely.

521 **Online resources:** [Note to editors and reviewers: if the manuscript is accepted the datasets and code, which  
522 have been submitted for review, will be uploaded to the Edinburgh Napier University repository, assigned a  
523 DOI, and cited accordingly]. During the review process, the R file and datasets are currently at:  
524 <https://github.com/melaniefindlay/CT-Detection>

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