Sooner, closer, or longer: detectability of mesocarnivores at camera traps

M. Tourani[1] (iD), E. N. Brøste[1], S. Bakken[1], J. Odden[2] (iD) & R. Bischof[1] (iD)

[1]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway
[2]Norwegian Institute for Nature Research, Oslo, Norway

Abstract

Camera trapping, paired with analytical methods for estimating species occurrence, population size or density, can yield information with direct consequences for wildlife management and conservation. Detectability, the ability to detect a species or individual if it is present, affects the reliability and efficiency of camera trap surveys and, in turn, varies across species, space and time. Greater detectability means greater sample size, and a common approach to boost detectability of wildlife by camera traps involves the application of olfactory lures. Using a camera trap study on sympatric mesocarnivores (European badger *Meles meles*, red fox *Vulpes vulpes*, pine marten *Martes martes* and domestic cat *Felis catus*), we quantified three elements of detectability: (1) the time until first detection ('sooner', conditional on being present), (2) the proximity to a focal point in front of the camera ('closer', conditional on being detected) and (3) the duration of exposure to the camera ('longer', conditional on being detected). A hierarchical analytical approach and a quasi-experimental setup allowed us to test for and quantify the species-specific effect of olfactory lures on these aspects of detectability. Depending on species, average median time to first detection ranged from 4 to 28 days, distance to the focal point from 0.3 to 0.8 body lengths, and median time to departure from 2 to 6 seconds. Credible intervals overlapped substantially between most species in all three measures, and variation between observations was extensive. We detected effects of lures on time to first detection for cats (castoreum; American beaver *Castor canadensis* scent), distance to focal point for badgers (striped skunk *Mephitis mephitis* scent) and martens (castoreum, fox and skunk scents), and the duration of exposure for foxes (fox and skunk scents). We discuss how a multifaceted perspective on detectability in camera trap studies, linked with species biology, can give investigators a more structured approach to selecting and testing measures intended to boost detection probability.

Introduction

Camera trapping is used worldwide as a non-invasive and cost-efficient tool for monitoring terrestrial mammals (Burton *et al*., 2015). The goals vary between studies, but chief among them are estimates of species distribution and relative or absolute abundance, all of which are useful in guiding wildlife management and conservation (Ahumada, Hurtado & Lizcano, 2013; Rovero *et al*., 2013).

Photographic detections (e.g. number of visits or photographs during a survey) continue to be used as proxies for certain focal parameters, such as species diversity or abundance, but there is a growing recognition for the need to cope with imperfect detection (Burton *et al*., 2015; Sollmann, 2018). The inability to detect every species or individual present in the study area (i.e. false negatives), together with

heterogeneous detection probability, has direct consequences for the reliability of inferences drawn from camera trap and other field surveys (Archaux, Henry & Gimenez, 2012; Guillera-Arroita *et al*., 2014). Analytical approaches such as capture–recapture and occupancy models account for imperfect detection when estimating focal parameters (MacKenzie et al., 2017; Sollmann, 2018; Hofmeester *et al*., 2019).

Despite the availability of hierarchical methods that estimate and control for imperfect and variable detection, investigators are keenly interested in maximizing detection probability. Increased detection probability results in larger sample sizes, thereby boosting precision (Gerber, Karpanty & Kelly, 2012) and in some cases accuracy of parameter estimates (Guillera-Arroita *et al*., 2014). Increased detection probability can also reduce the cost of surveys, for example by allowing shorter sampling periods in cases where a single detection of an

individual or species at a given site is sufficient, such as occupancy studies (Hamel *et al.*, 2013; Bischof *et al.*, 2014a; Kays et al., 2020).

The biology of study species is an important determinant of detectability (Fig. 1). The probability of encounter with a camera trap is directly affected by the density of a species and its use of the landscape (Neilson *et al.*, 2018). Behavioural characteristics such as exploratory behaviour and diel activity patterns also determine whether and when an animal enters the viewshed of a camera (Rowcliffe *et al.*, 2011). Speed of movement, size and appearance of a species influence whether the camera is triggered, and if so, whether a sufficiently clear image is captured to allow detection and identification. For example, rarity, shyness, furtiveness and small size are all characteristics that make species challenging camera trapping subjects (Fig. 1).

Investigators can address these challenges and take steps to boost detection probability. Cameras are often placed at microhabitat sites that are more likely to be visited by the focal species (or community), based on habitat selection and use of landscape features during travel (O'Connor *et al.*, 2017). Many studies employ baits (Moriarty *et al.*, 2018) or visual (McLean, Goldingay & Westcott, 2017), acoustic (Read *et al.*, 2015) and olfactory lures (Bischof *et al.*, ; Garvey *et al.*, 2017; Ferreras, Diaz-Ruiz & Monterroso, 2018), with the goal of attracting animals to the site and keeping it there long enough for photographic capture. Furthermore, camera design has improved substantially during the past decade, with features such as silent shutters and infrared (IR) or stealth IR mitigating the risk of spooking shy species (Glen *et al.*, 2013; Rovero *et al.*, 2013). These measures, such as the biological characteristics that they implicitly target, affect different aspects of the process of photographic capture, which are either directly or indirectly related to detectability (Fig. 1).

