# Using time-to-event analysis to complement hierarchical methods when assessing determinants of photographic detectability during camera trapping

**Richard Bischof[1]\*, Shoaib Hameed[2], Hussain Ali[2], Muhammad Kabir[2], Muhammad Younas[2], Kursheed A. Shah[2], Jaffar U. Din[2] and Muhammad A. Nawaz[2,3]**

[1]*Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway;* [2]*Snow Leopard Foundation, 17-Service Road North, I-8/3, Islamabad, Pakistan; and* [3]*Department of Animal Sciences, Quaid-i-Azam University, Islamabad 45320, Pakistan*

## Summary

**1.** Camera trapping, paired with analytical methods for estimating occupancy, abundance and other ecological parameters, can yield information with direct consequences for wildlife management and conservation. Although ecological information is the primary target of most camera trap studies, detectability influences every aspect from design to interpretation.

**2.** Concepts and methods of time-to-event analysis are directly applicable to camera trapping, yet this statistical field has thus far been ignored as a way to analyse photographic capture data. To illustrate the use of time-to-event statistics and to better understand how photographic evidence accumulates, we explored patterns in two related measures of detectability: detection probability and time to detection. We analysed camera trap data for three sympatric carnivores (snow leopard, red fox and stone marten) in the mountains of northern Pakistan and tested predictions about patterns in detectability across species, sites and time.

**3.** We found species-specific differences in the magnitude of detectability and the factors influencing it, reinforcing the need to consider determinants of detectability in study design and to account for them during analysis. Photographic detectability of snow leopard was noticeably lower than that of red fox, but comparable to detectability of stone marten. Site-specific attributes such as the presence of carnivore sign (snow leopard), terrain (snow leopard and red fox) and application of lures (red fox) influenced detectability. For the most part, detection probability was constant over time.

**4.** Species-specific differences in factors determining detectability make camera trap studies targeting multiple species particularly vulnerable to misinterpretation if the hierarchical origin of the data is ignored. Investigators should consider not only the magnitude of detectability, but also the shape of the curve describing the cumulative process of photographic detection, as this has consequences for both determining survey effort and the selection of analytical models. Weighted time-to-event analysis can complement occupancy analysis and other hierarchical methods by providing additional tools for exploring camera trap data and testing hypotheses regarding the temporal aspect of photographic evidence accumulation.

**Key-words:** Cox proportional hazards model, cumulative incidence, *Martes foina*, *Panthera uncia*, survival analysis, *Vulpes vulpes*, weighted observations

## Introduction

Camera trapping has become an important tool in ecological research, especially for monitoring rare and elusive species, because it can provide detailed visual information without requiring on-site human observers or physical capture. Developments and adaptations in analytical fields allow us to extract from photographic capture data information about activity patterns and behaviour (Maffei *et al.* 2005), species diversity/ inventory (Tobler *et al.* 2008), occupancy (Linkie *et al.* 2007),

abundance and density (Karanth & Nichols 1998), as well as vital rates such as survival and fecundity (Gardner *et al.* 2010). Like other evidence placing organisms in time and space, camera trap data originate from two processes: the ecological mechanisms determining abundance/occupancy and the process of observation determining our ability to detect an organism when it is present (Kéry 2011). Although ecological parameters are typically the focus, detectability permeates every aspect of camera trap studies and most other surveys of fauna and flora. Knowledge about detectability can help optimize study design (MacKenzie & Royle 2005), and detectability must be accounted for analytically to estimate the ecological parameter of interest (Kéry & Schaub 2012). In

*\*Correspondence author. E-mail: richard.bischof@umb.no*

addition, most studies strive towards achieving high detectability because this increases cost efficiency, improves the precision of the ecological parameter estimates and, in the presence of latent heterogeneity in detection probability, also reduces bias in the estimates (Lukacs & Burnham 2005).

We can express detectability (i) as the probability of making a detection in a given time period (e.g. 1 day) or (ii) as the time until a detection is made, both conditional on presence of the focal individual or species. Although these two measures are manifestations of the same binomial process, they provide different perspectives on detectability. Camera trapping typically involves periods of inactivity, interrupted by photographic captures of wildlife. An expansive statistical field, time-to-event analysis, more commonly referred to as survival analysis, deals with such situations. As the name suggests, the measure of interest is the time until some event occurs. In the case of camera trap studies, it is the time until a photographic capture is made, and we illustrate the use of this concept to gain additional insights about detectability during multispecies camera trap studies.

Using both occupancy analysis and time-to-event analysis, we explored empirical patterns in photographic detectability over species, sites and time for three sympatric carnivore species (snow leopard *Panthera uncia*, red fox *Vulpes vulpes* and stone marten *Martes foina*). We asked the following questions to guide our analysis:

*Q1.* How do the three carnivore species differ in their photographic detectability? We predict that widespread species known to be tolerant of human activity and environmental disturbance, such as red fox and stone marten (Adkins & Stott 1998; Herr *et al.* 2010), are more easily detected than the snow leopard with its reputation for being elusive (Janečka *et al.* 2011).

*Q2.* What are the determinants of detectability? Site selection is a key factor during camera trapping studies targeted at carnivores, and we expect species-specific responses of detectability to site covariates, such as terrain, habitat type and the presence/absence of carnivore sign in the area. We predict that the presence of carnivore sign and application of scent lures at camera traps improve detectability (higher detection probability, shorter time to detection).

*Q3.* How does photographic detection proceed over time? We predict that disturbances associated with placing camera traps in the environment, as well as changes in the potency of olfactory attractants due to scent dissipation, may lead to non-constant detectability over time.

*Q4.* What is the quantitative effect of longer survey duration on the probability of detecting a focal species at least once at a site if it is present? Hamel *et al.* (2012) recommended a 30-day survey duration when multiple species are targeted in one study to allow reliable parameter estimates (conditional on the number of sites surveyed). This would entail a two- to three-fold increase compared with the camera trapping duration in our study (10–14 days), which we anticipate would substantially boost the proportion of cameras with at least one detection and consequently increase the sample size.

We discuss implications of our findings for camera trap study design and data analysis and illustrate for the first time the utility of time-to-event analysis for complementing information about detectability gained from hierarchical models based on camera trap data.

