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Research article

An evidence-based approach to identifying resting sites of Eurasian otter *Lutra lutra* from camera-trap and field-sign data

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Mammals' resting sites (dens) are important features of their ecology. Eurasian otter *Lutra lutra* resting sites are strictly protected by UK and European legislation and are ostensibly identified from associated field-signs. This legislation is difficult to apply given the poor understanding of resting sites coupled with the lack of evidence supporting a field-sign signature. We aimed to use camera-trap data to identify resting sites, investigate whether field-signs differed between resting and non-resting sites and describe behaviours recorded on camera-traps that are associated with resting. An evidence-based approach to identifying resting sites of Eurasian otter *Lutra lutra* from camera-trap and field-sign data camera-trap data showed that otters frequently visited potential resting sites, characterised by a very short time within the structure (often < 4 min). Resting sites were characterised by longer durations (often hours) during the daytime and night-time. Based on these data, six of our 26 sites were identified as resting sites. Modelling suggested that no single field-sign had a clear association with resting sites. However, we found a hitherto unrecognised distinction between otter latrines (defecation sites) and spraint (scent-marking) sites, and that camera-trap observations of latrine behaviour and bedding collection were exclusive to resting sites. As bedding and latrines are not always visible, presence of either indicates a resting site but no interpretation can be drawn from their absence, so camera-trapping would be recommended to identify resting site status. Data simulations found that camera-trapping for 38 d in winter, followed by 38 d in spring, was the optimal approach for a 95% chance of detecting a rest across all resting sites. Ours is the first study to identify standards and expectations for surveys using camera-trap and field-signs at Eurasian otter resting sites. Our novel account of their resting activity facilitates better interpretation of legislation.

Keywords: camera-trap, field-signs, latrine, legislation, methodology, resting site



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Introduction

Eurasian otter dens, hereafter ‘resting sites’ are an important component of an otter’s habitat. In recognition of this, Council Directive 92/43/EEC (European Commission 1992) or the Habitats Directive, applicable across much of the otters’ range, directs member states to apply domestic legislation to protect otters and their resting sites even when the otter is not present. Despite this, there are currently no clear definitions of what a ‘rest’ or a resting site is. In ecological terms, a mammal den can be understood as a ‘site or structure’ used ‘for a prolonged bout of sleeping or resting’ and are used for breeding (Birks et al. 2005, p. 314). However, the directive is not otter-specific, covering over four-hundred species of different taxonomic groups and widely differing ecologies, thus the guidelines that support interpretation of the legislation have to be broad-brush.

Species of mammal that occupy their dens for significant periods usually have a build-up of field-signs and their dens can readily be identified by a field ecologist (Wilson et al. 2003, Gallant et al. 2012). The confident identification of otter resting sites is more problematic for several reasons. Firstly, they have a high number of resting sites which enables individuals to efficiently exploit resources within their large, usually linear, home-ranges, which can be 7–40 km of water-course (Green et al. 1984, Durbin 1996, Georgiev 2007, Néill et al. 2009). Secondly, these resting sites are used peripatetically when otters are without neonates, i.e. they change resting site frequently, often daily (Green et al. 1984, Rosoux and Libois 1996, Néill et al. 2009). Thirdly, their scent-marks, known as ‘spraints’ are frequently deposited throughout their home-range. These are easy for a field-ecologist to find and identify and are often used as a putative identifier of resting sites. However, sprainting behaviour is not fully understood and has been related to many variables including population density, season and food resources (Prigioni et al. 2006, Georgiev 2008, Remonti et al. 2011). Finally, current information on otter resting sites comes from radiotracking studies, but these studies do not inform more accessible approaches such as field-sign surveys and camera-trapping.

Camera-traps potentially offer an accessible method for identifying otter resting sites (Findlay et al. 2017) and also improve field-sign surveys by increasing understanding of any relationships between field-signs and resting behaviour. Before camera-traps can effectively be used as a tool to identify otter resting sites, research is required to inform how camera-trap data can distinguish a resting site from other features or structures that an otter might frequent which are not used for resting. Evidence is also needed to guide methodology, for instance, to reject a site as being a resting site, there needs to be a sampling protocol which gives an acceptable level of certainty that the site is not a resting site. A long-term study on a single otter holt demonstrated that activity data from camera-traps can be used to provide both a definition of a rest and evidence that the site could be defined as a resting site (Findlay et al. 2017). Aside from activity patterns, camera-traps could also record behaviours that are strongly associated with resting which could be

used as evidence of a likely resting site. These are important where it is difficult to capture sufficient temporal activity if the structure cannot be comprehensively camera-trapped, for instance resting sites with one or more underwater entrances. Ideally, any camera-trap observations relating to resting activity patterns or resting behaviour could be used to distinguish sites used for resting from those that are not.

We aimed to develop an evidence-based protocol using camera-traps to identify otter resting sites based on the duration an otter stayed within a structure. As detailed studies of otters at resting sites are not represented in published studies, we provide novel observations of behaviours and tested for any association with resting sites so that these may offer additional evidence of resting where complete temporal activity patterns are difficult to obtain with camera-traps. Our observations of resting patterns and behaviours contribute to a baseline of expected activity at resting sites which can be used as a reference for practitioners.

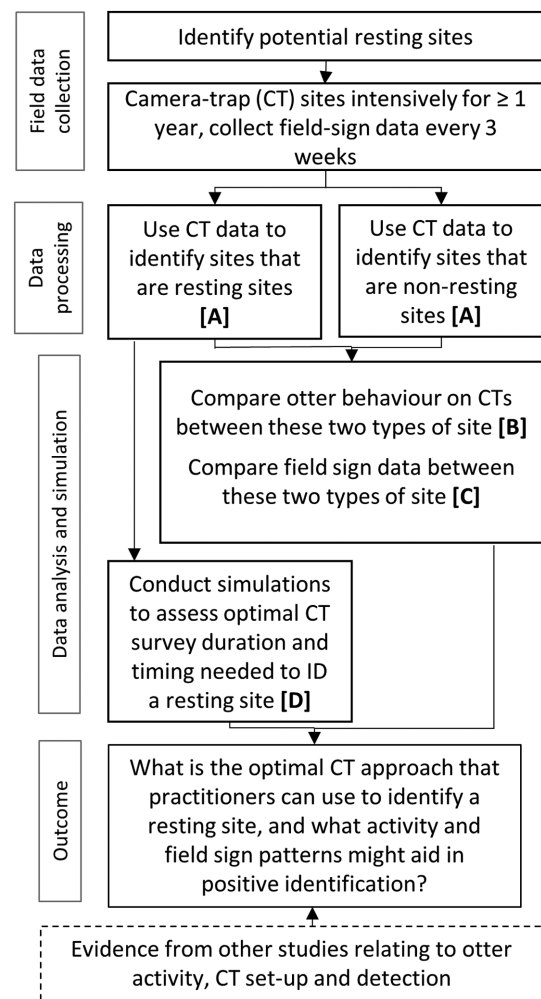


Figure 1. Framework of study to inform an optimal camera-trapping and field-evidence based approach for practitioners to identify otter resting sites, as per EU/UK legislation (see text). Letters in square brackets indicate the Methods/Results sections that describe those analyses. CT = camera-trap.

Using the temporal data from camera-traps to define which of our study sites were resting sites, we tested for any relationship between resting sites and types of field-sign.

The framework for this approach is summarised in Fig. 1. Camera-trap data and field-sign observations (e.g. spraints, otter paths, presence of bedding) were collected across the River Tweed catchment in Scotland from 26 potential resting sites, each monitored for a minimum of a year during a five-year period. We first used camera-trap observations to provide a quantitative definition of a rest event and, using this, we categorised 25 of the 26 study sites as a resting site or a non-resting site. The 26th site could not be assigned as either as there was an incomplete record of otter passes due to a concealed under-water entrance found during exceptional low water levels after the monitoring period. This site is excluded from analyses as appropriate. After categorising our sites, we looked for associations between selected behaviours observed on camera (specifically bedding collection, latrine behaviour and sedentary behaviours) and resting site status. We then modelled the relationship between individual field-signs (e.g. spraints, bedding and latrines) which were observed independently of camera-traps, and the function of the structure (resting site vs non-resting site) to assess whether any may be used as indicators for resting site identification. Finally, we present simulations on camera-trap data from the resting sites to determine the minimum survey effort which would have been required to have a 95% chance of detecting a rest.

