Optimisation of monitoring using camera-traps and field evidence when identifying Eurasian otter *Lutra lutra* resting or breeding sites

Melanie A. Findlay

A thesis submitted in partial fulfilment of the requirements of
Edinburgh Napier University, for the award of Doctor of
Philosophy.

April 2020

DECLARATION

I confirm that this thesis is my own work and the use of all material from other sources has been properly and fully acknowledged.

Please see co-authorship statements for Chapters 2 and 3 which have been published. The published papers are contained within the Appendices.

ABSTRACT

The Eurasian otter *Lutra lutra* and its resting places are protected by EU and UK legislation. Consultant ecologists must identify resting sites so they can be protected during developments. Currently, consultants usually use field-signs, but radio-telemetry studies indicate this may be unreliable. Camera-traps could be used to identify resting sites within the consultancy industry. This research aims to improve field-sign and camera-trap survey methods to identify otter resting sites. Firstly, camera-trap methodology is considered. Arrays of camera-traps were used with continuous CCTV as a control so the effect of variables on detection success of mammal passes could be modelled. A six-year camera-trap study of an active breeding and resting site was analysed to optimise set-up. Distance from the camera-trap had a negative effect on trigger probability but a positive effect on registration probability (i.e. the probability that an image or video is captured given a trigger). Slower animals had greater trigger and registration probabilities while otters had reduced detection after immersion in water. A reduction of video clip duration, and exclusion of daytime monitoring would have reduced the amount of time watching video footage with minimal data loss. These findings guided a camera-trap study of 26 potential resting sites where field evidence was recorded at 21-day intervals. The camera-trap data was also used to identify rests and any relationships between resting and field evidence were investigated. A rest could only be observed on CT footage and was defined as an otter being within a structure for ≥ 15min. According to this criteria, six of the 26 sites were resting sites, with 95% of rests occurring in winter and spring. Latrines were exclusive to resting sites, and presence of bedding material was strongly related to resting sites. Data simulations calculated that a period of 35 days of camera-trapping in winter, repeated in spring would have a 95% probability of detecting a rest. These findings contribute to the evidence-base for guidelines for ecologists to identify resting sites as required by law. The patterns of otter activity, behaviour and field-signs provide a comparison for further studies. The research focusses on otter, but the approaches and principles could be applied more widely.

ACKNOWLEDGEMENTS

This research has been supported by the many landowners, tenants, gamekeepers, estate office staff and fishing ghillies who have given their permission for me to set up study sites on land that they manage. I am grateful for their support and for all their otter-encounter stories which confirmed to me that people enjoy watching wildlife and generally like otters.

The research using CCTV and camera-traps was only possible with access to captive otters, and I am grateful to the Chestnut Centre for allowing a pilot study and then to Derek Gow and his staff in Devon for being so accommodating and answering all my questions about otter toilet habits. The two otters were charming, and watched us setting up our equipment with interest, and I thank them for not chewing the temperature logger in the pond and for not sprainting on the camera-traps. I also thank staff at Edinburgh Zoo, who facilitated the CCTV and camera traps being set up in a secure area near a badger sett.

“Alarms for Farms” supplied a DVR recorder, CCTV cameras and cable and Pakatak supplied four Acorn camera-traps.

I have had the support of several students who have helped with the laborious task of sorting videos into ones of foxes and badgers and ones of birds, rodents and moving vegetation. Also, I am grateful to Andy Tharme for changing the cameras and collecting data at Torquhan. Thank you to Roy Findlay for proof reading at very short notice.

Many of my field set-ups used the woodwork skills of Roger Ingledew who has provided endless practical and moral support throughout.

Finally, thanks to Dr. Pat White and Dr. Rob Briers, my research supervisors. I could not have had better, or more positive support and I am immensely grateful to them for guiding me through the research.

CONTENTS

PREFACE

As an ecological consultant, I have always had a special interest in otters. In 2009 I was commissioned to undertake surveys and an impact assessment for otter, for a proposed opencast coal mine which involved draining a 60ha, shallow, eutrophic loch which was formerly a fishery. As part of this contract, I used camera-traps to investigate the otter activity at a disused drift mine. I discovered that it was being used as a natal holt and was also used for rearing cubs. Interpretation of the camera-trap data was a challenge as there was no comparative information on breeding otters and otter activity at den sites. This was exacerbated by the newness of camera-traps as a tool in ecological consultancy yielding observations of activity and behaviour which would be impossible with other methods. The initial study was commended by Scottish Natural Heritage, and the contract was extended to 18 months. After the contract ended, I continued the study for my own interest and by the end of six years, I had accumulated a significant amount of data. I had documented activity patterns and observed behaviour which was contrary to published literature but did not then, have the skills to fully explore the data or publish the findings. This led me to approach Edinburgh Napier University to discuss potential research on otters by rolling-out this study to other sites, and to analyse the data from the long-term study site with the underlying aim of improving otter survey methods, primarily for consultancy applications. The long-term study site is presented as Chapter 3 of this thesis and the knowledge-gap encountered as a consultant precipitated the rest of the research presented here.

GLOSSARY

Capture probability	The combination of trigger and registration probability i.e. the probability that the camera trap will trigger and record an image of a mammal pass.
Couch	The traditional term for an otter den which is above ground.
Den	The generic and traditional term used for a place of rest and/or breeding which can be applied to all mammal species.
Holt	The traditional term for an underground den of an otter.
Latrine	A new field sign identified during this research referring to a mass of faecal remains deposited on top of each other, often appearing like a cow-pat. Individual dropping may be visible but a count of droppings is not possible.
Registration probability	The probability that an image/footage of an target animal is recorded once a camera-trap has been triggered.
Rest	A rest is where an otter stays within a structure for >15min (my own definition, as described in the thesis).
Resting site	The generic term used by the Habitat Regulations to describe places where a European Protected Species such as the otter is inactive, for otters, this includes holts and couches.
Spraint	The faecal scent-mark of an otter which is often small, black and tarry.
Structure	A fully or partially enclosed location considered suitable as an otter resting site as indicated by field signs, but not necessarily proven to be used for resting.