## Materials and methods

### STUDY AREAS AND CAMERA TRAPPING

Data analysed here were collected as part of a larger project studying carnivore guild ecology using non-invasive methods. Camera traps were deployed in four study areas situated in and around three national parks in the mountains of northern Pakistan. From west to east, the parks are Broghil National Park, with study area BNP (36º 50′ N, 73º 28′ E; 450 km$^2$; 3 217–5 696 m a.s.l), Qurumber National Park, with study area QNP (36º 42′ N, 73º 59′ E; 650 km$^2$; 2 474–5 914 m a.s.l), and Khunjerab National Park, with study areas KKH (36º 52′ N, 75º 07′ E; 1 025 km$^2$; 2 748–6 029 m a.s.l.) and SHS (36º 25′ N, 75º 23′ E; 475 km$^2$; 2 923–6 372 m a.s.l., Fig. 1). Broghil and Qurumber National Parks are located in the Pamir Mountains, whereas Khunjerab National Park is in the Karakoram Mountains. The landscape is rugged in all four study areas, dominated by narrow valleys, ravines, cliffs and ridges, and mostly glaciated mountain crests. Four vegetation zones can be distinguished along the elevation gradient: alpine dry steppe, subalpine scrub zone, alpine meadows and permanent snowfields.

Camera traps were deployed September 25–November 16, 2011, in KKH/SHS and June 18–July 30, 2012, in BNP/QNP. We selected camera trap locations within each study area based on terrain features favoured by medium to large mammalian carnivores (ridges, cliff bases, draws/valleys) and preferably the presence of carnivore and/or prey sign. Accessibility in rough terrain constrained site selection. Study grids (5 × 5 km, Fig. 1) were used as guides to spread camera traps across the landscape, but due to the variable terrain, mostly representing linear systems of narrow draws and ridges, grid cells are not true sampling units. We set 2 (occasionally 1 or 3) camera traps in each 5 × 5 km grid cell. Camera traps were separated by at least 1 km, with some exceptions due to constraints posed by terrain. Upon selecting a site, a single-motion-triggered digital camera with infrared flash (HC500/PC900; Reconyx, Holmen, WI, USA) was installed by affixing it at a height of *c.* 50–60 cm to a steel pole driven into the ground. Camera traps were set to take consecutive images (1-s picture interval) while being triggered and were typically kept active at a given location for 10–14 days.

### SPECIES STUDIED

We chose to include data from three species in this study (Fig. 1) as they were the most frequently captured carnivores during camera trapping. The red fox is one of the most widespread and adaptable carnivores and occurs throughout Pakistan (MacDonald & Reynolds 2008). The stone marten is common throughout Europe and Asia; its range in Pakistan includes the mountainous areas in the north and along the border with Afghanistan in the west (Tikhonov *et al.* 2008). Both red fox and stone martens are classified as species of least concern on the IUCN Red List, whereas the snow leopard is classified as endangered (IUCN 2012). In Pakistan, the snow leopard range covers part of the mountainous areas in the north with a countrywide population estimate of 200–420 individuals (Jackson *et al.* 2008).
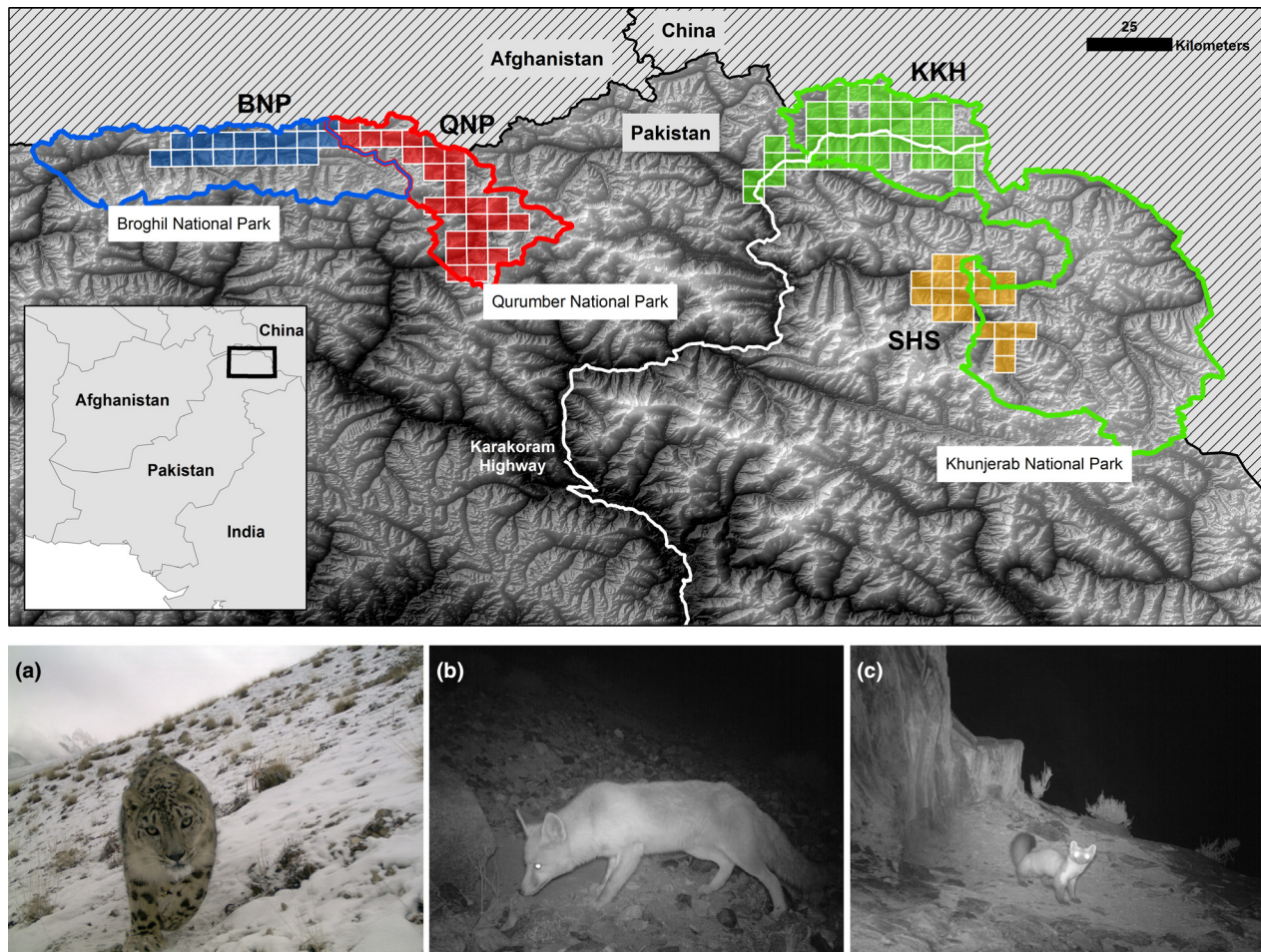
**Fig. 1.** Shaded relief map (top) showing four camera trap study areas (sectioned into 5 × 5 km grids) in relation to three national parks (solid boundaries) in northern Pakistan. The images below the map are examples of camera trap photographs of the three species included in the analysis: snow leopard (a), red fox (b) and stone marten (c).