Material and methods

Study catchment and study sites

The River Tweed catchment is approximately 4335 km² (Scottish Environment Protection Agency nd) and has a variety of river types from small, oligotrophic tributaries in the upper catchment, to the eutrophic reaches of the lower Tweed. It flows eastwards from the Lowther Hills in Peebleshire, Scotland into the North Sea at Berwick-upon-Tweed in England (Fig. 2). The River Tweed and its tributaries are protected as a special area of conservation (SAC) under UK law and the otter is one of the Tweed SACs qualifying interests.

Twenty-six potential otter resting sites were identified by two experienced surveyors from the author group using field-signs across the Tweed catchment. To increase the likelihood of independence between study sites we aimed to avoid monitoring sites concurrently that could fall in a single female otter's home-range (Ferdiá et al. 2011). Based on home-range estimates of females from radio-tracking studies of Eurasian otter (Green et al. 1984, Durbin 1996, Georgiev 2007, Néill et al. 2009, Quaglietta et al. 2015), we used a minimum distance between potential resting sites of 20 km via watercourses in oligotrophic systems and 8 km via watercourses in mesotrophic or eutrophic systems. Where potential monitoring sites were found that violated this distance criteria, the sites were monitored in different years. We acknowledge that

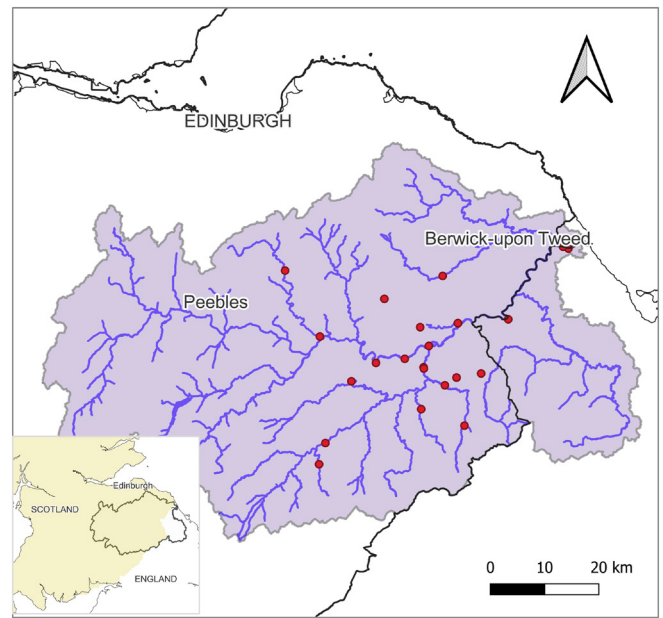


Figure 2. Study catchment and location of camera-trap sites (dots), some sites are overlain due to close proximity, but these were not monitored concurrently. Major channel and tributaries of the River Tweed are shown, and the River Tweed catchment is shaded. Inset map shows catchment in context with England and Scotland.

this approach may have resulted sites falling within the same male range, as home-ranges of male otters are typically larger and can potentially be 80 km (Durbin 1996, Kruuk 1995).

Camera-trap deployment and settings

Each potential resting site located was monitored with camera-traps for an average of one year. This was covered by licenses to derogate any accidental disturbance of otters during the research (Scotland: 20861; and England: 2016-26206-SCI-SCI). Camera-trap set-up followed evidence-based criteria but was adapted at each site due to variable topography and surrounding vegetation. The detection probability of otters in the detection zone of camera-traps is improved if there is more than one camera-trap with one camera-trap within 2 m of the structure entrance (Findlay et al. 2017). Therefore, we used a camera-trap within 2 m at each site, and if possible, a second camera-trap was used at a different angle and/or distance to increase detection probability. Ideally, camera-trap height should be just below the target species' shoulder height for maximum detection so that the body of the animal is in the centre of the detection zone, and the detection area should be parallel with the ground (Apps and McNutt 2018). The shoulder height of otter (estimated as 17–25 cm) was too low with respect to the summer vegetation height, so 20–30 cm was used. The camera-traps' fields-of-view were centred on the structure entrances where animals would linger, but with placement intentionally avoiding obstructing entry routes with the camera-trap itself.

Of the 26 structures monitored, 22 had the optimal two camera-traps. Two sites could only accommodate one

camera-trap which was set at 1 m distance from the entrance, to maximise trigger probability (Findlay et al. 2020). At three sites where there were multiple entrances, we decided to place three camera-traps. Examples of simpler and more complex two-camera deployments are shown in Fig. 3.

Overall data collection spanned five years (2015–2019 inclusive). Due to the long duration of the fieldwork, some camera-traps became faulty and had to be replaced with new camera-traps leading to three similar models being used (Bushnell Trophy Cams: models 119678, 119676 and 119776). All had low-glow 850 nm LEDs to minimise visible light. Hard fixings ensured consistency of the field-of-view and detection zone of the camera-trap between each maintenance visit and reduced the risk of theft.

At approximately three-week intervals (median = 21 days, IQR = 16–26 days) a ‘maintenance visit’ was undertaken when the camera-trap was replaced from a pool of camera-traps which was preloaded with fresh batteries and SD card. High river conditions or forecasted spates led to variation in the intended three-week interval. The time was recorded as Greenwich Mean Time (UTC ± 0) and camera-traps on the same site were synchronised as precisely as possible. The camera-traps were programmed to record 20 s of video and audio with minimal re-arming time of 1 s. At a known otter resting site, 20 s is indicated as the optimal video length in balancing use of power/memory with data quality (Findlay et al. 2017). Video was used rather than still images as it collects more data in terms of scent-marking behaviour, sexing otters and vocalisations than still images. From previous extensive camera-trap observations, otters were expected to loiter at the structures to sniff and scent-mark, increasing the time in front of the camera-trap which increases detection probability (Findlay et al. 2020). The sensitivity of the motion detector was set to ‘auto’ which is indicated by the manufacturer as being optimal where there is potential for variation in day and night-time temperatures. The footage from retrieved

camera-traps was reviewed briefly after each maintenance visit to assess how each camera-trap had performed and if any faults were indicated.

Whilst the aim was to monitor each site for approximately a year, monitoring at some sites had to be paused for short periods due to heavy rain and associated spates/floods. Sites were monitored for a median of 375 days (min = 95 days, max = 532 days). The monitoring periods for sites where resting activity was identified were extended for over a year to obtain more data on activity patterns at resting sites specifically. Monitoring ceased prematurely at two sites after four and five months of monitoring, when the structures were destroyed by severe storms in November 2015.

Data extracted from camera-trap footage

We deliberately triggered each camera-trap after setting it up in the field, and again just before collection, to assess if the camera-trap had functioned for the full monitoring period between maintenance visits. If a camera-trap had failed to record for the full duration of the monitoring period due to battery depletion for example, the date of the last video was noted to provide a record of minimum days working in the field for each camera-trap position.

Videos were watched and each registration of otter was documented. As 20 s video-clips and more than one camera-trap were used, multiple video-clips were often taken from the same continuous period of otter activity. Therefore, we used ‘events’ for the analyses, defined as ‘a unit of continuous activity, varying from the rapid pass of an otter to an otter loafing for an extended period comprising numerous video clips’ (Findlay et al. 2017). The event information used the combined data gained from both camera-traps. We used three categories of events representing the otters’ interaction with the structure being monitored: 1) ‘paired events’ where we observed an entry into the structure and subsequent exit,

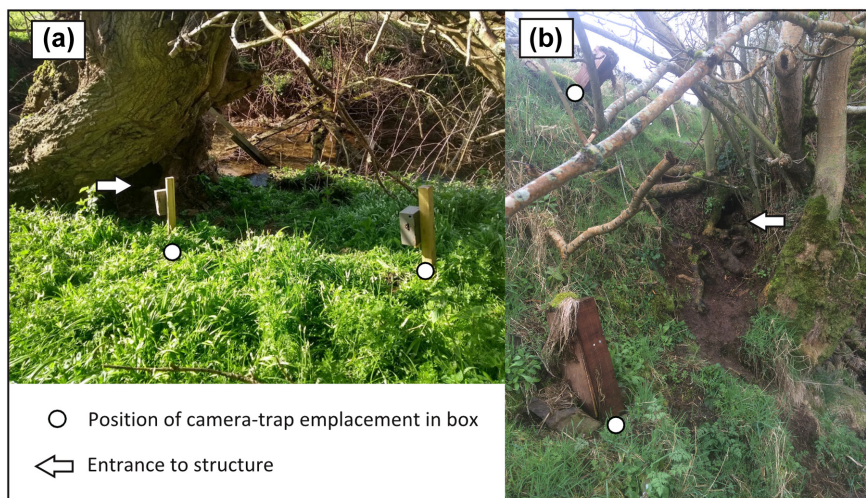


Figure 3. Deployment of dual camera-traps (CTs) at potential resting sites (a) on flat terrain which offers minimal constraints, and (b) on steep river-bank where the set-up has been modified but follows the same principles of having one close CT (≤ 2 m from the entrance) and a second CT with an alternative-view.

regardless of time elapsed as in this example: entry <tinyurl.com/uk3gtsw> and exit <tinyurl.com/v26w3aa>; 2) 'single events' when the time spent in the structure could not be determined, for instance if an otter was observed entering a structure but there was no footage of it exiting; and 3) a 'pass' when an otter did not enter the structure, but only interacted with the area at the entrance (e.g. sniffing, sprainting) as in this example: <tinyurl.com/ttubrs4>. Paired events were checked for obvious disparities, checking that the sex, age or any other identifier of the otter going in and exiting the structure were the same, also that the wetness of the exiting otters coat concurred with the amount of time it had been in the holt.