Trigger Probability	The probability that the camera-trap’s Passive Infrared sensor (PIR) senses a change in infrared from the pass of an animal which causes the CT to trigger.

Chapter 1 Introduction

1.1 Background

1.1.1 *Mustelidae, Lutrinae and* Lutra lutra

The Mustelidae are the most species-rich family within the order Carnivora, containing weasels, martens, wolverines, tayras, polecats, badgers and otters (Koepfli et al. 2008). Key family characteristics include a long body and flexible spine, short legs, five toes per foot and the presence of anal scent glands (Kollias and Fernandez-Moran 2010). The Lutrinae is a sub-family of the Mustelidae and contains 12 species of otter globally. The Lutrinae share a range of adaptations to exploit the underwater environment including webbed feet, ocular adaptations to facilitate sharp focusing under water and in air and highly insulative fur (Dunstone 1998). The Eurasian otter *Lutra lutra* (hereafter "otter") has a wide geographic distribution, spanning all three Palaearctic continents, Europe, Asia and Africa, but is assessed as "near threatened" by the International Union of Nature Conservation (IUCN) with a decreasing population trend (Roos et al. 2015).

1.1.2 *An overview of den use in Mustelidae and Lutra lutra*

A mammal den is a "*site or structure*" used "*for a prolonged bout of sleeping or resting*" and like many other carnivores, Mustelids also use dens for breeding (Birks et al. 2005, p. 314). Mammal dens are of greatest importance when a female has cubs (Fernández and Palomares 2000) offering protection from climatic extremes and protection from predators (Roper et al. 2002).

Some Mustelids, such as the Eurasian badger *Meles meles*, invest significantly in the construction of burrows which can be extensive with hundreds of metres of tunnel, many sleeping chambers and numerous entrances (Roper 1992). The badger social group has a relatively small number of these burrows (setts) which the social group use habitually, with the largest sett being occupied continuously and used for breeding. Similarly, other Mustelid species, such as the wolverine *Gulo gulo*, pine marten *Martes martes* and otter use a specific den for birthing and rearing neonates; at other times several different dens are used, leaving the natal den unoccupied. The female wolverine excavates an extensive breeding burrow into deep snowdrifts each year, which is used for birthing and early rearing (May et al. 2012). This repeated annual investment is rewarded by stable temperatures in the insulated subnivean environment (Marchand, Peter 1982). Radio-tracked pine marten in Scandinavia used arboreal cavities for birthing and caring for the young kits to avoid predation by red fox *Vulpes vulpes.* During the winter when the martens are not breeding, they use many arboreal and underground structures for resting. Energetic constraints give preference for underground sites which offer better insulation in the coldest temperatures (Brainerd et al. 1995). There is scant literature on activity at otter holts (or otter dens) and even less on natal holts (i.e. the holt in which the female otter gives birth). Whilst most (71%) fresh-water resting sites are on the river bank itself or on small islets (Green et al. 1984), natal holts tend to be away from open water and have been recorded almost 1km from the shore on Shetland Isles (Kruuk 1996). The cubs stay within this natal structure for approximately two months (Kruuk and Moorhouse 1991b). Few natal dens have been documented during radio-tracking studies but those that have, corroborate site selection away from the main river. A natal den was located within a nest structure in a reed bed, away from the main river (Taylor and Kruuk 1990), another in a pile of boulders, 150 m away from the main river (Durbin 1996a); the two natal holts found by Green, Green & Jefferies (1984) were 40 m and 100 m from the main river. However, a natal holt monitored by camera-traps during this research was 20 m from the main river, and the same holt was also used sporadically for rearing the cubs and was also used for resting by other otters (see Chapter 3).

The principal difference between denning behaviour in otter in the UK, and other mustelids, is that in many studies, otter do not appear to have a breeding season. Analysis of placental scarring during post-mortem examination of female otter killed by road traffic from mainland UK found no evidence to support a breeding season (Philcox et al. 1999; Chadwick and Sherrard-Smith 2010). Furthermore, females are thought to be continuously polyoestrous, coming into oestrous every 36 days (Trowbridge 1983). This contrasts with the delayed implantation present in many other mustelid species, including other species of Lutrinae, which facilitates seasonal breeding (Thom et al. 2013). However, in some parts of the otter's range, there are seasonal peaks in breeding, and these coincide with periods when food availability is highest (e.g. summer in Shetland (Kruuk et al. 1991)) and seasonal availability of prey species in Spain and Portugal (Ruiz-Olmo et al. 2007).

When otter do not have neonates, they exhibit peripatetic use of existing structures for resting (Green et al. 1984; Rosoux and Libois 1996; Néill et al. 2009) mirroring the use of multiple dens observed in pine marten and wolverine. The linear home-range of the otter along rivers systems can be as long as 80km (Kruuk 1996), exaggerating the need for numerous resting sites which enable individuals to efficiently exploit resources with their home-range. On river systems, otters are mostly nocturnal, see Chapter 3, alternating bouts of activity with nocturnal rests followed by retirement to a diurnal resting site, which can be above ground in the open in vegetation, or enclosed in a burrow or similar i.e. holt (Green et al. 1984). Radio-tracking studies indicate that otter use individual resting sites infrequently. Approximately a third of resting sites used by each of three otters radio-tracked for 22 days, 36 days and 98 days respectively were only used a single time (Green et al. 1984), and this proportion of single-use sites was also found in an Austrian study of four radio-tracked otters (Isabel and Freire 2011). Furthermore, use of the same resting site over consecutive days is rare, although resting sites on consecutive days can be in close proximity even if the daily range of the otter is large (Green et al. 1984). Whilst there was no re-use of some resting sites during these studies, some resting sites are used habitually. One third of resting sites identified by Green *et al*. (1984) were used for two thirds of recorded rests, and a study in France also found that a small number of resting places were used habitually (Rosoux and Libois 1996).