## COVARIATES

At each camera trap location, we recorded elevation, terrain feature (cliff base, ridge/slope, valley/draw), habitat type (barren, forest/scrub, pasture/grassland) and any potential carnivore sign (e.g. tracks, faeces, scrapes) found in its vicinity. Study area (BNP, QNP, KKH and SHS) was used as an additional predictor in the analysis to control for the collection of characteristics that separated survey bouts spatially and in time. Differences between survey years and seasons did not allow a reliable spatial comparison between SHS/KNP and BNP/QNP. Because snow leopard was only photo-captured at a single camera trap station in QNP and not at all in BNP, we only analysed data from KKH and SHS for this species.

To evaluate whether olfactory attractants boost detectability, camera traps were randomly assigned to one of three treatments: (i) castor-based scent lure (containing beaver *Castor canadensis* castoreum; Evanesce Lure, Kaatz Bros, Savanna, IL, USA), (ii) skunk-based scent lure (skunk *Mephitis mephitis* anal scent gland; Magnum-Call Lure, Blackie's Blend, Glenmont, OH, USA) and (iii) no lures/attractants (control). We used commercial scent lures manufactured for North American trappers targeting carnivores. At camera trap sites designated for lure application, a plaster tablet (diameter: 16 mm; thickness: 6 mm; USDA-Pocatello Supply Depot, Pocatello, ID, USA) soaked in

fish oil was placed in the centre of a cleared area (*c.* 75 cm diameter) and lightly covered with loose soil or sand to reduce the chance of detection and removal by birds. Plaster tablets were added as a short range attractant to draw potentially reluctant carnivores into the view of the camera. The designated scent lure (*c.* 3–5 mL) was applied as a long-range attractant to vegetation or rock adjacent to the cleared area at a height between 30 and 50 cm above the ground.

## DEFINITIONS

Before proceeding with the description of the analytical approach, we define the following variables:

- $P$ = detection probability, the daily probability of photographic detection of the focal species at a camera trap station at least once, conditional on the species being present.
- $T$ = time to detection, the time (e.g. in hours or days) until the first photographic detection of the focal species at a camera trap station, conditional on the species being present.
- $t_{0.5}$ = median time to detection, the time by which 50% of camera trap stations with the focal species present have made a photographic capture of that species.
- $P_t$ = the probability of at least one photographic detection of the focal species by a given time $t$ after camera activation,

conditional on the species being present. Alternatively, $P_t$ is the proportion of stations with at least one detection by time $t$.

## DETECTION PROBABILITY

We used single-species, single-season occupancy models to estimate detection probability $P$ (*Q1*) and the effect of site covariates (MacKenzie 2006; *Q2*). After constructing species-specific detection histories based on daily detection/non-detection at each camera trap (Fig. 2), we used function 'occu' in the R package unmarked (Fiske & Chandler 2011; R Development Core Team 2012) to fit separate occupancy models for each of the three focal species. We considered lure treatment, elevation, study area, terrain feature, habitat type and the presence/absence of potential sign of the focal species as covariates on $P$. The same covariates, except lure type, were also considered as predictors of occupancy ($\psi$). The need to set camera traps at locations that (i) were likely places for carnivores to visit and (ii) were accessible on foot, meant that the spatial distribution of camera traps was neither random nor systematic. The objective of the present analysis was to obtain conditional estimates of detectability and not to produce and compare absolute occupancy or abundance estimates, for which spatially explicit hierarchical models may be a more robust option (Royle *et al.* 2007). However, to partially account for the likely non-independence in occupancy between camera traps in each other's vicinity, we considered as an additional predictor on occupancy the distance to the nearest camera

trap station with at least one detection of the focal species. Both distance to the nearest camera trap with confirmed photographic capture and elevation were standardized (mean = 0, SD = 1) and modelled using smoothing splines with 2 d.f. (function 'ns' in R package 'splines'), because preliminary analysis suggested nonlinear relationships between these variables and real parameters. We used AIC for model selection, considering all possible combinations of terms, but limiting the maximum number of predictors on either real parameters to three. In cases where several models were within $\Delta$AIC 2 of the top model, we selected the model with the fewest parameters for inference. We performed goodness-of-fit tests with a parametric bootstrap and a chi-squared statistic following MacKenzie (2006) and Fiske & Chandler (2011).