We conducted a quasi-experimental camera trapping study of the mesocarnivore guild in southeast Norway and asked three questions (1) How soon is a given species detected at a camera trap?, (2) How close do individuals approach a target
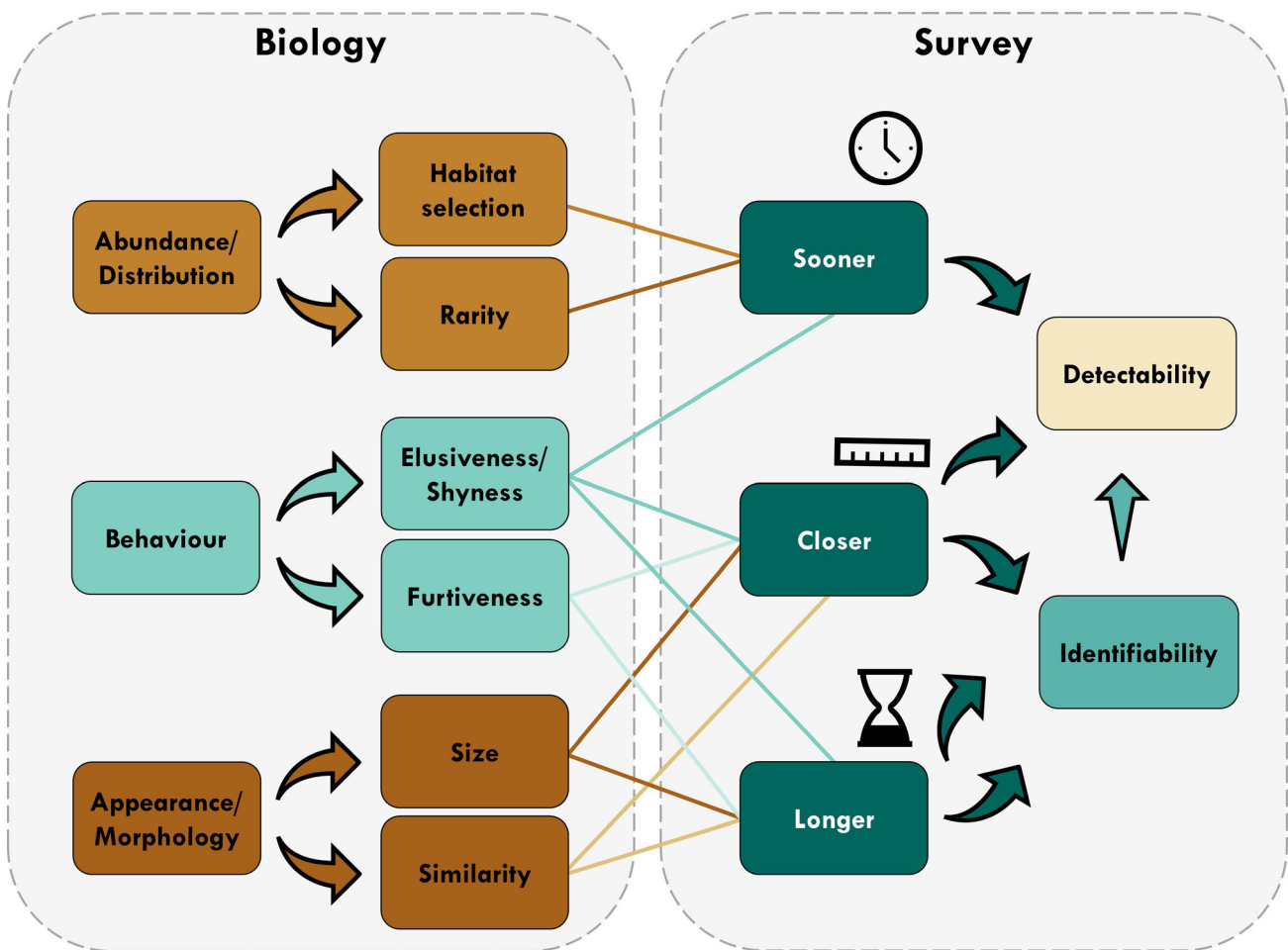

Figure 1 Conceptual diagram showing different aspects of detectability during camera trap surveys and the modulating effect of biological characteristics. In addition to direct impacts on detectability, a longer visit and a closer image of focal species increase the chance of identifying the visitor, thereby increasing detectability.

within the camera's field of view? and (3) How long do individuals remain within the camera's field of view? We used hierarchical models to quantify 'how soon', 'how close' and 'how long', thereby disentangling these three important aspects of detectability. Furthermore, we evaluated how these metrics are influenced by the study species and by using a widespread measure for boosting detectability: olfactory lures.

Material and methods

Study area and camera trapping

The study area (2400 km^2) is situated in south-eastern Norway (59.36-59.81°N, 10.60-11.60°E) where camera traps were placed to monitor the Eurasian lynx (*Lynx lynx*) as part of the SCANDLYNX project (http://viltkamera.nina.no/). The landscape varies from coastline, lakes and agricultural fields to valleys and wooded hills, between 0 and 400 m above sea level (Kartverket, 2017). Boreal forests dominate the area, and the climate is milder than in other areas of similar latitude, primarily due to warm winds and oceanic currents (Dannevig & Harstveit, 2013). The temperature varies throughout the year, with a mean temperature between −3 and −5°C in January and up to between 16 and 17°C in July (Dannevig, 2009). Average annual precipitation rate is 700–1000 mm (Moen, 1999), and the duration of snow cover (when snow covers at least 50% of the ground) ranges between 50 and 125 days per year (Moen, 1999).