Otters generally use existing structures or patches of dense vegetation for resting. There is little consensus in the type of feature selected for these resting sites. In Perthshire, Scotland, otters rested above ground in dense vegetation such as sallow beds (shrubby willow species), conifer plantations and dense willow beds and below ground in natural river bank cavities (Green et al. 1984). Otters in Austria preferred stick and log piles and tree root systems (Isabel and Freire 2011), whilst otters in Deeside, Scotland, used dense vegetation, small islands and artificial embankments with boulders and even a derelict car (Kruuk et al. 1998). Most of what is known about the internal architecture of underground resting sites (i.e. holts), comes from a study of seven holts in peatland habitat on Shetland which were excavated and described by Moorehouse (1998). He found that the tunnels often followed desiccation fractures in the peat, and the length of tunnel per holt ranged 11—57m. Underground water pools were present in four of the seven holts and latrines were found in all holts. Sleeping chambers were identified by the presence of bedding, but the shapes were irregular e.g. 1.65m x 0.28m. Holt entrances (n = 53) had a mean width of 27cm (range 11—65cm) and a mean height of 17cm (range 10—27cm). These holts were excavated by otter in deep peat, but in riparian areas otters usually utilise existing structures (Erlinge 1967; Green et al. 1984), so the internal architecture and dimensions are likely to vary.

Availability of den sites is a crucial component of a carnivore's home-range and can be a limiting factor (Halliwell and Macdonald 1996; Birks et al. 2005), especially in areas where there is human activity (Weinberger et al. 2019). Understanding denning habits of a species is critical when undertaking Ecological Impact Assessments for developments, also for conservation management. The predictable denning habits coupled with predictable breeding seasons of some mammal species has facilitated prescriptive guidelines in the UK for survey, resting site identification, impact assessment and mitigation e.g. Chiroptera (bats) (Collins 2016), great-crested newt *Tritturus cristatus* (Langton et al. 2001). Otters are far less predictable, use a wide variety of habitats and resting structures, are nocturnal and peripatetic, and lack a recognised breeding season over much of their UK range. Their management in the context of development works and impact assessment, and their conservation therefore present a particular challenge.

1.1.3 Scent marking in otter

Scent marking by mammals is characterised by several traits: it is oriented to specific objects, elicited by familiar landmarks and novel objects or odours and the same object is repeatedly scent marked. Additionally, it may be accompanied by distinct recognisable body movements (Kleiman 1966). Otter, in common with other Mustelidae, scent mark using anal sacs. Scent marking material from glands is stored in the sacs which are ducted into the alimentary canal and exuded onto passing faeces (Gorman et al. 1978). In otter, these deposits are commonly termed "spraints". Chemical analysis of spraints has demonstrated that each otter has a different chemical profile allowing individuals to be recognised by each other (Gorman et al. 1978; Bradshaw et al. 2011); this is also true for other Mustelids such as the American mink *Mustela vision* (Brinck et al. 1978). The age class of the otter that deposit a spraint (juvenile, sub-adult, adult) can be discriminated by humans with a reasonable level of success using colour differences and smell, probably due to different relative abundances of key compounds (Kean et al. 2011). Kean, Müller, & Chadwick (2011) also found a difference in the volatile organic compounds between the sex of adult otters, and distinguished differences between pregnant or lactating females and males or juveniles. Spraints can therefore confer sex, age class, breeding status of females and individual recognition of the depositing otter. In addition to anal sacs, Mustelids also scent mark using ventral glands which are on the underside of the body; the Eurasian otter is described as having ventral glands and interdigital glands (Hutchings and White 2000; Kruuk 2006a).

The function of spraints has been the subject of several studies, primarily seeking to relate spraint distribution and/or numbers to the environment or otter ecology. Mammals commonly use scent marking to communicate ownership of a territory to conspecifics (Macdonald 1980). Although there is some support for territorial marking in otter, from observations of increased marking at boundaries (Erlinge 1968; Green et al. 1984), not all studies concur. An observational study of sprainting activity on Shetland, Scotland, did not find evidence of scent marking at territorial boundaries but postulated that sprainting was associated with foraging energetics. Sprainting at feeding patches, specifically at intertidal pools, acted as a deterrent to further attempted exploitation of that feature when it was potentially depleted, thus benefitting the signaller and the receiver (Kruuk 1992). This association of sprainting with pools and greater prey abundance was corroborated in fresh-water habitats (Remonti et al. 2011; Almeida et al. 2012). However, Remonti et al. (2011) postulate that this could be a form of territorial marking or intra-specific resource defence: the linear shape of territories makes efficient boundary marking too costly, so key resources are marked within the territory as a deterrent to intruders.

Biological imperatives, such as breeding, may affect sprainting behaviour as spraint conveys the reproductive status of the female. The frequency of sprainting in both captive males and females was found to relate to the females oestrous cycle with sprainting frequency in both sexes being synchronised (Gorman et al. 1978). Observations in the wild also found no difference in sprainting frequency between sexes (Kruuk 1992). The number of spraints from groups of captive animals has been related to the birth and development of cubs, with a minimum number of spraints being deposited at parturition and the following month, with numbers peaking when cubs are five to six months old (Prigioni et al. 1995).

Therefore, sprainting patterns have been related to resource marking, reproduction and territorial demarcation. The relationship between spraint numbers and use of resting sites has not directly been addressed in published literature, however some studies observed that the female does not spraint at natal holts (Kruuk 2006b), and defaecates directly into water as a strategy to avoid detection by predators and an absence of spraints at a natal holt was confirmed by radio-tracking (Durbin 1996a)

1.1.4 Protection of otter during development projects

1.1.4.1 Legislative framework

The otter is listed on Annex 2 and 4 of the Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora, known as the "Habitats Directive", which was adopted by member States of the European Union in 1992. This directed member states to take measures to protect the species listed in the Annexes. In response to this, a European network of Special Areas of Conservation (SAC) was set up which were areas designated by domestic legislation by each country. The Habitat Directive was transposed into law in Scotland by the Conservation (Natural Habitats &c.) Regulations 1994, with similar regulations in other areas of the UK, which have been subject to various amendments. Maintenance of the Favourable Conservation Status (FCS) of otter is the primary aim. FCS is defined by the statutory authorities in the UK in terms of long-term maintenance of population dynamics, range and continuity of population (Joint Nature Conservation Committee 2007). The otter is also given "strict protection" by the various regulations to fulfil obligations for Annex 4 species of the Habitats Directive. The Habitats Directive continues to be the main legislative protection for the otter in EU countries. The UK left the EU on 31st January 2020; the environmental regulations underpinned by EU Directives have been adopted into domestic law; England and Wales passed The Conservation of Habitats and Species (Amendment) (EU Exit) Regulations 2019 and Scotland and Northern Ireland have equivalent legislation. As the former legislation has been adopted post Brexit, it is assumed that relevant guidance issued by the EU will also be applied.