## TIME TO DETECTION

Concepts and methods associated with time-to-event analysis are directly applicable to camera trapping. The measure of interest is the time until some event (also referred to as 'failure' or 'death') occurs to an individual. In our analysis, the individual for which the event occurs is a camera trap station, and the event is the first photographic capture of the focal species at that station. The follow-up period is the duration of time for which individuals are monitored, that is, the time from camera activation until takedown/deactivation. Censoring is an essential concept in time-to-event analysis; when monitoring ceases of an individual without having observed an event, we right-censor. Right-censoring allows for the inclusion of data from camera traps that did not
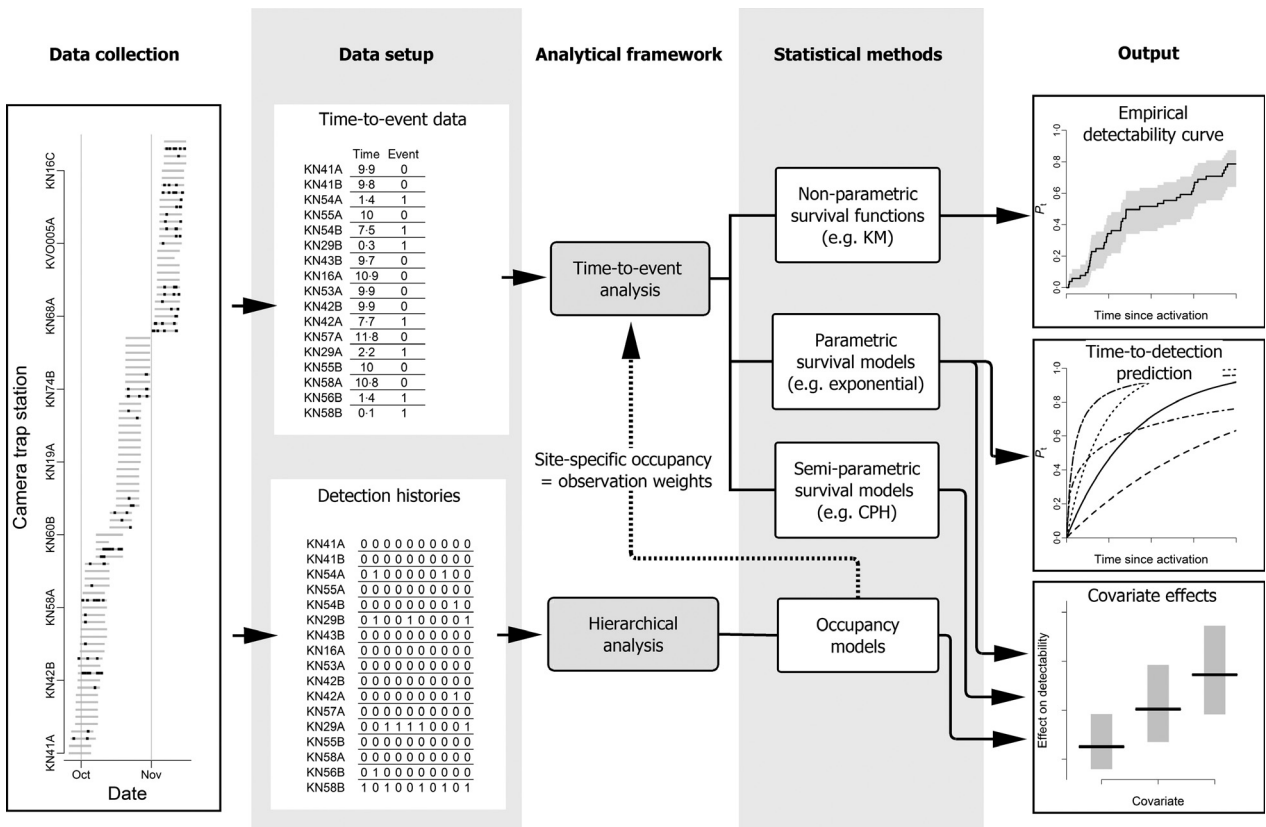


**Fig. 2.** Conceptual diagram of the approach taken to analyse camera trap data using time-to-event statistics and occupancy models. Each row in the graph to the far left represents the history of one camera trap station, with grey lines indicating time periods during which each station was active (*c.* 10 days) and black marks representing photographic captures of the focal species. Camera trap data were compiled into time-to-event data and detection histories (excerpts shown). Analytical steps (hierarchical analysis and time-to-event analysis) and their output are described in the text and Appendix S1.

detect the focal species by considering the time such camera traps were available for making a photographic detection.

We used Cox proportional hazards (CPH) models to confirm empirically that patterns in time to detection matched patterns in detection probability in terms of covariate effects (*Q2*). CPH models estimate the multiplicative effect of covariates on the baseline hazard (the instantaneous potential of detection), assuming only that hazards are proportional, but without having to specify the shape of the underlying cumulative distribution function (Cox 1972; Venables & Ripley 2002; Appendix S1). However, simply using the time until the first photo-capture of the focal species as the response and censoring all sites without captures ignore the fact that there are two possible causes for non-detection: the species either was present but missed, or was not detected because it was truly absent. From the top occupancy model that emerged during occupancy model fitting, we derived empirical Bayes estimates of site-specific occupancy at each camera trap location with functions 'ranef' and 'bup' in the R package unmarked (Fiske & Chandler 2011). We then proceeded to use these occupancy values (>0–1) as observation weights in the CPH regression, implemented through the 'weights' argument of the 'coxph' function in the R survival package (Therneau 2012). Covariate effects estimates derived from the weighted CPH model can be interpreted as effects on detectability conditional on presence, because sites less likely to be occupied have a correspondingly smaller contribution during fitting and hence smaller impact on the regression estimates. We used simulations to confirm that the weighted CPH approach reliably estimates conditional hazard ratios of detectability both qualitatively and quantitatively under an occupancy scenario (Fig. S1, Appendix S2). We fit species-specific CPH models using the same covariates identified in the top occupancy models (on detectability). Model diagnostics were performed following Fox (2002), including tests for proportionality of hazards using the 'cox.zph' function in the R survival package.

We used three steps to assess how the accumulation of photographic evidence proceeded in time:

Step 1: We constructed empirical detectability curves (DC) to visualize cumulative detection over time (*Q3*). Empirical DCs give the probability that the first photo-capture of a focal species occurs sometimes before $t$ (time after camera activation) and are equivalent to what are termed 'cumulative incidence curves' in time-to-event analysis. In the absence of competing risks, that is, when multiple events (photographic captures of different species) are not mutually exclusive, empirical DCs are complements of Kaplan–Meier (KM) survival curves. The latter are nonparametric maximum-likelihood estimates of survival over time ($S(t)$; Kaplan & Meier 1958; Venables & Ripley 2002; Appendix S1), that is, the probability that the event of interest has not yet occurred by time $t$, which can be calculated with the 'survfit' function in the R survival package. To construct empirical DCs that were conditional on presence at a site, we included site-specific occupancy estimates as observation weights during the calculation.