Recording behaviours

For each of the 26 sites we recorded if each of either sedentary behaviour (loafing, grooming, rolling), latrine behaviour (defecation at a latrine during a rest), bedding collection behaviour (otter seen carrying bedding material into a structure), or any had been observed at any point during the study period as follows:

Sedentary behaviours included 'loafing' (lying down, stretched out on back or on stomach and with little to no movement, occasionally shutting eyes, e.g. <tinyurl.com/wnv723s>), grooming (licking fur and/or extended periods of scratching e.g. <tinyurl.com/wnm7nsn>) and rolling (lying down and rolling on back, often on loose substrate such as fragmented bark, with the fur often wet at the start of the behaviour and notably less wet when rolling ceases, e.g. <tinyurl.com/sgfqchc>). Latrine behaviour was recorded when an otter defecated at a latrine site (example of latrine behaviour: <tinyurl.com/vq9kydq>; and example of sprainting behaviour as a comparison: <tinyurl.com/ul2ach2>).

Bedding collection was recorded when vegetation was pulled up and carried into the structure in the otter's mouth, with the otter moving uncharacteristically fast. Bedding collection occurred close to the structure, often with the otter not fully leaving the structure if it could pull vegetation from immediately outside the entrance (examples of bedding collection: <tinyurl.com/rhj75a9> and <tinyurl.com/tlge662>).

Field-signs data collection

At each maintenance visit, the structure was surveyed for field-signs of otter. On 19% (n = 396) of maintenance visits, this was not possible as water levels were too high. When recording field-signs, the aim was to record all observations but not to distinguish what evidence was new since the last visit, all field-signs were left in situ. The mean spraint count across the maintenance visits for each site was positively skewed, so the median was used to represent the expected value that a surveyor would detect at that site on any given visit. This was considered a methodologically useful measure since surveyors will be confronted with both newer and older field signs when surveying. Field-signs were recorded with no prior review of the camera-trap footage, ensuring independence between camera derived and field-sign derived data.

In addition to not clearing field-signs, disturbance was minimised by using non-invasive inspections (i.e. torches and endoscopes were not used). Field-signs were recorded to 5 m which was considered achievable for the topography and water-levels at all sites and it was assumed that signs beyond 5 m would be less likely to be associated with a structure by a field surveyor.

Most field-signs were identified (Brown et al. 2004) as present/absent within 5 m of the structure entrance namely: otter footprints, soft substrate such as silt or mud, a path linking structure to water and spraint piles (a collection of at least four spraints on top of each other without lateral spread). Historical deposits of spraint which had become fragmented and dispersed were excluded as this would have necessitated a more thorough, and potentially disturbing examination using a torch at some sites. It was accepted that the spraint counts would not be precise, but application of a consistent approach would enable valid comparisons. Spraints were counted within 1 m of the entrance and bedding (visible nests and/or clumps of loose vegetation out of context with surroundings) was recorded as present if within 1 m of entrance. During the fieldwork, substantial accumulations of faeces were found at some structures. These were large collection of droppings creating a continuous area of faeces with lateral spread over ground/substrate and were recorded as 'latrines' (Supporting Information), which are discussed in detail later. Nine of 26 sites did not have suitable substrate for footprints. Footprints were only observed on 5% of visits, so footprint data were not analysed further.

Capital letters (A–D) in each of the following four sub-headings represent data processing, analysis and simulation stages indicated in Fig. 1.

Identification of resting sites and non-resting sites [A]

Identification of resting sites from non-resting sites from the 26 study sites (Fig. 1A) was essential for subsequent analyses. A quantified definition of a resting site could also be used as a standard for camera-trap practitioners to use to identify resting sites. We calculated the duration of time that an otter was inside the structure by subtracting the time/date an otter entered the structure from the time and date it exited (Findlay et al. 2017). We hypothesised that our data would reflect the temporal patterns in Findlay et al., which distinguished short visits to holts and longer rests, and suggested a 15 min threshold to separate visits from rests.

We took all 1487 paired events in our dataset and ordered them by duration, from 0 to 1263 min (the maximum, equivalent to 21.1 h). We then simulated in R studio (<www.rstudio.com>) how many sites would have been defined as a resting site (i.e. at least one rest was observed) if we had set a threshold to define a rest as 1, 2, 3 min etc., up to 1263 min, and plotted the theoretical number of defined 'resting sites' against the theoretical threshold defining a 'rest'.

To see if there were a natural multi-modal distribution that might distinguish short visits from longer rests, we plotted the distribution of durations of all 1487 paired events. We also looked for differences in durations of time spent in

structures during the day compared to during the night. To do so, we took the coordinates at the approximate centre of our study site (the town of Kelso, Scottish Borders) and using the *sunriseset* function in the *maptools* package of R (Bivand and Lewin-Koh 2016) we calculated the times of sunrise and sunset of the exact day for each rest and compared them to the midpoint of that rest. If the mid-point fell between sunrise and sunset, it was regarded as a diurnal rest while the mid-point of a nocturnal rest fell between sunset and sunrise. When plotting our histogram of duration of paired events, we stacked the data by diurnal and nocturnal rests.

Comparison of otter behaviour recorded by camera-traps at resting and non-resting sites [B]

Having classified 25 of 26 sites as resting or non-resting sites from temporal data, we compared behavioural observations on camera-trap footage (Fig. 1B) to see if there were any clear differences which might be used by practitioners to identify resting sites.

For each of the 25 sites, we recorded if latrine behaviour (defecation at a latrine during a rest), bedding collection behaviour (otter seen carrying bedding material into a structure) or sedentary behaviour (loafing, grooming, rolling) had been observed at any point during the study period. We generated 2×2 contingency tables (with total frequency equal to the 25 sites) of site type (non-resting site, resting site) and behaviour (not seen, seen) and used a Fisher-exact test (Crawley 2007) with the *fisher.test* function in R to see if frequencies differed significantly to what would be expected if sites were distributed randomly with respect to the two variables; this was repeated for each behaviour type. A significant result would mean there was an association between observing one of these behaviour types at a site and whether or not it was a resting site.

Comparison of field evidence at resting and non-resting sites [C]

Field-sign evidence, collected independently of camera-trap data was compared between sites that we had identified as resting and non-resting sites (Fig. 1C) to investigate if any field signs might be useful to practitioners to indicate resting sites and focus survey effort.

We constructed a set of six univariate candidate models based on hypotheses of which field-signs were related to whether a site was a resting site or not. Field-signs included as explanatory variables were presence/absence of otter path, presence/absence of latrine, presence/absence of bedding, presence/absence of spraint piles, median count of spraints within 0–1 m (see Field signs data collection). A null model was included for comparison.

A binary response variable called RS was used (1 = site defined as a resting site from camera-trap footage, 0 = site defined as a non-resting site). Small sample size in logistic regression can lead to increased bias, but it has been shown that Firth's penalised maximum likelihood correction (Firth 1993) can greatly reduce this bias and the variance of the maximum likelihood estimator (Rainey and McCaskey 2021). Due to our sample size of 25 sites, we used the *logistf* function to run our models in R (Heinze et al. 2022), which

applies this correction. Only six sites were positively identified as resting sites, and a low number of events per variable (EPV) can inflate type 1 error and bias regression coefficients (Peduzzi et al. 1996, van der Ploeg et al. 2014), so we only included univariate models to maintain $EPV = 6$. Peduzzi et al. (1996) suggest that in logistic regression that EPV should ideally be ≥ 10 although they found that there was an improvement in bias and sample variance of regression coefficients between 2 and 5 EPV. For each site, the median spraint count and the mean of the other variables was calculated across all the maintenance visits at that site, representing the expected value of that field-sign that a surveyor would detect at that site on any given visit.