The strict protection includes several prohibitions, one of which is the prohibition of "*deterioration or destruction of breeding sites or resting places*". The European Union produced a guidance document on interpretation and definition of terms of the Habitats Directive (EU 2007, p. 23) which is in context of species listed on Annex 4 which includes species as diverse as the fresh-water pearl mussel *Margaritifera margaritifera,* otter, leatherback turtle *Dermochelys coriacea* and great-crested newt *Triturus cristatus*. The salient points pertaining to breeding and resting sites are thus summarised. Protection should aim "*to safeguard the ecological functionality*" of breeding and resting places (EU 2007, p. 41). Breeding sites are defined as areas used for courtship, mating, the parturition site and parturition site when occupied by young, although it is acknowledged that only some of these criteria may be applicable to each species depending upon the species ecology. For example, breeding in great crested newt is confined to a pond, and this is where all of the stages of breeding occurs such as courtship, egg laying, egg fertilisation, hatching and maturation of the young during the first few months of its life. The pond is therefore considered the breeding site (Langton et al. 2001). In otter, it is not feasible to protect areas used for courtship and mating as these are not thought to be spatially limited and are rarely observed. The breeding site includes the place of parturition and the parturition site when it is occupied by young. It is reasonable that the environs of the natal holt are also protected to safeguard its ecological functionality, however the EU and also the UK do not offer guidelines on this. Resting places are defined as "*areas essential to sustain an animal or group of animals when they are not active*". The main criteria in defining a breeding or resting site in this context is that there is a "*reasonably high probability that the species concerned will return*" to use the site/place (EU 2007, p. 41). Resting sites that are frequently used either within, or between years should be protected, and this includes periods when they are not in use. The guidance also advises that in the case of widely ranging species, the definition of a breeding and resting site should be "*restricted to a locality that can be clearly delimited: e.g. the roosts for bats or the holt of an otter*" (EU 2007, p. 45).

In England, Wales and Northern Ireland, the otter is also protected by the Wildlife and Countryside Act (1981), as amended which broadly reflects the protection to otters and their resting sites afforded by the Habitat Regulations.

1.1.4.2 Derogation Licenses

The legislation includes the option of granting derogation from the strict protection (i.e. an exemption that allows an action which would ordinarily be unlawful) provided that the action can be demonstrated to fulfil strict criteria on the need for the action, the lack of alternatives and that the action will not adversely affect the favourable conservation status of the species. Article 16 of the Habitats Directive directs member states to report the number of derogation licenses issued per year. The number of licenses issued for each UK region each year from 2011-2016, with the licensable purpose being "*in the interests of public health and safety, or for other imperative reasons of overriding public interest, including those of a social or economic nature and beneficial consequences of primary importance for the environment*" (i.e. for development purposes), are summarised in Figure 1-1). Note that the figures refer to the number of licenses issued; the number of resting sites affected cannot be extracted from online data for all regions for all years, for example, in 2016 in Scotland, 57 licenses were issued to cover 89 resting sites.

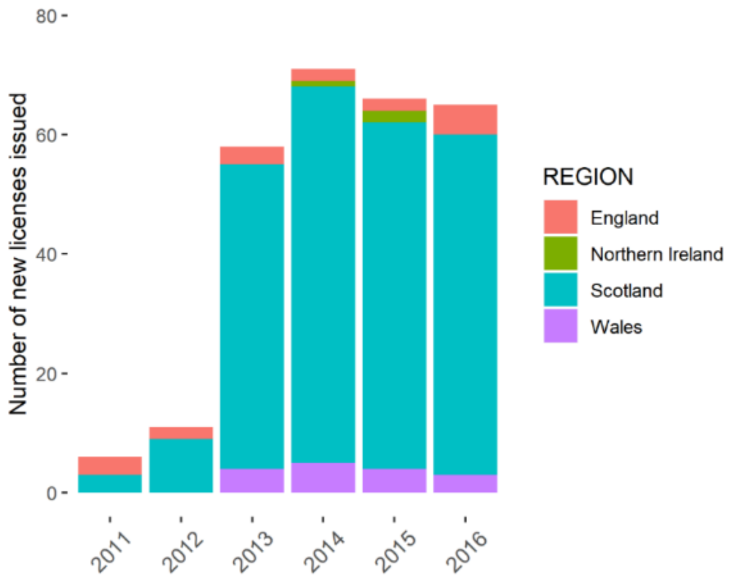


Figure 1-1 Number of derogation licenses issued for development purposes per year between 2011-16 for each of the UKs regions (European Commission nd)

1.1.4.3 The role of the consultant ecologist

Ecological consultants are qualified individuals who are paid to provide expert services and advice on the impacts of development projects on biodiversity. Development projects can be small and localised such as the renovation of a property, or spatially large with impacts that extend beyond the construction period of the project, such as large housing developments, quarries and national infrastructure projects. The legislative framework must be applied to any intended developments that may impact upon otter. Ecological consultants usually undertake field surveys of otter to provide the data for the above processes, these surveys underpin ecological impact assessments, derogation license applications and mitigation. Regardless of the magnitude of the project, the strict protection afforded to otter has to be applied and the ecological consultant must provide advice on how to meet legislative requirements, both for the broad conservation of the species and to protect the developer from acting illegally. Therefore, the ecological consultant undertakes fieldwork to determine presence of otter and, more crucially, to identify resting and breeding sites as presence in suitable habitat in the UK is usually assumed. The survey results are used by the consultant to advise on any requirement for a derogation license, but there is no clear and specific guidance on identification of resting or breeding sites, just an assumption that they will be found and identified correctly (Scottish Natural Heritage; e.g. Northern Ireland Environment Agency 2017). Furthermore, the International Union for the Conservation of Nature (IUCN) Otter Specialist Group, in their Research Guidelines, state that “there is an urgent need for accurate science-based knowledge to underpin ecological impact assessments” (Kruuk 2011).