We deployed 30 motion-triggered digital Reconyx cameras (five different models: HC500 HyperFire Semi-Covert IR, HC600 HyperFire High Output Covert IR, PC800 HyperFire Professional Semi-Covert IR, PC900 HyperFire Professional Covert IR and PC850 HyperFire Professional White Flash LED) from 15 September to 20 December 2017, specifically with the goal to photo-capture lynx. Therefore, cameras were installed in steep terrain, on ledges or at the base of (and facing) cliffs. Placement was often close to wildlife trails, with one camera trap per location and a minimum distance of 2.3 km between neighbouring camera trap sites. Cameras were aimed perpendicular to the wildlife trail at locations where a wildlife trail was present. Each camera was mounted on a tree between 0.2 and 1 m above the ground, depending on terrain. Notwithstanding occasional failures (empty batteries, etc.), all cameras were operating for 24 hours per day every day during the study period. Cameras were set to take three photographs per trigger event with up to two photographs per second. The no-delay function was used to enable the cameras to continue taking photographs while being triggered. In addition to motion-triggered capture, the time-lapse mode was used to take one photograph per day to allow identification of time periods during which cameras were non-functional.

Lure treatment

At each camera trap location, a scent station was installed at 2 to 6 m from the camera. The area between the scent station and the camera was cleared by removing tall vegetation. The scent station consisted of one scent lure stick (untreated Norway spruce *Pica abies*; 40 x 4.7 x 2.2 cm), hammered 20 cm into the ground (tapered end), leaving 20 cm exposed above the ground (Fig. 2). As a lure receptacle, a 3 cm deep and 1 cm wide hole angled 45 degrees downwards was drilled into each lure stick on the narrow side 2.5 cm from the top of the stick. The lure sticks were placed with the drilled hole facing the wildlife trail if the trail was present in front of the camera and facing the camera where wildlife trails were absent. The lure sticks were treated with a scent lure, applied with one cotton swab (with paper core) cut in half and soaked in the lure, containing ~0.5 mL of lure (or control), and placed in the drilled hole of the lure stick. The five treatments were (1) skunk-based scent lure (essence of striped skunk *Mephitis mephitis* anal scent glands), (2) fox-based scent lure (ground red fox *Vulpes vulpes* scent glands), (3) castor-based scent lure (castoreum; essence of anal sacs from American beaver *Castor canadensis*), (4) synthetic fermented egg (SFE) and (5) distilled water as a control. All four scent lures are commercially available products and were obtained from F & T Fur Harvester's Trading Post, Alpena, MI, USA.

As the lure sticks were novel objects in the environment, they may influence animal behaviour even without scent lures; we thus used distilled water instead of lures on scent poles as the control treatment. Each scent station was randomly assigned to one lure (or water) at a time, which was replaced with a different treatment and a fresh scent stick every 14 days (±3 days) until all five treatments had been used at each site. After use, the lure sticks were disposed outside the study area. Clean plastic gloves were used in all handling of cameras, lure sticks and lures to prevent cross-contamination between lure treatments.

Analysis

We only included photographs of European badger (*Meles meles*), red fox, pine marten (*Martes martes*) and domestic cat (*Felis catus*) in the analysis, as these were the most common free-ranging mesocarnivores in the study area. Photographs of a given species that were taken within a five-minute interval were classified as belonging to the same visit. We performed three Bayesian analyses as explained below and assessed model convergence by inspecting trace plots and by using the R-hat statistic, where models with R-hat ≤1.1 are considered converged (Brooks & Gelman, 1998). The number of Markov chain Monte Carlo (MCMC) samples/iterations was based on convergence requirements identified in preliminary analyses. Parameter estimates were provided as the mean and 95% credible interval (CI) of their respective posterior distribution.

Sooner: time to first detection

We fitted separate occupancy models for each species in a Bayesian framework following Bornand *et al.* (2014). We estimated the effect of lure treatments on the time (in days since lure treatment application) until the first photographic capture

Figure 2 Example camera trap photographs of the four study species in southeast Norway; clockwise from the top left: European badger (*Meles meles*), red fox (*Vulpes vulpes*), domestic cat (*Felis catus*) and pine marten (*Martes martes*). We measured distance as the number of body lengths between the lure stick and the part of the animal closest to the lure stick in each photograph (indicated by arrows).

of the focal species at each camera, conditional on occupancy of the site by the focal species.

The occupancy state z_i of a given site i is the result of a Bernoulli trial where ψ is the probability of occurrence.

$$z_i \sim Bernoulli(\psi) \qquad (1)$$

We adopted an exponential distribution and modelled the time to detection as a censored random variable stratified by lure treatment (Poisson rate λ for a given lure l) and a constant hazard in continuous time. Detection probability p until time t is a function of the detection rate λ and the survey time t:

$$p_l = 1 - exp(-\lambda_l t) \qquad (2)$$

We defined a censoring indicator variable d, where $d = 1$ indicated that the time-to-detection observation at site i was censored (hence, the species had not been detected before the end of the survey period T) for a given lure and $d = 0$,

otherwise. There were two ways in which an observation could become censored ($d = 1$) at a given site i, either because the species was absent at that site ($z_i = 0$) or because the species was present ($z_i = 1$) but was not detected by the end of the observation period (following a given lure treatment).

We fitted species-specific models using the R2jags package in R (version 3.5.2, R Development Core Team, 2018; Su & Yajima, 2012) and JAGS (Plummer, 2003). We drew 200 000 MCMC samples from three chains, thinned by three and we discarded the initial 50 000 samples as burn-in. The model definition is provided in the electronic Supporting Information Appendix S1.