We fitted the candidate models to the data in R studio (<www.rstudio.com>) and used the package *MuMin* (Barton 2016) to generate a model comparison table. Models were compared using small sample AICc, and models with a $\Delta AICc$ of ≤ 2 were considered as having good support (Burnham and Anderson 2004).

Estimating the optimal camera-trap sampling strategy to detect a resting event [D]

Having identified a sample of confirmed resting sites, we simulated different camera-trapping strategies to assess if there was an optimal duration and timing of camera-trap survey that would have a high probability of detecting resting behaviour while eliminating the need for year-round monitoring, which is likely to be logistically unfeasible for many surveyors.

Since 95% of days when a rest occurred at our monitored sites were in winter or spring it would be most efficient to restrict sampling to this period (Dec–May inclusive). To acknowledge that efficiency of resource use is important, we restricted scenarios to either a single duration of monitoring over the whole winter–spring period, or to two equal-length durations, one in winter (Dec–Feb) and one in spring (Mar–May).

We had recorded rests during eight winter–spring periods, hereafter 'site-periods' from six sites, which varied widely in the number and distribution of rests. Four sites each had one site-period, and two sites had two. For the latter, we treated each winter–spring as an independent sample, although we highlight these pairs in the results. In R Studio, we ran simulated camera-trapping monitoring windows of every possible number of consecutive days of camera-trapping, starting on every possible date for each site-period, i.e. a simulated camera-trap window of 3 days could start on any day in a given season (depending on the simulation either winter–spring, winter or spring) but could not start later than 3 days before the end of that season, as it would then go beyond that season. For each camera-trapping monitoring window duration (from 1 day upwards), we recorded the proportion of simulations when resting was recorded, to calculate the number of camera-trap days that would be required to have a 95% probability of detecting a rest across winter–spring for that site-period. We then modified the simulations to calculate camera-trap days that would be required to have a 95% probability of detecting

a rest if there were two equal periods of camera-trapping, one in winter and one in spring. (Full details of the simulations are provided in the Supporting information).

For a single simulated period of camera trapping (winter–spring), the number of simulations across all possible camera-trapping window durations and start dates varied between 4753 and 16 653 (median 15 233). For two equal simulated periods of camera trapping (one in winter, one in spring) the number of simulations across all possible camera trapping window durations and combinations of start dates varied between 38 640 and 255 255 (median 222 578).

We then used the simulations from all the site-periods to compare the efficiency in detecting a rest of either having a single period of camera-trapping in the winter–spring period or having two equal periods of camera-trapping, one in winter and one in spring.

Results

Identification of resting sites and non-resting sites [A]

When we plotted the theoretical threshold defining a rest (in minutes) against the number of our study sites that would thus have been defined as resting sites (having observed at least one rest there), there was a clear plateau at six resting sites, whereby we would have demarcated our study sites in the same way if we had selected a threshold of 4 min or 803 min (13.4 h) (Fig. 4). This suggests a clear, natural distinction among our sites.

When we plotted the distribution of the durations of paired events ($n = 1487$), separated by whether they were diurnal or nocturnal, there appeared to be three broad peaks. Firstly, a peak of ca 1000 events of five minutes or less (Fig. 5a), which was about three-quarters nocturnal activity. Then, looking at only events of at least 1 h in duration, there was an apparent peak at 1–3 h, which was dominated by nocturnal rests and a

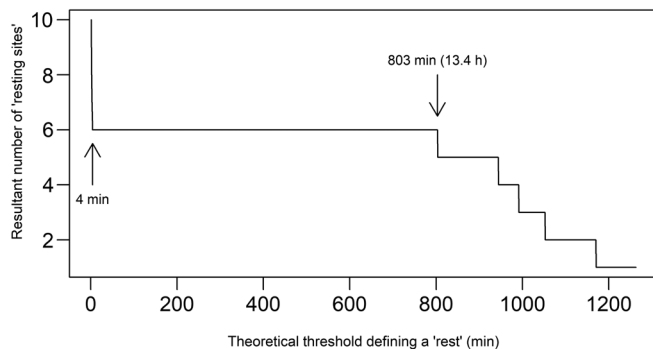


Figure 4. The theoretical number of sites we would have defined as 'resting sites' (where at least one 'rest' is observed) if we had set the threshold for defining a 'rest' as an event where an otter remained in a structure (based on camera-trap observations) for between 1 and 1263 min (the longest duration of any event). There were 25 sites in total, although 15 are not shown as they had no events that lasted 1 min or more. Between thresholds of 4 and 803 min, the same six sites would have been defined as resting sites, indicated by the arrows.

less distinct, broader peak of events at approximately 12–16 h, which was mostly made up of diurnal rests (Fig. 5b).

Comparison of otter behaviour recorded by camera-traps at resting and non-resting sites [B]

There were significant associations between whether a site was a resting site or not and observation of each of latrine, bedding collection and sedentary behaviours seen on camera-traps (Table 1). This was most stark for latrine and bedding collection observations, where there were no cases of these behaviour types being seen at non-resting sites and only one case each of these behaviours not having been seen at an assigned resting site. The latter was a different site for each behaviour type, so latrine behaviour was recorded as the only behaviour at one site, bedding collection as the only behaviour at another site, and both behaviours were observed at four sites. Observation of sedentary behaviour had a significant association with whether a site was a resting site or not, but there were five sites where sedentary behaviour was observed at non-resting sites. There were no resting sites where sedentary behaviour was not seen. When we considered whether any pair of behaviour types was observed on camera traps (latrine activity and bedding collection; latrine activity and sedentary behaviour; or bedding collection and sedentary behaviour) there were no instances of resting sites without any two behaviour types observed, and equally no non-resting sites with two of these behaviour types observed. Note that this means that the two behaviours could have been seen at any time, not necessarily concurrently or within a close time period of each other.

Summary of resting patterns at identified resting sites

Figure 6 summarises periods of observation and activity types for each of the six resting sites. Across all six resting sites, the percentage of days (i.e. 24 h period) when a rest (nocturnal and/or diurnal rest was recorded (as a proportion of observation days) was much higher in winter and spring (10%, $n = 1709$) than summer and autumn (<1%, $n = 1011$).

Comparison of field-signs at resting and non-resting sites [C]

The model comparisons did not suggest any field-sign was a good predictor of resting/non-resting sites since the null model was within $\Delta AICc \leq 2$ ($\Delta AICc = 0.85$ and $w_i = 0.30$; Table 2). The best model containing median count of spraints within 1 m of the entrance had a w_i of 0.45 but the 95% confidence interval of the odds ratio overlapped one.

Estimating the optimal camera-trap sampling strategy to detect a resting event [D]

Reduced data quality due to battery depletion or other camera-trap malfunction was negligible, as five site-periods experienced no loss of camera-trap days and the maximum loss from any one site-period was 6%. Occasional gaps in camera-trapping days were present when there were elevated water levels affecting two sites leading to a loss of 14% of data at site 1 and 18% data at site 5a. Additionally, at site 6, human error caused a loss

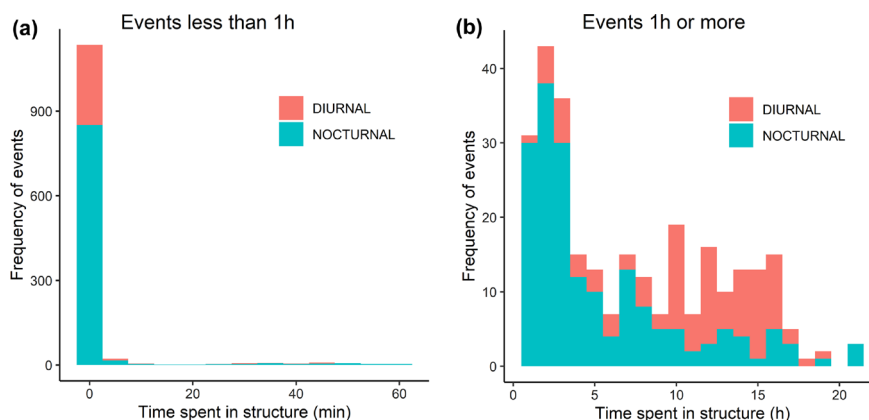


Figure 5. The distribution of time an otter remained in a structure for 1487 paired events where an otter was seen to enter and exit a structure. Due to a large peak at 0–5 min we have separated the distribution into (a) events of < 1 h and (b) events \geq 1 h. Note differing scales for ease of interpretation. Events are indicated as diurnal or nocturnal depending on whether the midpoint of the event fell between sunrise and sunset, or sunset and sunrise respectively on the date that the event occurred.

of data from 20 continuous days which was 10% loss. No sites had losses due to both battery depletion and high-water events.