Step 2: We fit parametric survival models to the time to first detection to determine whether there was evidence for non-constant detectability over time (*Q3*). We quantitatively compared the performance (AIC) of the model assuming constant detection over time (exponential cumulative distribution function) with models representing four alternative cumulative distribution function shapes that allow for non-constant detectability: Weibull (with scale parameter $\neq 1$), Gaussian, log and log-logistic. All survival models were fitted with the function 'survreg' in the R survival package, with site-specific occupancy estimates as observation weights. In addition to AIC-based model comparison, we visually

compared empirical DC (Step 1) with predictions from the model assuming constant detectability over time (exponential DC).

Step 3: We used parametric survival models to a) estimate $t_{0.5}$ as an alternative means to compare detectability among species (*Q1*) and b) predict $P_t$ if we extended the camera trapping duration to 30 days (*Q4*). Both $t_{0.5}$ and $P_t$ assuming a 30-day camera trapping duration were estimated using the exponential survival model fitted separately to each species' time-to-detection data ('survreg' function in R survival package).

Additional details about the analytical approach are provided in Appendix S1 and an overview in Fig. 2. We again used simulations to confirm that detectability, conditional on presence, was correctly represented by DCs constructed from observations weighted according to their site-specific occupancy estimates (Fig. S2).

## Results

We set 198 separate camera traps (BNP: 31, QNP: 47, KKH: 85; SHS: 35) for a total of 2 287 camera trap days. Of the three focal species, red fox was the most frequently captured species (8·6 capture trap days per 100 trap days and 2 055 photographs at 93 camera traps), followed by stone marten (2·6 capture trap days per 100 trap days and 520 photographs at 36 camera traps) and snow leopard (1·3 capture trap days per 100 trap days and 1 093 photographs at 23 camera traps).

### DETECTION PROBABILITY

Occupancy analysis revealed species-specific differences in detection probability and the covariates affecting detectability (Table 1, Fig. 3).

*Q1*. In the areas where we photographically captured all three species, $P$ for snow leopard was noticeably lower than that for red fox, but comparable in magnitude to $P$ for stone marten (Table 1).

*Q2*. For snow leopard, the strongest determinant of photographic detectability was the presence of potential sign indicating activity in the vicinity of the camera trap prior to set-up (9·3 times greater odds, 95% CI: 2·2–39·9). Skunk-based lures had a positive effect on $P$ of red fox (2·6 times greater odds, 95% CI: 1·7–4·1), and castor-based lures were intermediate in their effect (Fig. 3). Both snow leopard and red fox had lower

**Table 1.** Estimates of daily detection probability ($P$; from occupancy models) and median time to first detection ($t_{0.5}$; from survival models) by species and study area (95% CI limits in parentheses)

| Study area | Snow leopard | Red fox | Stone marten |
|---|---|---|---|
| Detection probability $P$ | | | |
| KKH | 0·037 (0·032–0·047) | 0·163 (0·152–0·179) | 0·048 (0·047–0·055) |
| SHS | 0·036 (0·029–0·049) | 0·181 (0·161–0·209) | 0·032 (0·031–0·05) |
| BNP | – | 0·131 (0·116–0·154) | 0·136 (0·127–0·153) |
| QNP | – | 0·072 (0·065–0·084) | 0·099 (0·095–0·107) |
| Median time to first detection $t_{0.5}$ (in days) | | | |
| KKH | 19·89 (11·99–32·99) | 4·65 (3·43–6·32) | 13·39 (6·97–25·73) |
| SHS | 23·27 (10·46–51·8) | 4·43 (2·79–7·03) | 16·57 (5·34–51·38) |
| BNP | – | 7·18 (4·33–11·91) | 5·19 (2·6–10·38) |
| QNP | – | 9·79 (6·17–15·54) | 5·43 (3·33–8·87) |

odds of being detected by camera traps set on ridges/plateaus than by camera traps set along the bases of cliffs; odds of stations set in draws/valleys were intermediate (Fig. 3). Study area affected $P$ of red fox and stone marten. Effects of predictors retained in each species' top occupancy model are shown in Fig. 3, and results of model selection, in Table S1.

Hierarchical modelling also yielded species-specific estimates of $\psi$ and associated covariate effects. Although occupancy itself was not the focus of the present study, site-specific occupancy estimates were used as observation weights during the time-to-event analysis and are shown in Fig. S3. Overall occupancy estimates (Table S2) should be interpreted with caution (e.g. as site/area use, rather than as occupation) due to violation of closure assumptions caused by the likely observation of individuals with large home ranges at multiple sites.

### TIME TO DETECTION

*Q1*. Patterns in median time to detection were consistent with patterns in detection probability across species and study areas: low $P$ was associated with long $t_{0.5}$ and *vice versa* (Table 1). Species-specific DCs predicted with parametric survival models tracked DCs based on estimates of $P$ obtained from occupancy models (Appendix S1), which is further empirical evidence of the connection between the two measures of detection.

*Q2*. The results from the weighted CPH regressions closely matched those from the occupancy analysis (Fig. 3), and simulations confirmed that using occupancy estimates as observation weights in CPH regression led to reliable estimates of covariate effects on hazards, conditional on presence (Fig. S1).

*Q3*. Comparison of empirical DCs (black lines, Fig. 4) with DCs assuming an exponential survival model (red lines, Fig. 4) gave little indication of systematic deviations from constant detectability over time. In one case (red fox in BNP), the Weibull cumulative distribution function resulted in a better fit ($\Delta$AIC = −4) than the exponential one. Simulations confirmed that empirical DCs constructed using occupancy estimates as observation weights matched the DCs constructed using perfect knowledge about occupancy (Fig. S2).