Closer: distance to the focal point

To obtain a relative measure of an individual's proximity to the lure stick, we measured distance in units of body lengths of the animal visible in the photograph (Fig. 2). When an

event resulted in several photographs, we measured distance as the minimum distance over all photographs of the event. Body length has been used as a measuring unit in other studies in behavioural ecology (Macdonald *et al.*, 2004). We measured the body length from the base of the ear to the base of the tail. We recorded distance as the number of body lengths (with ½ body length resolution) between the lure stick and the part of the animal closest to the lure stick (Figs. 2 and 3). Contact between the animal and the lure was recorded as zero body lengths. We fitted species-specific Bayesian generalized linear mixed models using brms R package (Bürkner, 2018), with an identity link (Gaussian family), to quantify the effect of lure treatment on log of distance of the focal species to the camera (+0.01 body lengths to deal with zeros). We included camera station as a random effect on the intercept to account for non-independence between observations associated with the same camera trap. Individual animals may be detected during multiple visits at one or multiple camera traps; this source of non-independence could not be accounted for here, due to the inability to distinguish individuals. We also fitted one model testing differences between species (regardless of lure treatment) with the specifications described above. We drew 2000 MCMC samples from four chains, and we discarded the initial 1000 samples as burn-in.

Longer: duration of exposure

Apparent time spent at camera stations was defined as the time difference (in seconds) between the first and last photograph showing the species during a visit. The time an animal spent at scent lures has been used to evaluate attraction and avoidance in both captive (Saunders & Harris, 2000) and wild carnivores (Andersen, Johnson & Jones, 2016), suggesting that longer visits at a scent station could indicate attraction, while shorter visits could indicate avoidance. We fitted species-specific Cox proportional hazard models using the spBayesSurv package in R (Zhou, Hanson & Zhang, 2020) to quantify the effect of lure treatments on duration of exposure for the focal species. We used treatment as a categorical covariate (5 levels) and compared effect of the 4 lure treatments to water. In addition, we included a random effect of camera trap (station) in our model. We drew 20 000 MCMC samples from four chains, and we discarded the initial 5000 samples as burn-in.

Results

Of 1876 trap nights (operational cameras), 336 were associated with the control treatment (water), 357 with SFE, 369 with castor-based lures, 360 with fox-based lures and 420 with skunk-based lures. Focal species were recorded in 1279 (68.2%) camera trap photographs (520 badger, 122 cat, 560 fox and 199 marten). We recorded 40 camera station visits by cats, 60 by badger, 108 visits by fox and 32 by marten across all treatments. Red foxes were photo-captured at 27 of the 30 camera trap locations, badgers at 14, domestic cats at 10 and pine martens at 12 camera trap locations. Based on R-hat

values, convergence was reached by all Bayesian models used for inferences.

Sooner: time to first detection

Median time to first detection, that is the time by which 50% of occupied sites had made their first detection of the focal species was 4 days with 95% credible interval (CI) of 2.2 to 41.4 for martens, 28 days for cats (95% CI = 4.1 to 108), 7.3 days (95% CI = 3.3 to 49) for badgers and 8 days (95% CI = 5 to 18) for foxes (Fig. 3). These estimates assume an exponential hazard function. In addition, they are conditional on the site being occupied and thus account for imperfect detection. The only species for which we detected a significant effect of lure on time to first detection was the domestic cat. Exponential hazard rate (λ) of domestic cat was higher at stations treated with castor-based lure (mean $\lambda = 1.5$, 95% CI = 0.3 to 3.6) compared to control treatment water (mean $\lambda = 0.2$, 95% CI = 0.03 to 0.5). This translates into a 4.3-day reduction (95% CI = 1 to 27 days) in the median time to first detection (Fig. 4).

Closer: distance to the focal point

The shortest distance from the focal point within the camera's viewshed (expressed in body lengths of the individual in the image; Figs. 2 and 3) varied substantially between observations and their posteriors overlapped between species: 0.84 median body lengths for cat (95% CI = 0.3 to 2.1), 0.75 median body lengths for fox (95% CI = 0.43 to 1.4), 0.3 median body lengths for badger (95% CI = 0.13 to 0.55) and 0.4 median body lengths for marten (95% CI = 0.2 to 1). Martens kept a longer distance from the lure stick when the scent station was treated by fox-based lure (mean regression coefficient $\beta = 4$, 95% CI = 1.9 to 6.3), skunk-based lure (mean $\beta = 3.2$, 95% CI = 0.8 to 5.6) or castor-based lure (mean $\beta = 4$, 95% CI = 0.7 to 7.4) compared with the control treatment (water). Conversely, badgers moved closer to lure sticks when they were treated with skunk-based lure (mean $\beta = -2$, 95% CI = -3.5 to -0.5) compared to the control treatment (Fig. 4, Tables S1-S4 in Appendix S2).