There was considerable variation between sites in the number of days of camera-trapping required for a 95% probability of detecting a rest, both when a single (Fig. 7a) or two equal (Fig. 7b) windows of camera trapping were simulated. The total number of days required to have \geq 95% probability of detecting a rest was smaller when two equal sampling windows were used at five site-periods, while for two site-periods (sites 4 and 5b) the single window approach was marginally more efficient, but only by 1 day at each. At site 6 which had a continuous data gap of 20 days, the single window was more efficient by 56 days but these data contained a continuous gap of 20 days. The single monitoring period needed to have a 95% probability of detecting a rest ranged from 12 to 108 days (site 6 = 98 days) in comparison with the dual monitoring period which ranged from 8 to 38 days (site 6 = 77 days) for each of the two camera-trapping periods.

Discussion

Identifying rests and resting sites from camera-trap data using duration of time spent within structures

Our data showed that there was a clear distinction between 19 sites that were, during our monitoring, only ever entered

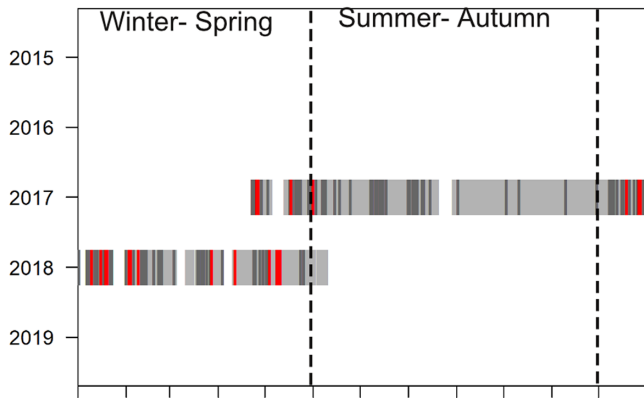
for short periods of time (< 4 min), and six sites that had much longer events of multiple hours that clearly were rests (Fig. 4). Further investigation of the distribution of entries into structures revealed non-random use of structures. The short visits were predominantly nocturnal, reflecting the nocturnal habit of otters. Of the shorter rests which were most commonly 1–3 h, most were nocturnal which concurs with a radio-tracking study that found that otters will rest for periods during the night between bouts of foraging (Green et al. 1984). The longer rests of > 10 h, were mostly diurnal, again reflecting the nocturnal activity of the otter and its need to seek shelter during daylight, and also that otters rarely change diurnal resting site within a given day unless they are disturbed (Green et al. 1984).

We found our sites would be defined as resting sites or non-resting sites whether we had set a threshold for defining a rest at 4 min or 13 h. However, this is based on exceptionally long monitoring periods per site (averaging over one year per site), meaning at all six resting sites in our study a rest of > 13 h was observed. As nocturnal and diurnal rests were observed at all sites, we would not suggest setting the threshold for defining a rest this high because during shorter monitoring periods it may be that only a shorter rest is observed, for example a nocturnal rest of just a few hours of the type we frequently observed in our study (Fig. 5). In a previous study (Findlay et al. 2017) we set a data-driven threshold of 15 min

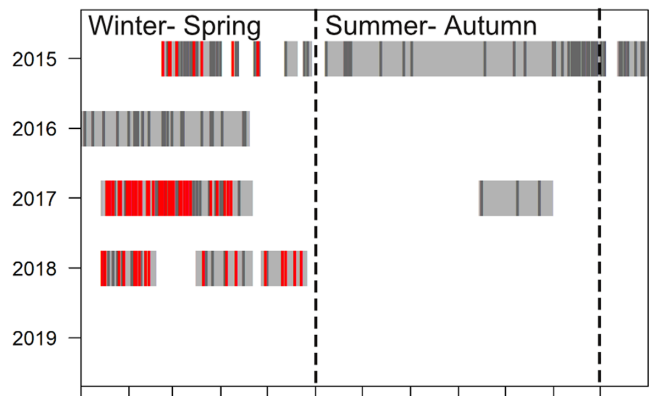
Table 1. Contingency tables and Fisher-exact test p-values for behaviours seen on camera trap footage at 25 sites during the study (no, yes) and whether that site was identified independently as a non-resting site or resting site via the use of paired entry-exit observations. In addition are included data for any combination of two behaviours seen and all three behaviours seen (at any point during monitoring, not necessarily concurrently).

	Behaviours seen on camera trap									
	Latrine		Bedding		Sedentary		Any two		All three	
	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes
Type of site										
Non-resting site	19	0	19	0	14	5	19	0	19	0
Resting site	1	5	1	5	0	6	0	6	2	4
p-value	< 0.001		< 0.001		0.003		< 0.001		0.001	

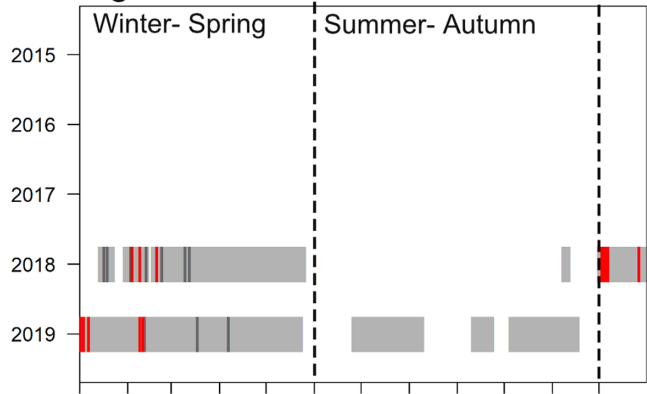
Resting site 1



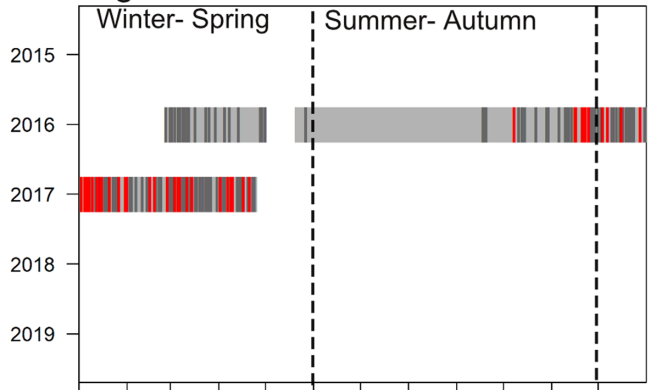
Resting site 2



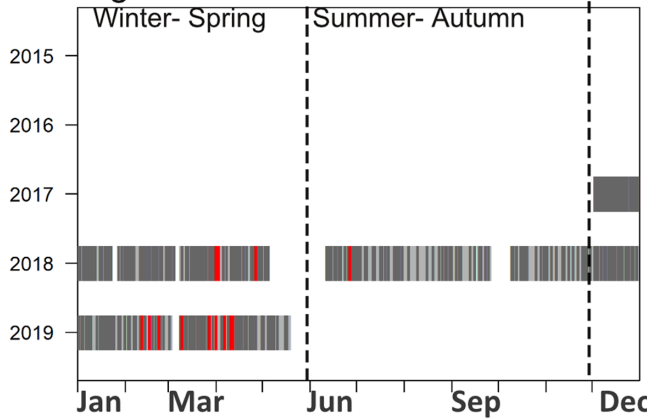
Resting site 3



Resting site 4



Resting site 5



Resting site 6

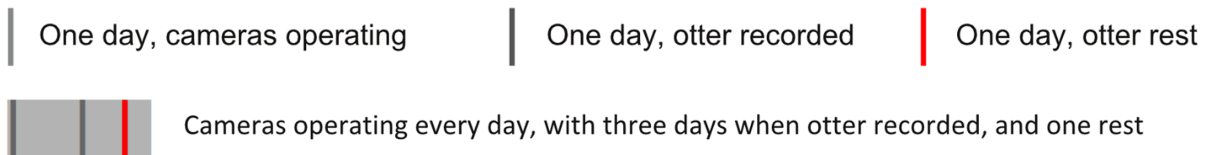
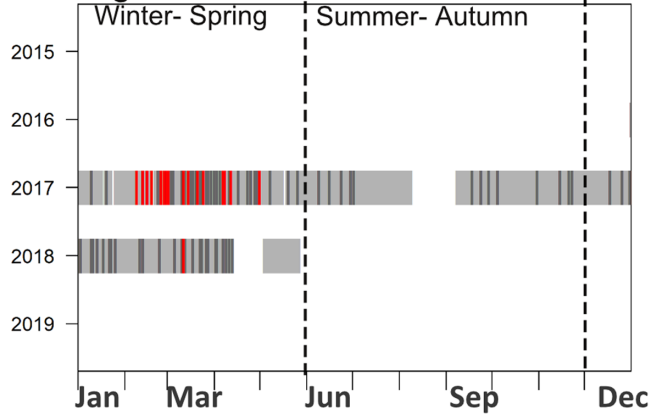


Figure 6. Daily activity type (otter recorded or otter rest detected) in context with monitoring periods at each site used for resting. Gaps in recording are left as blank space. Over 95% of camera-trap days where a rest was observed (black bars) occurred in the winter–spring period (Dec–May inclusive).