*Q4*. The proportion of stations that would detect a focal species at least once during a 30-day camera trap period varied dependent on the pattern in species- and area-specific detectability. For example, for snow leopard, the species with the lowest detection probability increasing the camera trapping duration from 10 to 30 days in KKH would result in a predicted increase in $P_t$ from 0.29 to 0.65, whereas for red fox and stone marten, a corresponding extension of camera trapping duration would lead to an increase in $P_t$ from 0.78 to 0.99 and 0.4 to 0.79, respectively (Fig. 4).

## Discussion

### SPECIES-SPECIFIC DIFFERENCES IN DETECTABILITY (*Q1*)

Our results confirm the need to account for imperfect and variable detectability when analysing camera trap and other observation data (see also Kéry & Schaub 2012). It is tempting to analyse camera trap data by comparing photographic capture rates and ignoring the hierarchical origin of the data. However, comparisons of rates could be deceiving because systematic variation in detection probability will result in biased estimates of differences (Kéry 2011). In our study, detection probability varied between species and over several of the site covariates that we evaluated (Fig. 3). Because occupancy varied as well, models ignoring the hierarchical process would have led to potentially erroneous predictions (Figs S1 and S2).

### SITE SELECTION AND ATTRACTANTS AS DETERMINANTS OF DETECTABILITY (*Q2*)

Many species with the greatest conservation need are difficult to detect and monitor. The key factor in determining detectability in most field studies remains location; for carnivores, this means selection of sites that lie along possible movement paths, are near preferred terrain/habitat features and ideally contain signs of use by carnivores or their prey. Determinants of snow leopard detectability, the presence of sign and terrain feature, are particularly noteworthy in the light of the international interest in snow leopard monitoring and conservation and the species' notoriety for elusiveness (Janečka *et al.* 2011). The nine-fold greater odds of photo-capturing snow leopards at stations with snow leopard sign than without may seem trivial in the context of occupancy studies (i.e. why not just use sign data for determining occupancy in the first place), but are relevant for photographic mark–recapture studies that distinguish between individuals.

During camera trapping, enticements such as lures and baits can boost the probability of a visit and thereby detectability. We found that red foxes were more likely to be detected at camera trap stations treated with lures. Lures can increase detectability, but might also lead to a change in spatial sampling units (by drawing animals in from a wider area) and to non-constant detection probability over time (e.g. through initial attraction, followed by scent dissipation). During a camera trap study of Malagasy civets *Fossa fossana*, Gerber, Karpanty & Kelly (2012) found that the application of lures did not bias density estimation through effects on immigration and emigration; instead, it led to an increase in precision of the estimates by increasing the number of recaptures. In addition to the benefits of a larger sample size, more frequent and potentially longer visits increase the chance of making an individual identification, observing behaviour and reproductive status, and provide greater opportunity to collect genetic samples at the site. Furthermore, by shortening the time to first detection, lures can help reduce survey durations and thereby help meet closure assumptions and reduce costs.

### DETECTION PROCESS OVER TIME (*Q3*) AND CAMERA TRAPPING DURATION (*Q4*)

Time to detection in our study showed little systematic deviation from the exponential cumulative distribution function (i.e. constant detectability), with the exception of red fox in BNP.
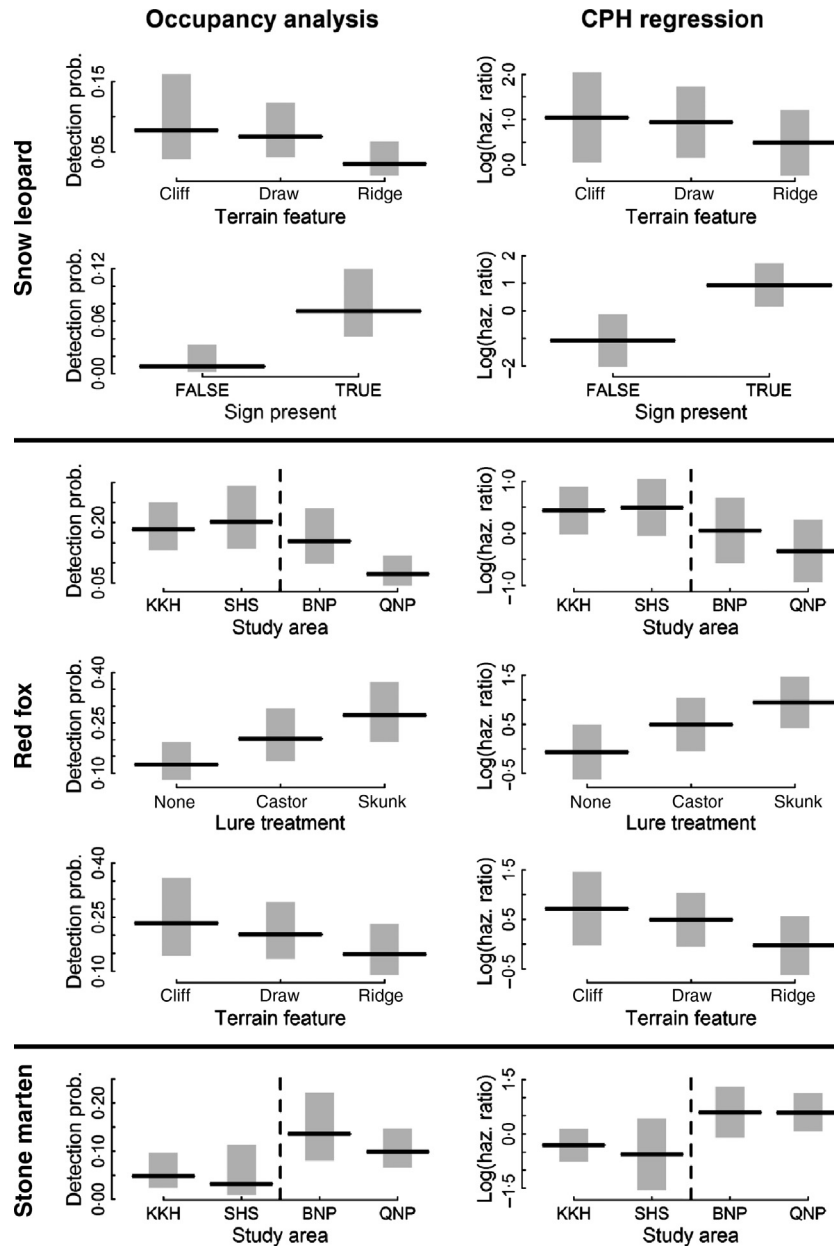
**Fig. 3.** Predictions for covariate effects on detectability estimated from top occupancy models (left column) and Cox proportional hazards regression (right column) for three carnivore species (grey bars: 95% CI). Panels in the left column show covariate effects on daily detection probability. Panels in the right column show covariate effects on the log hazard ratio. For predictions of a given covariate effect, all remaining covariates are held either at the mean (continuous variables) or at an arbitrary level (categorical variables). The focus is on the relative position of the estimates, not their absolute value. Vertical dashed lines in the study area effect plots indicate that surveys were implemented in different seasons and years in KKH/SHS vs. BNP/QNP.