Longer: duration of exposure

Median time to departure after the first image had been captured (i.e. the time by which half of the documented visits by the focal species had ended) was 6 seconds for badgers (95% CI = 3 to 16), 5 seconds for martens (95% CI = 3 to 14), 3 seconds for foxes (95% CI = 0 to 4) and 2 seconds for cats (95% CI = 0 to 4; Fig. 3). Foxes had the longest visits at scent stations that were treated with fox-based lure (mean hazard coefficient = -0.8, 95% CI = -1.5 to -0.2) or skunk-based lures (mean hazard coefficient = -0.8, 95% CI = -1.4 to -0.2) compared to the control (water). We detected no significant difference in duration of visits between control and lure treatments for the other species (Fig. 4, Tables S1-S4 in Appendix S3).
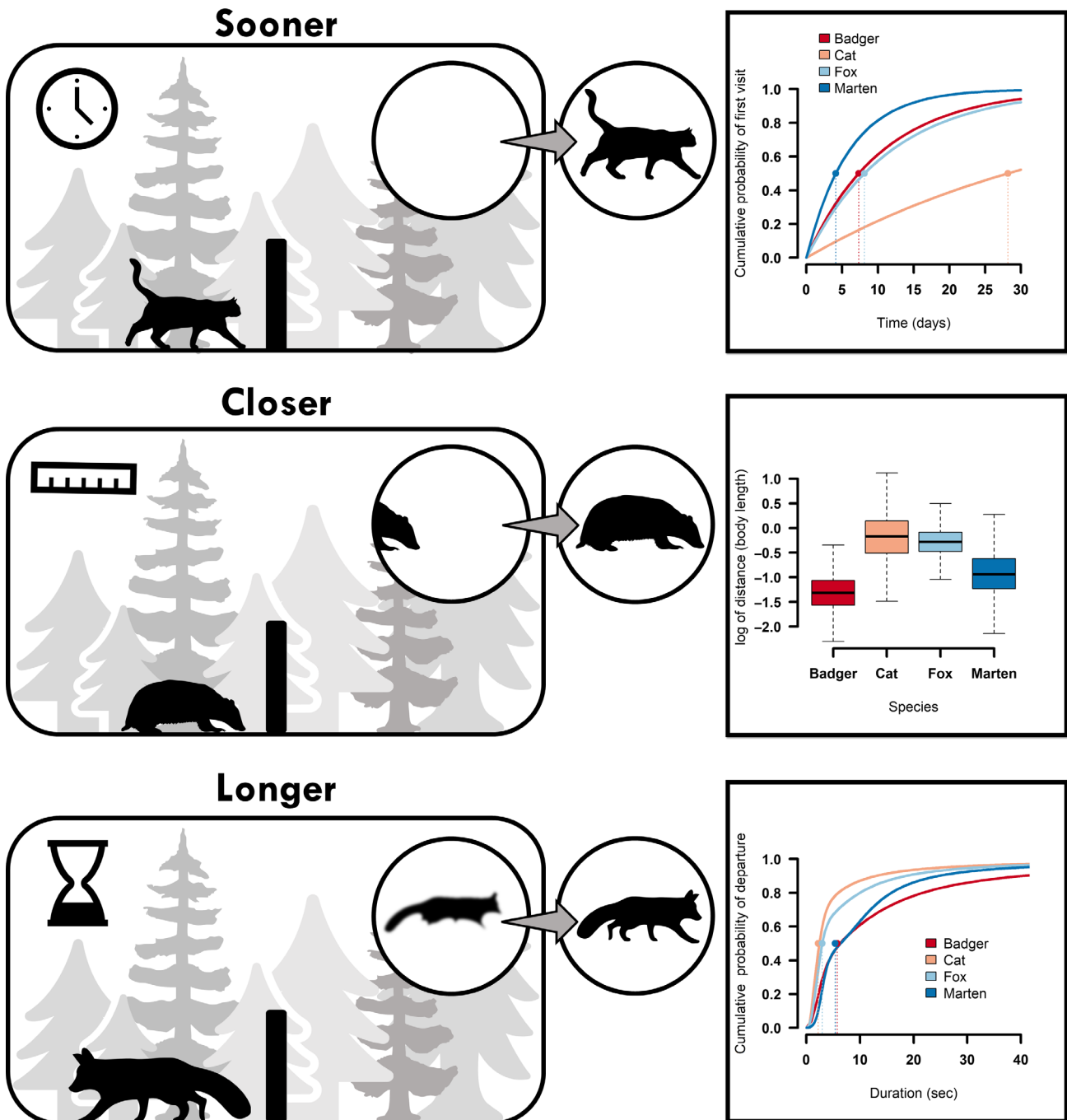
Figure 3 The workflow of our study and potential impact of behavioural response to reduce false absences in camera trapping. Boxes on the right show posterior time to first detection (days), distance from camera's focal point (body length) and duration of visits (seconds) for the focal species: European badger (*Meles meles*), domestic cat (*Felis catus*), red fox (*Vulpes vulpes*) and pine marten (*Martes martes*). Time to detection (top-right) is conditional on a site being occupied.