Table 2. Model selection, parameter estimates and model fit information across six binomial generalised linear models with logit link function and Firth’s penalised maximum likelihood, to assess field signs as predictors of whether a site was a resting site (1) or non-resting site (0). CI = confidence interval, AICc = corrected Akaike information criterion, Δ AICc = difference in AICc between that model and the model with the lowest AICc, w_i = Akaike’s weight, $-\ln(L)$ = negative log likelihood of the model.

Model	Intercept (\pm 95% CI)	Slope (\pm 95% CI)	95% CI of odds-ratio	AICc	Δ AICc	w_i	$-\ln(L)$
Spraints (null)	-1.49 ± 1.28	0.17 ± 0.34	0.85–1.67	27.34	0.00	0.45	-11.40
Path	-1.10 ± 0.89	–	–	28.20	0.85	0.30	-13.01
Spraint piles	-1.64 ± 1.44	1.20 ± 2.08	0.43–32.3	30.71	3.36	0.08	-13.08
Bedding	-1.52 ± 1.35	1.37 ± 2.76	0.23–74.25	31.45	4.10	0.06	-13.45
Latrine	-1.71 ± 1.15	3.45 ± 3.33	1.78–8631.5	31.55	4.21	0.06	-13.50
Latrine	-1.51 ± 1.06	2.79 ± 2.93	1.06–633.08	31.62	4.28	0.05	-13.54

to define a rest, and we would argue that, although this precise value is somewhat arbitrary, this figure still appears reasonable, in that it would clearly separate the large peak of short visits we observed (Fig. 5a) whilst still identifying sites which may only be used for shorter nocturnal rests.

Can behaviours observed by camera-traps be used as indicators of resting activity?

Camera-trap observations of specific behaviours could potentially be used as indicators of resting as they were associated with whether a site was a resting site or not. However, for each behaviour type (bedding collection, defecation at a latrine and sedentary behaviour) there were instances where that behaviour was not observed at a resting site (bedding collection,

defecation at a latrine) or where that behaviour type was observed at a non-resting site (sedentary behaviour). If we considered whether any two of those behaviour types was observed on camera-traps at any time during monitoring, there was a perfect association with resting sites (i.e. all resting sites saw at least two of those behaviour types, and no non-resting sites saw two of those behaviour types). This indicates that behavioural observations at sites have potential to be used as indicators to positively identify resting sites, and might make good indicators where paired entry-exits cannot easily be used to identify a resting site (e.g. sites with hidden underwater entrances). However, some caution is recommended with this pattern, since these are based on an average of over one year’s monitoring per site, so camera-trapping for a shorter period and not observing these behaviours would not rule out a resting site, and our sample size of resting sites is relatively small.

Using this behaviour-based approach would have indicated that our 26th site (which had an underwater entrance) was a resting site in the absence of paired entry-exits as latrine behaviour was observed on footage and the latrine was also observed as a field-sign. Therefore, assessment of rests based on paired entry-exit events, having camera trapped for a suitably long period of time is still the best way to assign status to a structure as resting or non-resting, but behavioural observations can also be used as indicators of resting.

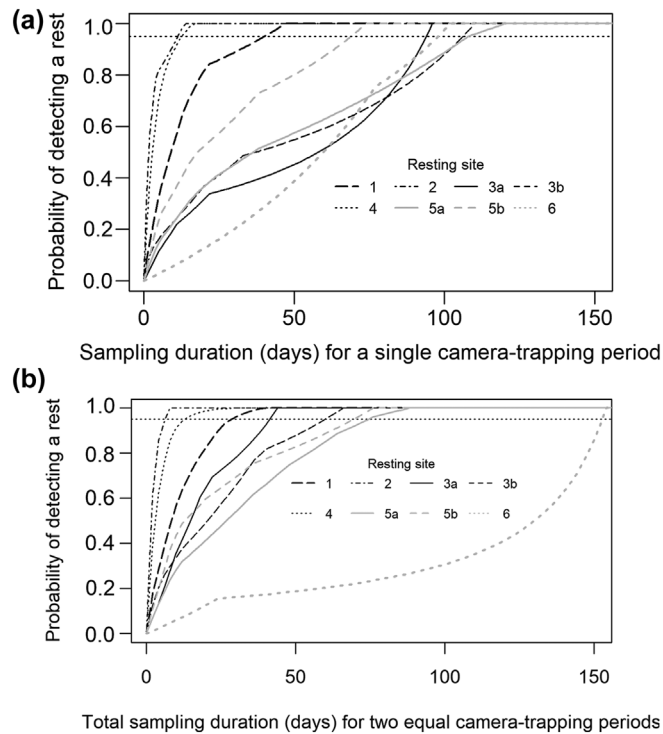


Figure 7. The probability of detecting a rest during eight winter–spring periods at six resting sites based on simulated camera-trap monitoring for different survey window durations (in days) for: (a) a single monitoring window (at any point in winter–spring), and (b) for two equal monitoring windows one in winter and one in spring. A 95% probability of detecting a rest is indicated by the horizontal dotted line.

How helpful are field-signs in identifying an otter resting site?

We did not find a reliable field-sign indicator, but our sample size and events per variable in the analysis were low, resulting in low statistical power. In contrast, our camera-trapping data shows that bedding collection and latrine behaviour are strongly associated with resting sites. These behaviours would have to consistently give rise to field-signs that had longevity and could be found without an invasive survey to be used for as a reliable field-sign signature of a resting site. The presence of latrines, and/or bedding as field-signs are therefore suggested to be indicators of a resting site when present, but an absence of these field signs should not lead to the conclusion that a structure is not a resting site. This also illustrates the need for ecologists to undertake invasive surveys using high powered torches or endoscopes, which may increase the likelihood of finding these field-signs. No other field-signs had a strong enough

association with resting sites to be used as indicators. The current absence of a known consistent and reliable field-sign indicator which can be used to assess the likelihood of every structure as a resting site, where latrines and bedding are absent, demonstrates the need for additional methods to identify otter resting sites which have more certainty, such as camera-trapping.

Spraint sites and latrines: different field-signs

We suggest that latrines are a new type of field-sign for Eurasian otter and differ in function and form from spraint sites. Differentiation between the appearance of a spraint site and a latrine (Supporting information) has been missing in earlier studies although both terms have been used to describe a small number of spraints deposited together (Green 2000, Ruiz-olmo et al. 2001, Depue and Ben-David 2010, Remonti et al. 2011, Almeida et al. 2012, Parry et al. 2013, Yoxon and Yoxon 2014). In these studies, the function of all faecal deposits (latrines and spraint sites) is described within the context of scent-marking. Scent-marking is characterised by a token amount of material orientated to specific objects which is repeated frequently (Kleiman 1966). Our camera-trap observations, on the other hand, indicate a distinction between sprainting behaviour which is characteristic of scent-marking, and digestive elimination which was observed at resting-site latrines. Latrines and scent-marking sites are, in fact, differentiated in other species, such as pine marten *Martes martes* (Kleef and Tydeman 2009) and Eurasian badger *Meles meles* (Böhm et al. 2008) so this functional difference is not atypical for mustelids. The differences between the characteristics of a spraint site and latrine were observational and more quantitative data would be required to describe the variation in their form.