1.1.5 Methods to identify resting and breeding sites

In the EU and the UK, there is a legislative imperative to confidently identify resting and breeding sites of otter for developments so these sites can be protected. The current approach in the UK consultancy industry (Section 1.1.4.3), is largely reliant on interpretation of field-signs; for example, the presence of spraint at an apparently suitable structure is taken as evidence that it is a resting site. However, the relationship between presence, quantity of spraint at a structure and resting behaviour has never been tested; this relationship is very much assumed by practitioners. Several methods of studying otter have been used in academic studies of otter; direct observation, radio-telemetry, non-invasive genetic sampling and camera-trapping. The feasibility of these for commercial applications are discussed.

1.1.5.1 Direct observation

Direct observation of otter has been used in a small number of fresh-water studies (Jenkins 1980; Ruiz-Olmo et al. 2005; Kruuk 2014), but this method is constrained by otter’s primarily nocturnal activity; it is also time consuming. Both these logistical constraints are relevant to consultancy, there are health and safety considerations for consultants working at night by water, night vision equipment is expensive, and consultancy work is time-charged which would make fees overly expensive. Direct observation studies of some populations of coastal otters are more feasible where otters are active diurnally and nocturnally (Moorehouse 1988) and have smaller home-ranges (Kruuk and Moorhouse 1991a), such as on the Scottish isle of Mull and the Shetland Isles. It is possible that direct observation could be applied in situations where impacts are predicted to be high and where it is logistically possible, therefore justifying high consultancy fees. An example would be large developments in the Shetland Isles, the most northerly population in the UK, thus indicating potential impact on the range of otter. The fees for direct observation monitoring are otherwise likely to be considered as disproportionately high, especially for large infrastructure projects where there may be many structures requiring monitoring. Additionally, there may be potential for the observer's presence to affect patterns of otter resting. Disturbance by observers has been noted during radio-tracking surveys (Green et al. 1984; Isabel and Freire 2011).

1.1.5.2 Radio telemetry

Radio telemetry is a method to follow the movements of individual otters by tracking the position of a radio transmitter which is attached to the animal (Néill et al. 2009). Radio-telemetry enables resting sites to be located (Green et al. 1984; Isabel and Freire 2011). The initial trapping of otter is controversial, box traps are inefficient whilst Hancock traps and leghold traps are more efficient but potentially stress the animals more and cause injury (Neill et al. 2007). Harnesses, or neck collars that carry transmitters can also be lost or removed by otters as they have a small head in relation to their neck and harnesses are also prone to snagging on underwater debris (Green et al. 1984; Ó Néill et al. 2008). More recent radio tracking studies use intraperitoneal implants, which involves trapping, anaesthesia, surgery and release of the animals (Ferdia et al. 2011; Quaglietta et al. 2014). After the otter is released after surgery, it will invariably enter water; the residual effects of the anaesthesia, lack of a sub-cutaneous fat layer and potential for chilling and potential for infection must all be considered.

Radio tracking offers the best method for finding and confirming resting and breeding sites. It is occasionally used in consultancy to assess individual movements of and impacts on other species such as Chiroptera (bat species). However, it's use is limited to large projects with potentially significant impacts on rarer species of bat, for example a new bypass road development for Galway, Ireland (Galway County Council 2018).

In 2007-2010, radio tracking was used to study the simultaneous movements of 16 otters in Southern Portugal (Quaglietta et al. 2014). Such an inclusive study would offer robust findings to assess impacts of a large development, in context with movement patterns, numbers affected as well as resting and breeding sites. However, the cost would be prohibitive, health and safety risk may preclude such work by some companies and there may be difficulties in obtaining a license to undertake trapping, anaesthesia and surgery on animals for development purposes. Radiotracking is therefore likely to remain largely inaccessible as a method to survey otter for consultancy purposes.

1.1.5.3 Non-invasive genetic sampling

Environmental DNA (eDNA) is an emerging discipline to identify species from genetic material shed into the aquatic environment (Goldberg et al. 2015) and is routinely used in consultancy to detect presence of great crested newt *Triturus cristatus* in ponds (Rees and Gough 2018). The application of eDNA for otter in the UK is limited, as it can currently only detect the presence of a species. Additionally, in lotic systems, eDNA is subject to a number of processes which can transport it downstream (Shogren et al. 2017) with distances of up to 10 km recorded in one study with modelled detection to far greater distances depending upon species and season (50 km) (Deiner and Altermatt 2014). As spraints can readily be found *in situ* and identified by experienced surveyors by their appearance and smell, more costly methods that can only determine presence are redundant.

Non-invasive genetic sampling (NGS) can also be used to analyse genetic information from spraints which contain epithelial cells, and thus DNA, which are shed from the gut lining (Prigioni et al. 2006). As a non-invasive study method, there would be no issues relating to animal welfare. This method is now routinely used by ecological consultants to identify species of bat using droppings found at roost sites, and a small number of laboratories offer species-identification which is affordable even for small projects. To be of use for otter, this method needs to offer more than species identification. Population density, sex ratio in a population, relatedness of individuals, ranging behaviour and genetic diversity are possible (Park et al. 2011). The cost of collection and laboratory analysis may be justified in assessments with potentially large impacts such as national infrastructure projects, especially where SACs designated for otter may be impacted. However, this method can also be prone to bias. Over-estimations are possible from contaminated samples, genotyping errors and inclusion of samples from transient or dead otters. Likewise, under-estimations can arise by failing to collect samples from all individuals; the probability of detecting and collecting spraint from each otter in the study area is unlikely to be equal (Arrendal et al. 2007), also poor quality samples can lead to errors in analysis (Park et al. 2011). Application of this method to identification of resting and breeding sites is significantly curtailed by the lack of knowledge relating to sprainting behaviour at resting sites, and by a lack of knowledge and uptake both in the consultancy sector and statutory authorities.