Discussion

Our study yielded quantitative information about three different aspects of detectability during camera trapping (Figs. 1 and 3): (1) the time until first detection, (2) the proximity of the subject to a focal point in the viewshed of the camera and (3) the duration of exposure to the camera. Variation in these measures was substantial and to some extent explained by species and lure treatment (Fig. 4).
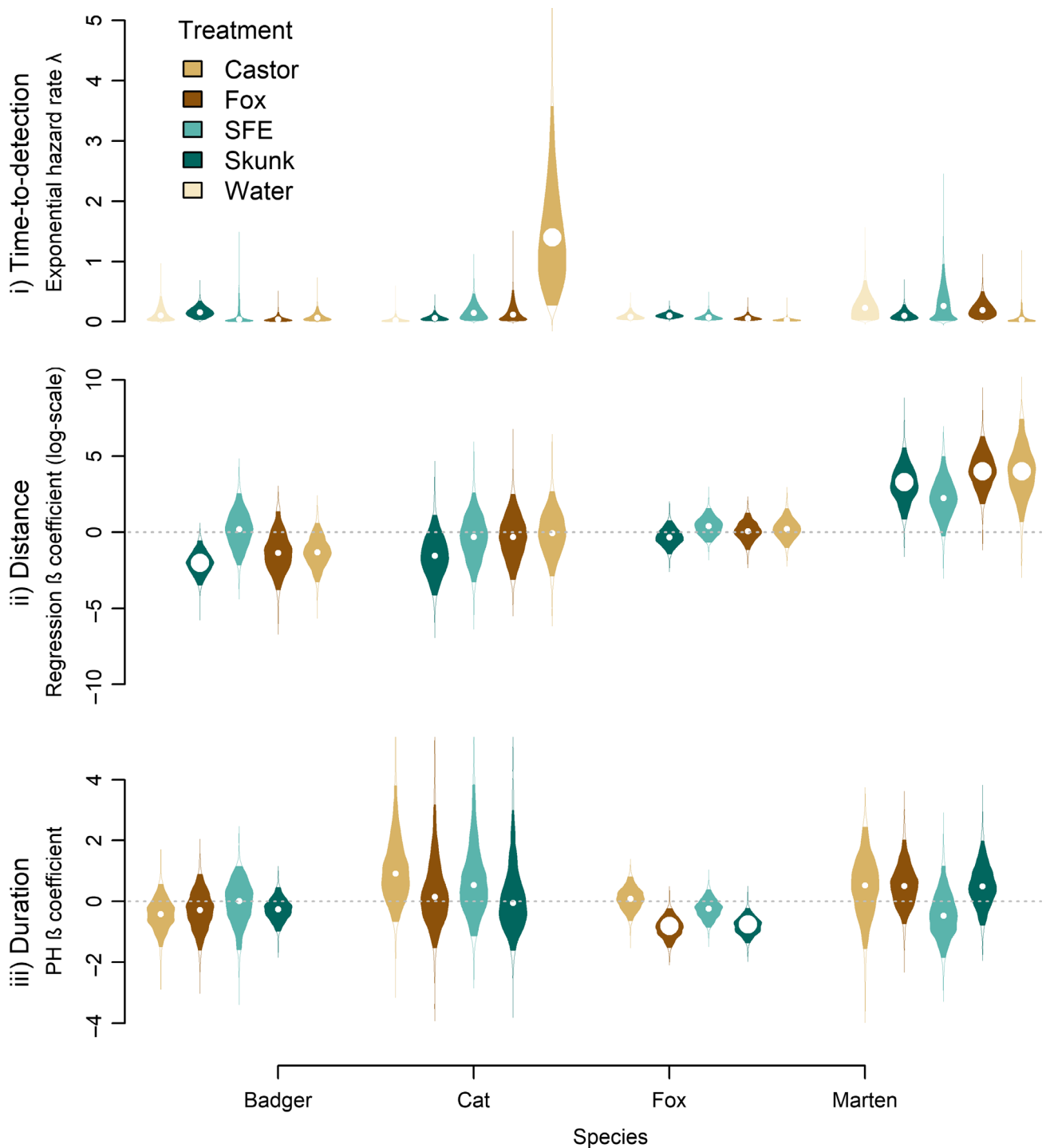
Figure 4 The effect of scent lure treatment (castoreum, fox gland, synthetic fermented egg [SFE], skunk gland) on (a) time to first photo-capture of the study species (λ: exponential hazard rate), (b) distance of focal species to the lure stick (linear regression β coefficient of each lure treatment on log of distance) and (c) duration of visit (proportional hazard β coefficient of each lure treatment effect on time to departure; higher coefficients mean shorter durations). Each violin shows posterior distribution (with 95% credible interval) of coefficients of one lure treatment (colour coded) effect on one species, and the median is shown by a white dot (larger dots for results that are significantly different from 0). Violins for the control (water) are only shown in the 'time to first detection' analysis; violins in the other two plots are coefficients, compared with the control.

Sooner: time to detection

Time to detection is directly related to the probability of detection (Garrard *et al.*, 2008). Factors that influence the propensity for and frequency of visits (e.g. density, movement patterns, curiosity) affect the time until the initial detection or the interval between consecutive detection events. We found that time to detection varied substantially between observations in our study but detected only one significant effect: free-ranging domestic cats appeared to visit sites during the castoreum lure treatment sooner than during other scent applications (Fig. 4). An affinity of felines to castoreum lures has been reported previously (McDaniel *et al.*, 2000). However, given the spectrum of scents used in this study and previous reports from similar work (Bischof *et al.*, 2014a), a lack of additional effects on time to detection was surprising. Our study was conducted late autumn to early winter which might have influenced the effective sampling distance by cold weather. Alternatively, we used a comparatively small amount of lure (~0.5 mL) which could explain the paucity of effects.

Investigators have multiple options for manipulating the time to detection. They can try to reduce it, as we attempted here, by using olfactory or other attractants which may draw animals from a wider area or increase the propensity for approaching the camera by exploiting the interest in food, potential mates or curiosity in general. Although the effect was not pronounced in our study, based on findings from other studies, lures can be an effective tool for increasing detectability and thus decreasing time to detection (Bischof *et al.*, 2014a; Ferreras *et al.*, 2018; Mills *et al.*, 2019). Other measures are aimed at reducing the risk of avoidance behaviour by preventing contamination of the site with human scent, hiding or camouflaging cameras, using illumination outside the visible spectrum of the target species, and minimizing sounds generated by the camera. Most important perhaps is the selection of sites (O'Connor *et al.*, 2017); placing cameras at locations the target species' range and in preferred microhabitat increases exposure to individuals in the population and thus reduces time to detection (Fig. 1).