Methodological implications

Our data indicate that camera-traps should be considered an essential tool to identify otter resting-sites over and above field-sign surveys, but practitioners will need evidence-based principles of deployment and sampling for this to be effective. Camera-trap height (Apps and McNutt 2018), mass of the target animal (Anile and Devillard 2016, Hofmeester et al. 2017), distance to and speed of the target animal and camera-trap settings (Findlay et al. 2020) have been shown to be important in detection success of the animal when it is in front of the camera-trap, but an effective sampling strategy is also important (Hamel et al. 2013). We found most rests occurred in winter and spring (Dec–May) and this reflects the pattern of resting use of a holt in another area of Scotland over six years (Findlay et al. 2017). Increased frequency of resting in enclosed structures when riparian vegetation is at a seasonal low has been found by radio-tracking (Weinberger et al. 2019). This suggests that otters have more specific requirements for sheltered resting sites in winter–spring and, furthermore, this

may increase fidelity to certain structures which fulfil those requirements. We found fidelity to all resting sites within each winter–spring period, but also from year to year where sites were monitored across multiple winter–spring periods (Fig. 6). These resting sites could be considered more important to individual otters' survival than resting sites that are not repeatedly used. Whilst we separate field-sign surveys from camera-trap surveys in our approach, the selection of sites to monitor with camera-traps inevitably starts with a field-based assessment of field-signs and/or the suitability of a particular place or structure for resting. Often resting sites that are not in a structure have no associated field-signs (Green et al. 1984), so resting sites that are not associated with a suitable structure (which are more prevalent in summer and autumn), are unlikely to be identified using field-signs or camera-traps.

We suggest that in riparian habitats in temperate latitudes it would be more efficient to camera-trap potential resting site structures in the winter–spring period, although it is acknowledged that this is based on six confirmed resting sites in this study and a six-year study elsewhere in Scotland (Findlay et al. 2017). Six months (182 days) is a large monitoring duration if camera-traps are continuously running, requiring substantial investment of time in maintenance visits and data extraction. Our simulations calculated that 38 days (ca 5.5 weeks) of camera-trap monitoring in winter and repeated in spring would be required to have at least a 95% probability of detecting a rest across all our sites and monitoring periods. This is 30% less than the estimated optimal duration of a single monitoring period of 108 days, and 58% less than the total winter–spring period (if no strategy other than restricting monitoring to the whole winter–spring season were used). However, the optimised duration of two periods of 38 days would represent the longest duration required, as monitoring could potentially be curtailed, and the site defined as a resting site, as soon as one incident of resting was confirmed. The full 76 days (ca 11 weeks) would only be necessary to report, with reasonable confidence, that the site was not a resting site. Ecologists would still need to report on their data quality, that their camera-traps were functioning for the majority of that period, and that camera-traps were placed in locations close to entrances so as to ensure high detection probability (Findlay et al. 2017, 2020), or else such a decision may not be reliable.

Ours was a catchment-scale study across several years, but there may be variation in frequency and pattern of resting site use according to country, catchment or habitat, which might affect the optimal camera-trap sampling timing and duration. This could be the subject of further research, and our simulation approach could be adapted to estimate the optimal monitoring strategy for populations elsewhere.

Wider application

Camera-traps are comparable to or outperform a range of alternative methods (Wearn et al. 2019). They have been shown to have improved detection rates of north American river otter

Lutra canadensis at latrine sites when compared to scat counts (Day et al. 2016). Our study shows how camera-traps can be used as a validation tool for indirect survey methods such as those relying on field-signs. Our potential resting sites, by necessity, were found by two experienced otter surveyors locating suitable structures with associated field-signs of otter. The six confirmed resting-sites (out of 26 potential resting sites) were used repeatedly by otters. Radio-tracking studies have shown that otters favour some resting sites over others, with approximately a third of resting sites only used once during observations (Green et al. 1984b, Freire 2011). Our data suggest that only habitually used resting sites are likely to be found by a field-surveyor and confirmed using camera-traps. These sites would fulfil the criteria of a resting-site of a 'wide-ranging species' in EU and UK legislation (EU 2007). These would therefore have strict protection which prohibits disturbance to otters occupying a resting site and protects the resting site from damage or obstruction regardless of occupation. Amending guidance to include a quantitative definition of a resting site, as here, would provide a clear standard for surveys.

However, two scenarios are likely to be excluded from strict protection. The busiest of our 26 sites recorded otter presence on over 90% of observation days, yet the paired entry-exit camera-trap data showed clearly that it was not used for resting. Such frequently visited structures must have a different function (e.g. essential grooming), but the lack of knowledge of that purpose and inferred significance makes it difficult to place these sites in the current legislative framework. Additionally, the resting-sites that are likely to be rarely used, as indicated through radio-tracking studies (Green et al. 1984, Freire 2011), are unlikely to be identified as resting-sites by either field signs or camera-trap surveying, yet potentially make-up a large proportion of resting sites in an otter's home-range, and so cannot be dismissed. Such sites arguably do not fulfil the criteria of a protected resting-site defined by legislative guidance (EU 2007) where there is expected re-use. These are likely to be unwittingly lost to development in riparian and coastal areas, which may be detrimental to otter populations. A future study that combines individual-focussed radio-tracking with site-focussed camera-trapping within otter territories might disentangle some of these unknowns, such as the function of frequently visited non-resting sites, methods to characterise rarely used resting sites, and the spatial relationships between different types of structure and other territorial resources such as food supply.

Our approach of detecting paired entries and exits using correctly placed camera-traps could readily be applied to potential dens of other species to establish resting behaviour patterns. Repeating this at otter resting sites over a larger geographical area, including parts of the Eurasian otter's range that experience wet and dry seasons as opposed to temperate latitudes, would enable refinements to sampling protocols and gain insight into resting site usage. Furthermore, our framework of simulations to optimise sampling duration to detect a specific event could be used to rationalise sampling protocol to detect species' presence, breeding or another specific type of observation.

Further investigation into the distinction between latrines and scent-mark sites, such as biochemical differences and morphological characteristics would provide further insights into scent-marking behaviour and surveying methodology for otter. It may also have a significant bearing on studies where spraints are collected for dietary analyses (Kemenes and Nechay 1990, Kloskowski 2005, Lyach and Cech 2017), especially those investigating the impact of otter predation within commercial fisheries. Further research is needed to characterise latrines of otter to avoid possible confusion to other species.

Conclusions and recommendations

This catchment-scale camera-trapping study of 26 potential resting sites used by otters, each surveyed intensively for over a year on average is unique in its insight of activity and behaviour of Eurasian otters at both resting sites and non-resting sites. Notably, we provide novel and clear criteria by which resting sites, protected under EU and UK law, can be identified, including placement of camera-traps, duration of monitoring and interpretation of their data. We also demonstrate that using field-signs alone to identify resting-sites is likely to generate false-positives and/or false-negatives. While our recommended approach will aid in the protection of resting-sites that fit the definition under EU law ('reasonably high probability that the species concerned will return to use these sites and places' (EU 2007, pp. 45 and 41)), our data have also revealed sites that are frequently visited but not rested in. There may well be some unknown function of such sites, which future research may reveal, and the legislation may need to be amended to protect these, alongside resting sites that are used too infrequently to detect easily.

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Author contributions

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Investigation (supporting); Methodology (supporting); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (lead); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (lead). **Roger P. Ingledeu**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (equal); Software (supporting); Supervision (supporting); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Patrick J. C. White**: Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (lead); Resources (equal); Software (equal); Supervision (lead); Validation (lead); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead).

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The peer review history for this article is available at <<https://publons.com/publon/10.1002/wlb3.01036>>.

Data availability statement

Data are available from the Github Repository: <<https://github.com/melanieCTfindlay/otter-restingsites>> (Findlay et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Almeida, D., Barrientos, R., Merino-Aguirre, R. and Angeler, D. G. 2012. The role of prey abundance and flow regulation in the marking behaviour of Eurasian otters in a Mediterranean catchment. – *Anim. Behav.* 84: 1475–1482.

Anile, S. and Devillard, S. 2016. Study design and body mass influence RAls from camera trap studies: evidence from the Felidae. – *Anim. Conserv.* 19: 35–45.

Apps, P. J. and McNutt, J. W. 2018. How camera traps work and how to work them. – *Afr. J. Ecol.* 56: 702–709.

Barton, K. 2016. MuMIn: multi-modal inference. – R package ver. 1.42.1, <<https://CRAN.R-project.org/package=MumIn>>.

Birks, J. D. S., Messenger, J. E. and Halliwell, E. C. 2005. Diversity of den sites used by pine martens. – *Mammal Rev.* 35: 313–320.

Bivand, R. and Lewin-Koh, N. 2016. maptools: tools for reading and handling spatial objects. – <<http://CRAN.R-project.org/package=maptools>>.