1.1.5.4 Camera-trapping

A camera-trap (CT), or trail camera, is an automatically triggered camera that takes photographs or videos of passing animals (Rovero et al. 2013). A CT is usually a single unit integrating a camera, a passive infrared motion detector (PIR) and an array of LED bulbs to illuminate the area being photographed (Apps and McNutt 2018b). The PIR receives infrared energy (IR) emitted by the background surfaces of the area in front of the CT which is focussed through a specialised lens onto a pyroelectric sensor. Any rapid change in the IR falling on the sensor causes a signal to the camera to take an image or video (Welbourne et al. 2016). Mammals moving in front of the PIR can cause such a change and thus have the potential to be captured by the camera in any footage/images.

The development of CTs opened new avenues of study and the twenty-first century has marked a rapid proliferation in their use in ecological research (Rowcliffe and Carbone 2008). CTs are commonly used for species inventories (Tobler et al. 2008; Mugerwa et al. 2013) and have generated records of mammal species in geographic areas where they were formerly considered absent (Ambarli et al. 2010; Khanal et al. 2017). They are used for abundance estimates of species with pelage marks that identify individual animals, utilising capture-recapture analysis (Rovero et al. 2013) and methods are being developed to estimate species densities of mammals without unique markings (Rowcliffe et al. 2008; Hofmeester et al. 2017). CTs compare well with radio and satellite tracking for studying range, habitat associations and landscape scale analysis but also allow studies of specific behaviours and multiple taxa and allow independent data verification (Caravaggi et al. 2017). CTs avoid having to trap and handle target animals and any subsequent effects on the target animal from backpack or collar deployment (Caravaggi et al. 2017).

The ability to make observations of mammals at close quarters suggests good potential for monitoring behaviour and activity patterns at den sites. CTs performed better than human observers in a study of peak counts of kit fox *Vulpes macrotis* at their dens (Kluever et al. 2013). This study found that the main advantages of CTs over human observers at den sites included constant surveillance by CTs compared to a sampling protocol using human observers, the ability to make nocturnal observations with CTs, the ability for a single person to simultaneously monitor many dens, and recording the foxes with a CT at 2m from the main den entrance compared with an average of 224m by human observers using binoculars to avoid disturbance. The low power consumption of the CT when it is not taking pictures, enables continuous monitoring for weeks at a time. This facilitates studies of rare behaviours such as predation at den sites (Brzeziński et al. 2014; Arbon 2019). Whilst radio-telemetry methods track individuals, CTs monitor all activity within a small area facilitating observations of species interactions such as den sharing (Mori et al. 2015).

The advantages of CT are significant, but there are also potential sources of bias including potential disturbance, imperfect detectability, effects of sampling design and trapping effort, and these may affect the use of camera-traps as a research tool (Sollmann and Kelly 2013; Gužvica et al. 2014). CTs are often described as non-intrusive or non-invasive (Lim and Ng 2008; Adamič and Smole 2011; Swinnen et al. 2014; Rowcliffe et al. 2016), but it is not universally accepted that CTs are unnoticed by all mammal species and do not affect them as CTs potentially harbour human scent and emit mechanical noise that can potentially be detected by some species of mammal (Meek et al. 2014b). The wavelength of the LEDs illuminating the field of view also has potential to be seen and disturb behaviour (Gibeau and McTavish 2009).

Camera-trap studies, like other wildlife monitoring methods are not immune to sampling error such as imperfect detection. A review of CT studies found that more than half CT studies ignored imperfect detection (Burton et al. 2015). Many variables are known to affect detection success, with variables acting at different spatial scales. Six orders of scale have been identified; the geographic range of a study species, the landscape, the habitat patch, microsite and the area being monitored by the CT and the image or video that is captured (Hofmeester et al. 2019). The importance of bias at these scales varies according to the type of study however, all study types including species distribution, activity patterns, behaviour and abundance/density are affected by detection in front of the CT and in the image (Hofmeester et al. 2019).

The methods summarised here, each have their strengths depending upon study aims. Considering the outlined methods for monitoring potential otter resting and breeding sites (i.e. direct observation, radio-telemetry and non-invasive genetic sampling), camera-trapping is the most plausible in terms of time, cost and is within the skill range and available resources of consultant ecologists. However, as with all monitoring equipment, the generated data and conclusions from commercial CT studies will only be fit for purpose if the CTs are properly deployed and with a working understanding of potential bias.

1.2 Research questions

The overarching objective of this research is to increase the evidence base for methods used to identify otter breeding and resting sites, thus improving the potential for ecological consultants and other conservation practitioners to identify and protect these sites. I have used two intrinsically-linked approaches: the first is to increase understanding of optimal deployment and efficacy of camera-traps (Chapters 2 and 3), and the second is to provide an evidence base for identifying the function of a structure (resting or non-resting) from camera-trap activity (Chapter 4) and assess the potential for reaching the same identification using field evidence (Chapter 5).

I have therefore addressed the following research questions:

What factors affect the occurrence of false-negatives when an animal passes in front of the camera-trap?

A false-negative occurs when the camera-trap fails to capture an image of a passing animal. I quantify how data quality is affected by key environmental and animal-based variables by comparing the capture success of animal passes in front of CTs with continuously running CCTV. This informs a framework of practical considerations to minimise false-negatives for camera-trapping surveys of otter, and two similar sized mammals, red fox *Vulpes Vulpes* and Eurasian badger *Meles meles*. This is addressed in Chapter 2.

How can monitoring of resting sites using camera-traps be optimised?

Using a 6-year camera-trapping dataset of an otter holt which was used for resting and breeding, I develop a method to assess the duration that otters stay inside the structure, and from this I define a resting event. I look for any changes in activity patterns of otters at the holt that could be caused by researcher visits to maintain the camera-traps. I describe variation in resting activity at the holt in relation to seasons and breeding, and present findings to estimate survey effort that would be required to have at least a 95% probability of detecting a rest. Data is analysed to find if CT deployment and settings could have been optimised: the quality of data from a two camera-trap set up was compared to a single camera-trap set up and the optimal video duration to balance data quality and analysis time was determined. This is addressed in Chapter 3.

Using data from camera-trap monitoring, are there differences in otter activity between sites used for resting by and sites that are not?