Regardless of the biological characteristics that influence time to detection and the measures taken to reduce it, it has already been recognized as an intuitive and useful measure of detectability (Garrard *et al.*, 2008; Bornand *et al.*, 2014; Bischof *et al.*, 2014a; Halstead, Kleeman & Rose, 2018). Specifically, time to event analysis has been used previously in wildlife camera trapping studies to quantify the effect of lures and other covariates on time to detection (Bischof *et al.*, 2014a). Among previous studies that employed time to detection, we can make a coarse distinction based on accounting for imperfect detection (Garrard *et al.*, 2008; Bornand *et al.*, 2014; Bischof *et al.*, 2014a). Accounting for imperfect detection, which includes the present study, has the distinct advantage that we estimate time to detection conditional on the site being occupied, rather than apparent time to detection conditional on the detection having been made. Time to detection without accounting for imperfect detection is liable to underestimate time to detection, as it ignores sites without detections (Bischof *et al.*, 2014a). Alternatively, one may estimate time to detection using right-censoring of sites without detections, which leads to overestimation of time to detection.

Here, we included an exponential hazard model for time to detection besides a binomial component to account for detection conditional on presence (Garrard *et al.*, 2008; Bornand *et al.*, 2014). This allowed us to account for non-detections that were due to true absences, while analysing the effect of lure treatment on the time to detection. The hazard rate parameter (λ) estimated by the model translates directly into detection probability (equation 2) but offers a different perspective on detectability (Garrard *et al.*, 2008).

Regardless of the type of time-to-detection model used, we recommend that it is made part of a hierarchical approach that accounts for imperfect detection. When it comes to measures intended to reduce time to detection, investigators should consider not only the strength of the effect, but also potential unintended consequences these measures may have for the interpretation of survey results. For example, lures may change the size of the area sampled, thereby affecting assumptions of the analytical methods (Larrucea *et al.*, 2007; Rowcliffe *et al.*, 2008) or they could cause changes in the study population (e.g. territory maintenance, energy expenditure). Furthermore, many camera trap studies target multiple species and lures that attract one may repel another (Rocha, Ramalho & Magnusson, 2016; Mills *et al.*, 2019).

Closer: distance to the focal point

Once an individual has been attracted to a camera trap site, detection will depend on whether the individual enters the camera's field of view in a way that (1) triggers the camera and (2) results in a photograph (or video) with enough detail to make an identification. Distance of a visitor to the camera trap is one of the most important covariates of a successful trigger (Randler & Kalb, 2018). Since most camera traps in use today operate on a passive infrared sensor that detects heat of a moving object, the probability of missing a visit increases with distance from the sensor.

Our analysis showed species-specific differences in proximity to the focal location at camera trap stations, modulated by lure type. When lure sticks were treated with the control (distilled water), pine martens approached the sticks more closely than the other three species (Tables S1-S4 in Appendix S2). This pattern reversed, when lures were applied, with marten exhibiting avoidance behaviour towards gland-based lures (castoreum, fox and skunk). Certain species could display aversion towards lures; for example odours from predators or potential competitors can act as deterrent to subordinate species, and hence, their detectability could decrease when using lures (Rocha *et al.*, 2016). Red foxes represent an interspecific threat to the smaller marten, which may explain apparent avoidance behaviour (Lindström, Brainerd & Overskaug, 1995; Monterroso *et al.*, 2020). The similar response to castoreum or skunk-scented sticks is more difficult to explain, as neither striped skunks nor American beaver are native to Europe and do not occur in our study area.

By contrast, badgers approached lure sticks treated with skunk anal scent gland significantly more closely than the control. Similar communication systems in closely related species (Hughes,

Price & Banks, 2010) may facilitate bidirectional olfactory communications within species assemblage (Nielsen et al., 2015). Although striped skunk does not occur in our study area, both skunk and badger are mustelids, which may explain interest by badgers. Alternatively, skunk-based lure, a novel stimulus, may elicit curiosity (Harrington, Harrington & Macdonald, 2009). Other studies have reported little effect of scent lures from sympatric predators on badger attraction (Monterroso et al., 2011; Suárez-Tangil & Rodríguez, 2017), possibly indicating a greater role of the novelty and curiosity aspects.

Detection probability decreases or becomes biased as the chance of misidentification (false positive) increases with the number of related and similar-looking species co-occurring in the same area (Rowcliff & Carbone 2008). Similarly, animals that are hesitant to fully enter the camera's viewshed or keep their distance are less likely to trigger the camera or yield photographs that allow identification, which translates into lowered detection probability. These challenges are further amplified for small-bodied (Tobler et al., 2008) and furtive species (Glen et al., 2013). The choice of camera (focal length, shutter speed or frame rate, image resolution, choice of still vs. video, etc.), camera placement (e.g. relative to a path), installation (height, aim) and the application of attractants give investigators some control over the position of target animals within the camera's viewshed. Attractants may in addition help keep fast-moving species still enough to minimize motion blur.

As our results show, lures may not only facilitate increased proximity but could also prompt avoidance behaviour, manifested as increased distance from the focal point. As mentioned earlier, this could be especially relevant in studies targeting multiple species, where finding a lure or bait that attracts some or all, but does not repel any target species may be challenging if not impossible (Rocha et al., 2016). Furthermore, leaving DNA at the camera's focal point (e.g. scats or hair samples), where it can be detected and used as an additional source of information can aid individual identification (see also next section).