Böhm, M., Palphramand, K. L., Newton-Cross, G., Hutchings, M. R. and White, P. C. L. 2008. The spatial distribution of badgers, setts and latrines: the risk for intra-specific and badger-livestock disease transmission. – *Ecography* 31: 525–537.

Brown, J. R., Lawrence, M. J. and Pope, J. 2004. Animal tracks, trails and signs (Hamlyn Guide). – Octopus Publishing Group.

Burnham, K. P. and Anderson, D. R. 2004. Multimodel inference: understanding AIC and BIC in model selection. – *Sociol. Methods Res.* 33: 261–304.

Crawley, M. 2007. The R book. – Wiley.

Depue, J. E. and Ben-David, M. 2010. River otter latrine site selection in arid habitats of western Colorado, USA. – *J. Wildl. Manage.* 74: 1763–1767.

Durbin, L. S. 1996. Individual differences in spatial utilization of a river-system by otters *Lutra lutra*. – *Acta Theriol.* 41: 137–147.

EU 2007. Guidance document on the strict protection of animal species of community interest under the Habitats Directive 92/43/EEC: 88. – EU.

European Commission 1992. Council Directive 92/43/ECC. – *Off. J. Eur. Union* 94: 40–52.

Ferdia, M., Ó Néill, L. and Deirdre, L. 2011. How to calculate range and population size for the otter? The Irish approach as a case study. – *IUCN Otter Spec. Group Bull.* 28: 15–22.

Findlay, M. A., Briers, R. A. and White, P. J. C. 2020. Component processes of detection probability in camera-trap studies: understanding the occurrence of false-negatives. – *Mammal Res.* 65: 167–180.

Findlay, M. A., Briers, R. A., Diamond, N. and White, P. J. C. 2017. Developing an empirical approach to optimal camera-trap deployment at mammal resting sites: evidence from a longitudinal study of an otter *Lutra lutra* holt. – *Eur. J. Wildl. Res.* 63: 96.

Findlay, M. A., Briers, R. A., Ingledeu, R. P. and White, P. J. C. 2022. Data from: An evidence-based approach to identifying resting sites of Eurasian otter *Lutra lutra* from camera-trap and field-sign data. – Github, <<https://github.com/melanieCTfindlay/otter-restingsites>>.

Firth, D. 1993. Bias reduction of maximum likelihood estimates. – *Biometrika* 80: 27–38.

Freire, S. I. M. 2011. Day resting site use and fidelity of Alpine otters *Lutra lutra* in southeast Austria. – MSc thesis, Univ. of Lisbon.

Gallant, D., Slough, B. G., Reid, D. G. and Berteaux, D. 2012. Arctic fox versus red fox in the warming Arctic: four decades of den surveys in north Yukon. – *Polar Biol.* 35: 1421–1431.

Georgiev, D. 2007. Study on the home range of the resident female otter *Lutra lutra*, (Mammalia: Carnivora) in south-east Bulgaria. – *Acta Zool. Bulg.* 59: 165–172.

Georgiev, D. 2008. Seasonality in marking activity of the Eurasian otter *Lutra lutra* in southern Bulgaria. – In: Velcheva, I. G. and Tsekov, A. G. (eds), Proceedings of the anniversary scientific conference of ecology, Plovdiv, pp. 236–240.

Green, J., Green, R. and Jefferies, D. 1984. A radio-tracking survey of otters *Lutra lutra* on a Perthshire river system. – *Lutra* 27: 85–145.

Green, R. 2000. Sexual differences in the behaviour of young otters *Lutra lutra*. – *IUCN Otter Spec. Group Bull.* 17: 1–9.

Hamel, S., Killengreen, S. T., Henden, J. A., Eide, N. E., Roed-Eriksen, L., Ims, R. A. and Yoccoz, N. G. 2013. Towards good practice guidance in using camera-traps in ecology: influence of sampling design on validity of ecological inferences. – *Methods Ecol. Evol.* 4: 105–113.

Heinze, G., Ploner, M. and Jiricka, L. 2022. logistf: Firth's bias-reduced logistic. – <<https://cemsis.meduniwien.ac.at/en/kb/science-research/software/statistical-software/firth-correction/>>.

Hofmeester, T. R., Rowcliffe, M. J. and Jansen, P. A. 2017. A simple method for estimating the effective detection distance of camera traps. – *Remote Sens. Ecol. Conserv.* 3: 81–89.

Kemenes, I. and Nechay, G. 1990. The food of otters *Lutra lutra* in different habitats in Hungary. – *Acta Theriol.* 35: 17–24.

- Kleef, H. L. and Tydeman, P. 2009. Natal den activity patterns of female pine martens *Martes martes* in the Netherlands. – *Lutra* 52: 3–14.
- Kleiman, D. G. 1966. Scent marking in the Canidae. – *Symp. Zool. Soc. Lond.* 18: 167–177.
- Kloskowski, J. 2005. Otter *Lutra lutra* damage at farmed fisheries in south eastern Poland, II: exploitation of common carp *Cyprinus carpio*. – *Wildl. Biol.* 11: 257–261.
- Kruuk, H. (1995). *Wild Otters: Predation and Populations*. – United Kingdom: Oxford University Press Oxford.
- Lyach, R. and Cech, M. 2017. Do otters target the same fish species and sizes as anglers? A case study from a lowland trout stream (Czech Republic). – *Aquatic Living Resour.* 30: 11.
- Néill, L. Ó., Veldhuizen, T., de Jongh, A. and Rochford, J. 2009. Ranging behaviour and socio-biology of Eurasian otters *Lutra lutra* on lowland mesotrophic river systems. – *Eur. J. Wildl. Res.* 55: 363–370.
- Parry, G. S., Bodger, O., McDonald, R. A. and Forman, D. W. 2013. A systematic re-sampling approach to assess the probability of detecting otters *Lutra lutra* using spraint surveys on small lowland rivers. – *Ecol. Inform.* 14: 64–70.
- Peduzzi, P., Concato, J., Kemper, E., Holford, T. R. and Feinstein, A. R. 1996. A simulation study of the number of events per variable in logistic regression analysis. – *J. Clin. Epidemiol.* 49: 1373–1379.
- Prigioni, C., Remonti, L., Balestrieri, A., Sgroso, S., Priore, G., Mucci, N. and Randi, E. 2006. Estimation of European otter *Lutra lutra* population size by fecal DNA typing in southern Italy. – *J. Mammal.* 87: 855–858.
- Quaglietta, L., Hájková, P., Mira, A. and Boitani, L. 2015. Eurasian otter *Lutra lutra* density estimate based on radio tracking and other data sources. – *Mammal Res.* 60: 127–137.
- Rainey, C. and McCaskey, K. 2021. Estimating logit models with small samples. – *Polit. Sci. Res. Methods* 9: 549–564.
- Remonti, L., Balestrieri, A., Smioldo, G. and Prigioni, C. 2011. Scent marking of key food sources in the Eurasian otter. – *Ann. Zool. Fenn.* 2450: 287–294.
- Rosoux, R. and Libois, R. M. 1996. Use of day resting places by the European otter *Lutra lutra* in the Marais Poitevin (France). A radiotracking study. – In: Mathias, M. L., Santos-Reis, M., Amori, G., Libois, R., Mitchell-Jones, A. and Saint Girons, M.-C. (eds), *European Mammals: Proceedings of the 1st European Congress of Mammalogy*. Museum Nacional de Historia Natural, Lisboa., pp. 199–212.
- Ruiz-olmo, J., Saavedra, D. and Jiménez, J. 2001. Testing the surveys and visual and track censuses of Eurasian otters *Lutra lutra*. – *J. Zool.* 253: 359–369.
- Scottish Environmental Protection Agency Flood risk management strategy: Tweed Local Plan District. Section 1
- van der Ploeg, T., Austin, C. P. and Ewout, W. S. 2014. Modern modelling techniques are data hungry: a simulation study for predicting dichotomous endpoints. – *BMC Med. Res. Methodol.* 14: 137.
- Weinberger, I. C., Muff, S., Kranz, A. and Bontadina, F. 2019. Riparian vegetation provides crucial shelter for resting otters in a human-dominated landscape. – *Mammal. Biol.* 98: 179–187.
- Wilson, G. J., Delahay, R. J., de Leeuw, A. N. S., Spyvee, P. D. and Handoll, D. 2003. Quantification of badger *Meles meles* sett activity as a method of predicting badger numbers. – *J. Zool.* 259: 49–56.
- Yoxon, P. and Yoxon, K. 2014. Estimating otter numbers using spraints: is it possible? – *J. Mar. Biol.* 2014: 1–6.