Using CT data collected at 26 study sites across the River Tweed catchment, I describe variation in otter activity at a range of potential resting structures. I use the method developed in Chapter 3 to define rest events and categorise sites as resting sites or non-resting sites. I describe patterns of resting events relating to season and night/day. I analyse patterns of selected behaviours, specifically bedding collection, latrine behaviour and sedentary behaviours in relation to the function of the structure (resting site vs non-resting site). Simulations on camera-trap data from resting sites are used to determine the survey effort required to have a good chance of detecting a rest. This is addressed in Chapter 4.

Is there a relationship between field-signs and resting use of a structure, and are there field-signs that can reliably be used to differentiate structures used for resting from structures that are not used as such?

Having defined which of the 26 River Tweed sites were resting sites, I test whether field-sign evidence, collected concurrently with the CT footage, could have reliably identified those sites, thus testing the efficacy of using field-signs to identify resting sites which is a common approach in consultancy applications. This is addressed in Chapter 5.

Finally, in Chapter 6, I evaluate what this research has added to the understanding of resting and breeding site use and camera-trap methodology, how this can be applied to the ecological consultancy industry and identify areas for further research.

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

The following chapter was published as:

Findlay, M. A., Briers, R. A. & White, P. J. C. (2020) Component processes of detection probability in camera-trap studies: understanding the occurrence of false-negatives Mammal Research 65 167—180 Doi 10.1007/s13364-020-00478-y

The publication is included in Appendix III. It has been modified slightly for the thesis. Author contributions are as follows:

MAF conceived the idea and undertook the fieldwork. MAF conducted the analysis with advice from PJCW and RAB. MAF wrote the manuscript with advice from PJCW, and PJCW and RAB contributed guidance and revisions. After peer-review, MAF responded to the reviewer's comments and prepared the revised manuscript.

2.1 Abstract

Camera-trap studies in the wild record true-positive data, but data loss from false-negatives (i.e. an animal is present but not recorded) is likely to vary and impact data quality. Detection probability is defined as the probability of recording an animal if present in the study area. I propose a framework of sequential processes within detection - a pass, trigger, image registration, and images being of sufficient quality. Using Closed Circuit TV (CCTV) combined with camera-trap arrays I quantified variation in, and drivers of, these processes for three medium sized mammal species. I also compared trigger success of wet and dry otter *Lutra lutra*, as an example of a semi-aquatic species. Data loss from failed trigger, failed registration and poor capture quality varied between species, camera-trap model and settings, and were affected by different environmental and animal variables. Distance had a negative effect on trigger probability and a positive effect on registration probability. Faster animals had both reduced trigger and registration probabilities. Passes close to the camera-trap (1–2m) frequently did not generate triggers and there was over 20% trigger failure for all species across all distances. Our results, linked to the framework describing processes, can inform study design to minimise, or account for data loss during analysis and interpretation.

2.2 Introduction

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

Field data from CTs can only include true-positives: when an animal pass elicits a trigger which results in registration of the animal as recorded footage. In order to achieve a true-positive, a number of sequential processes have to occur, all of which must have a successful outcome (Figure 2-1), and these sequential processes underlie a series of measurable conditional probabilities. False positives, such as misidentification of species, sex or individual, are errors by the observer of the footage, and not the CT itself. Some species may be more prone to being incorrectly identified, such as Scottish wildcat *Felis silvestris silvestris*, where the phenotype of the “pure” species and the hybrid are very similar. True negatives are the result of an absence of footage in an area where a species is absent. False-negatives can arise from failure of any processes in Figure 2-1. True and false-negatives cannot be distinguished from each other which is why it is important to try to understand and account for the latter.

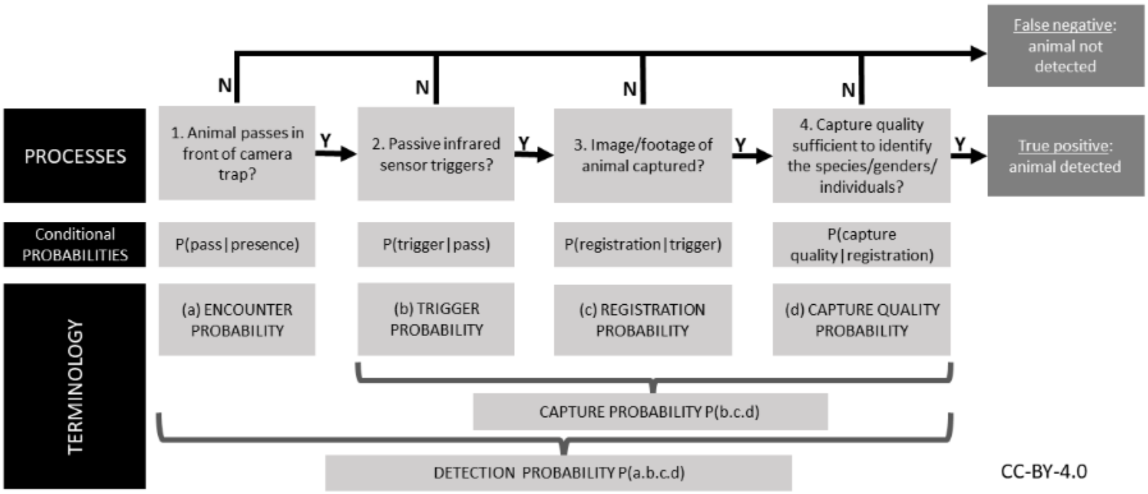


Figure 2-1 The sequential processes required to detect an animal on a camera-trap given that it is present. Failure of any of these processes leads to a false-negative therefore detection success requires a positive outcome from all the component processes. Specific terminology we use in this study to quantify these processes is also shown. ‘Detection probability’ can thus be considered the product of a series of conditional probabilities representing each of these processes.

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

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

Process 3: Registration probability P(registration|trigger). A CT trigger is not sufficient alone to record an animal – the animal must also be visible on the CT image or video.