Longer: duration of exposure

In many cases, the time spent in the camera's viewshed is directly related to the number of images or the number or length of video recordings. More abundant visual documentation translates into a higher probability of making an identification and ultimately greater detection probability. We found that red foxes spent significantly more time getting their picture taken during skunk and red fox scent gland treatments than the control treatment (Fig. 4). Fox reaction to conspecifics and skunk can be attributed to information gathering (e.g. communication with conspecifics and competitors) or novelty investigation behaviour.

We detected no significant response to SFE by foxes or any other species in our study. SFE contains some of the components of carrion scent (Bullard, 1982) and has been reported as effective for attracting canids such as red fox (Saunders & Harris, 2000; Hunt, Dall & Lapidge, 2007), kit fox *V. macrotis*, and coyote *Canis latrans* (Roughton, 1982; Bullard, Turkowski & Kilburn, 1983), as well as dingo *C. lupus dingo* and

feral dog *C. l. familiaris* (Hunt *et al.*, 2007). The lack of a response to SFE in our study may be due to the very small amount of lure used at scent stations (~0.5 mL), compared with other studies, that is 2–10 mL (Monterroso *et al.*, 2011; Stratman & Apker, 2014; Bischof *et al.*, 2014a; Díaz-Ruiz *et al.*, 2016; Suárez-Tangil & Rodríguez, 2017). In addition, our study was conducted during the autumn, whereas others reported that red fox spent more time with SFE during winter and spring than summer and autumn (Saunders & Harris, 2000). Seasonal variability in the energetic state of the animal, and thus, the marginal value of carrion, will likely affect the efficacy of SFE and other food-based scent lures.

There is another potentially important and unaccounted-for aspect that could have influenced behaviour during our study: the mutual influence between species visiting the camera trap. Carnivores, intentionally or unintentionally, leave scent at camera trap stations which is liable to be picked up during subsequent visits to the same station by conspecifics and other species. For example, a lure that attracts species A and prompts it to leave a scent mark, may attract or repel species B. This is also one of the reasons (aside from the inability to distinguish individuals) we refer to our study as quasi-experimental, as mutual interactions were neither controlled for during the study nor accounted for during the analysis but may have contributed to the observed patterns.

Investigators may be especially interested in measures to increase the duration of visits to camera traps when working with fast-moving species or species that are difficult to identify due to their morphology (similarity with conspecifics, lack of unique markings, etc.). Particularly capture–recapture methods that require individual identification and rely on unique markings such as pelt patterns, may benefit from boosting the number of images taken and thus the chance of identification (Garrote *et al.*, 2012; Gerber *et al.*, 2012; Dorning & Harris, 2019). For species without visible markings, longer visits may increase the probability and amount of DNA left behind, such as in hair (Burki *et al.*, 2010), faeces and urine (Wikenros *et al.*, 2017), and glandular secretion in case of marking (Clapham *et al.*, 2014).

While lengthening exposure time to the camera will increase detection probability, sample size (visual documentation), and detail, it may also artificially increase encounters between individuals of the same or different species, thus impacting the study system. In addition, it may constitute a manipulation of time budgets. These and other potential impacts should be considered when measures are taken to keep animals in front of the camera for an extended time.

Conclusions

An important conclusion regarding measures to boost detection probability in camera trapping studies is that one measure does not fit all. Biological differences in distribution, abundance, behaviour, and morphology result in different challenges to detectability (Fig. 1). Disentangling and quantifying components of detectability, as we did here, offer investigators a framework for organizing study and species-specific impediments to detection and to come up with strategies to cope with them.

In addition to biological considerations, the impediments and choice of measure for overcoming them will depend on the goals of a given camera trapping study. Studies that require individual identification, such as capture–recapture for abundance estimation, may place high importance on 'closer' and 'longer' in order to make reliable individual assignments (Guthlin, Storch & Kuchenhoff, 2014). Similarly, studies focusing on assessments of behaviour (Caravaggi *et al.*, 2017; van Ginkel, Smit & Kuijper, 2019) and body condition (Carricondo-Sanchez *et al.*, 2017) that want to distinguish reproductive status (Trolle & Kéry, 2003; Canu *et al.*, 2017) and sex (Monterrubio-Rico *et al.*, 2018) will be interested in boosting the quantity and level of detail of information obtained during a given visit to a camera trap. Conversely, studies on presence–absence or species assemblages (Kays et al., 2020) will initially be focused on maximizing the probability of a visit to the camera trap station, especially when rare species are involved ('sooner').

Finally, measures taken to boost different aspects of detectability may have other, unintended effects. Camera trapping is generally hailed as a non-invasive ecological survey method (Burton *et al.*, 2015, but see Meek *et al.*, 2016). The use of lures and baits, as discussed above, could have unintentional consequences for movement and activity patterns, as well as intra and interspecific communication (Neilson *et al.*, 2018). Such changes not only make camera trapping intrusive but could also impact the assumptions of the approach used for drawing inferences (e.g. the size of the site in occupancy analysis). In addition, a measure that improves detection of one species or demographic group may have the opposite effect for another species or group. We recommend that investigators take a comprehensive look at both the biological and study-specific impediments to detectability and potential strategies for overcoming them.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Time to first detection.
Appendix S2. Distance to the focal point.
Appendix S3. Duration of exposure.