Regardless of this finding, we encourage investigators to check their camera trap data for non-constant detection probability over time, because the shape of the DC could influence selection of the appropriate model for analysis as well as decisions about effective survey length. For example, when hazards are initially low due to avoidance, but then increase as the target species becomes accustomed to the camera trap or, when human scent has dissipated, lengthening the camera trapping duration to include the period of elevated detection will increase the average daily probability of detection during the survey.

The duration for which a camera trap is kept active at a given site is an important consideration when planning camera trap studies (Hamel *et al.* 2012). Resource limitations (available staff, time, camera traps) and analytical assumptions (e.g. demographic closure in capture–recapture studies; Karanth, Nichols & Kumar 2011) may favour shorter overall study periods, whereas the need to increase $P_t$ and thereby the accuracy and precision of parameter estimates may require longer camera trapping durations (Hamel *et al.* 2012). Survival functions and their complements constructed from camera trap data can provide an analytical and visual tool to help with decisions
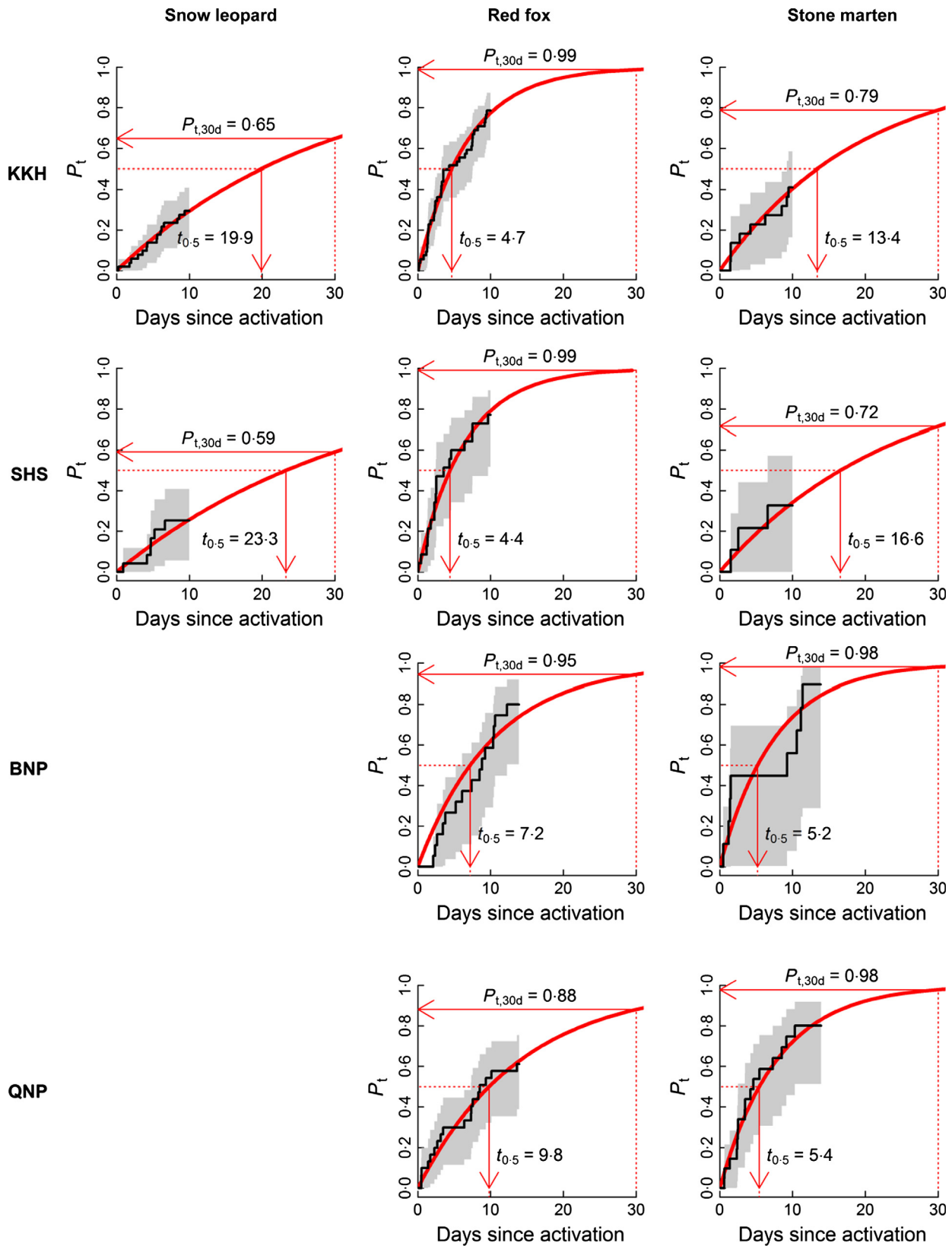
**Fig. 4.** Detectability curves (DC) for three carnivore species in four study areas, showing the probability $P_t$ of at least one photographic detection by a given time $t$, conditional on presence. Empirical DCs (solid back lines, with 95% confidence bands in grey) were estimated as the complement of Kaplan–Meier survival curves, with camera traps weighted according to their site-specific occupancy estimates. Bold red lines are DCs predicted with parametric survival models assuming constant detectability over time. Red arrows indicate the median time to detection ($t_{0.5}$, pointing down) and $P_t$ assuming 30 days of camera trapping (pointing left).

about camera trapping duration consistent with the recommendation by Garrard *et al.* (2008) to use detectability curves for determining effort needed during floral surveys. Hamel *et al.* (2012) recommended a 30-day camera trapping duration at a site when multiple species are targeted in one study, which depending on the study area would lead to projected $P_t$ between 0·59 and 0·65 for snow leopard, 0·88 and 0·99 for red fox and 0·72 and 0·98 for stone marten. Survival functions can also help view the effect of covariates from a different perspective: for example, the median time to first detection of red fox depends on the application of olfactory attractants, with direct consequences for survey efficiency (Fig. 5).

### ANALYTICAL CONSIDERATIONS

Important concepts and methods in time-to-event analysis, such as survival functions, hazards and censoring, find direct application during the analysis of camera trap data. Using a Bayesian approach, Garrard *et al.* (2008) and McCarthy *et al.* (2013) combined an exponential failure time model with a binomial component to account for the time to detection conditional on presence, as well as non-detection due to true absence during floral and faunal surveys. As an alternative approach for modelling time to first detection conditional on presence, we have weighted observations according to their site-specific occupancy estimates during time-to-event analysis. Although there are inherent benefits in integrating all components of an analysis within a single framework/paradigm as done by Garrard *et al.* (2008) and McCarthy *et al.* (2013), there are several advantages associated with our approach. These include the benefits of using nonparametric and semi-parametric models that do not require that the shape of the cumulative distribution function be specified, as well as access to the built in functionality of the R survival package (Therneau 2012). In addition, our approach is more accessible for investigators who rely on frequentist methods for inference. As our validation has shown, weighted DC construction and CPH regression resulted in reliable conditional parameter estimates, apparently unbiased with respect to the true parameter and estimates obtained assuming perfect knowledge about occupancy (Figs S1 and S2). Furthermore, predictions of covariate effects (CPH models) and species-specific time to detection (parametric survival models) showed strong correspondence with results obtained from occupancy analysis. Time-to-event analysis of camera trap data as described here considers the first detection at each camera, whereas occupancy or other forms of mark–recapture analysis use also subsequent captures (albeit pooled into discrete occasions). Recurrent event survival analysis (Cook & Lawless 2007), may present a solution where this is a concern because it allows for events that can occur more than once.

Because the sample size available for analysis is directly related to the magnitude of the real parameters ($\psi$ and $P$), so is our ability to detect and/or reliably quantify covariate effects. The relationship between the magnitude of the real parameters and statistical power should be considered when comparing patterns in covariate effects between species, especially because
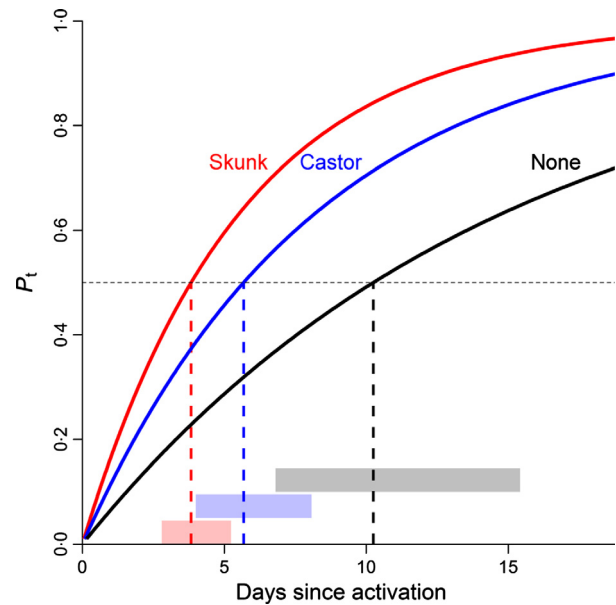


**Fig. 5.** Parametric detectability curves showing $P_t$ for red fox as a function of camera trapping duration. Predictions assuming constant detectability over time were made for three different lure treatments. Dashed vertical lines indicate the predicted median time to event (i.e. foxes are detected at 50% of the stations at which they are present) together with 95% CIs (shaded horizontal bars).

the absence of evidence of a significant effect cannot be taken as evidence for the absence of an effect. Ironically, we can expect to obtain less reliable and less detailed information on factors influencing detection probability for rare and elusive species where we could potentially gain the most from understanding and manipulating detectability (such as through site selection or the use of attractants). In the extreme, we have to accept that photographic captures of some species may be too scarce to allow parameter estimation with useful precision. Even if parameter estimation seems feasible, covariate effects or potential deviations from model assumptions may be difficult to detect when sample sizes are low. For example, the comparatively small number of photographic captures of snow leopard and stone marten is a cause for caution when interpreting tests of proportionality of hazards (CPH models) or deviations from the exponential cumulative distribution function (parametric survival functions).

## Conclusions

The technical developments and growing popularity of camera traps have brought about an unprecedented amount of detailed visual information about wildlife (O'Connell, Nichols & Karanth 2011). Detectability, although a so-called nuisance parameter, is nonetheless of considerable importance when it comes to designing, analysing and interpreting camera trap studies. Combining analytical tools that target different expressions of detectability – detection probability and time to detection – can give a comprehensive picture of how photographic evidence accumulates during camera trap studies and the factors determining detection. As a follow-up to our study, we

suggest investigations that search for variation in the shape of cumulative incidence of detection over time and evaluate its implications for the design and analysis of camera trap data.

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## Supporting Information

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

**Appendix S1.** Details of applying time-to-event analysis to camera trap data.

**Appendix S2.** R code for simulating occupancy data with exponential time to detection and conducting occupancy and weighted time-to-event analysis.

**Fig. S1.** Validation of weighted Cox proportional hazards regression predictions for photographic detection, conditional on presence.

**Fig. S2.** Validation of cumulative incidence curves for detection, constructed from observations weighted according to site-specific occupancy estimates.

**Fig. S3**. Map of site-specific occupancy estimates at camera trap locations.

**Table S1.** Model selection results from occupancy analysis.

**Table S2.** Overall occupancy estimates by species and study area.