Trigger latency or trigger speed is the interval of time between PIR trigger and initiation of the camera (Rovero et al. 2013) which can vary widely between CT models (Randler and Kalb 2018). A slow trigger speed coupled with fast moving animals means that not all triggers lead to registration as the animal has passed through the field-of-view before the camera has been activated (Rovero et al. 2013). The field-of-view of the camera is not necessarily the same width as the detection zone monitored by the PIR motion detector (Rovero et al. 2013; Trolliet et al. 2014; Rovero and Zimmermann 2016), thus affecting registration probability. Thus, if the detection zone is wider than camera field-of-view, a trigger can occur while the animal is not visible to the camera. Registration probability is then affected by the duration of the video or the number of photos taken per trigger as well as the gap between triggers which could be either due to the technology (i.e. the re-arming time), or due to the user setting. Previous studies, without use of a control (to identify scenarios where an animal triggers the camera but is not recorded) have only been able to measure the combined detection of processes 2 and 3 (Rowcliffe et al. 2011; Hofmeester et al. 2017). So while body mass, season and relative position of an animal with respect to the camera are likely to influence across processes 2 and 3 (Rowcliffe et al. 2011), these may operate on trigger probability, registration probability, or both.

Process 4: Capture quality probability P(capture quality|registration). Not all footage/images of a study species are of equal value, as images of a given quality may be required depending on a study's objectives. 'Quality' here refers to the contents of the footage/images rather than image resolution per se. For example, if aiming to identify individuals, reliable unique markers need to be visible, so a given angle of view or fully body image may be required (Foster and Harmsen 2012). Similarly, in species where it is possible to determine sex, and the study aims require this, footage containing sufficient views of an animal in terms of primary and/or secondary sexual characteristics may be required (Findlay et al. 2017), and whilst video may be better than stills for observations that determine sex such as the source and direction of urine streams, sexing animals may not be possible for every registration.

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

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

I used CCTV as a control to record all passes of our target species through the putative detection zones of arrays of CTs in order to observe at which process CTs produced false negatives. CCTV explicitly allowed me to observe all passes, even when these did not elicit a trigger, or did elicit a trigger but not a registration. Without such a control, recordings where an animal is not seen may be a false-negative caused by an animal triggering the CT but not being recorded in the footage or may be a 'false-trigger'. The term 'false-trigger' describes when a CT is triggered by extraneous stimuli such as moving vegetation and result in recordings that are empty of animals. A greater number of false-triggers can be due to a high PIR sensitivity setting (Apps and McNutt 2018b).

They can be a drain on resources in CT studies as they deplete batteries and fill memory cards. They can also increase the amount of time needed to process images or videos to a level considered unacceptable (Swinnen et al. 2014). False-triggers can be reduced by careful CT deployment by ensuring that the CT itself does not move in windy conditions and by avoidance of dense vegetation within the detection areas which can be achieved by cutting an area of vegetation back (Apps and McNutt 2018b). Using a control such as CCTV enables video or images where an animal is not visible to be classified as a false-negative or a false- triggers in addition to false-negatives caused by trigger failure.

Two CT models were chosen to contrast field-of-view and detection zone differences, one with a more standard detection zone and field-of-view (Bushnell) and one with wide detection and field-of-view (Acorn). I was able to separately investigate variation in trigger probability, registration probability and elements of capture quality probability for one semi-aquatic (Eurasian otter *Lutra lutra*), and two terrestrial (red fox *Vulpes vulpes* and Eurasian badger *Meles meles*) mammal species of a similar size (hereafter 'otter', 'fox' and 'badger'). I hypothesised that the variables driving success in processes 2, 3 and 4 would be different, for example trigger probability would be influenced primarily by distance, whilst registration probability would be most influenced by movement patterns, such as speed. Furthermore, I hypothesised that trigger probability of wet otters would be lower than that of dry otters (Lerone et al. 2015). The findings are used to suggest key considerations of study design and potential sources of bias in CT studies.

2.3 Materials and Methods

2.3.1 Data collection

There were two study sites. The first was a wild area in SE Scotland (55.9°N, 3.2°W). I targeted a mammal run in woodland known to be used by both badger and fox. The second was a captive otter enclosure (50.6°N, 4.2°W) in SW England. The enclosure was approximately 700m^2, with a pond accounting for approximately a third of the area. The enclosure included two wooden hutches for denning, termed 'holts'. A male and a female otter lived in the enclosure; they were not intended for release and were habituated to humans. In both study areas we set up two CCTV cameras (Swann SRPRO-

842) at approximately 2m above ground to continuously record to a CCTV recorder (M2/UTC-FDVR-4). The CCTV used IR illumination at night and was able to observe 24h per day. Both sites had flat topography and work was undertaken in winter when vegetation would be at minimum density and height (otter: 14 Nov–5 Dec 2017, fox & badger: 21 Feb–14 April 2017). At both sites, four CT stations were set up, subsequently referred to as CT ‘positions’, within the CCTV field-of-view with the PIR at 27cm above the ground approximating average shoulder height of the three species studied (Figure 2.2), also see section 2.3.2. CTs were aimed parallel to the ground and placed in security boxes so that they could be replaced at the same height and angle.

For both trials I used Bushnell Aggressor (model 119776) CTs programmed to record 5s video with an interval of 5s between recordings. Video potentially captures more data than still images and use of video is likely to increase due to technological advances (Swinnen et al. 2014). Whilst the resolution of still images can be better than video in good light (i.e. daytime conditions or using white flash), the better resolution of stills is lost during night-time conditions if using IR illumination (pers. obs.). As fox, badger and otter are primarily nocturnal the resolution of still image versus video was therefore not a consideration in the choice of capture mode. In the otter enclosure, at each recording station, I also set a Bushnell CT to record a burst of 3 still images with a 5s interval between bursts and a Little Acorn (model 5310 WA [Wide Angled]) CT to record 5s video with a 5s interval. Single CTs were therefore deployed at each position in the set-up for fox and badger, and three CTs were deployed at each position in the set up for otter, see Figure 2-2. The sensitivity setting of the PIR on the Bushnell CTs could potentially have been set to high, normal, low or ‘auto’, and the Acorn to high, medium or low. The choice of sensitivity settings allows practitioners to balance detection success and excessive false- triggers according to their aims, environment, and focal species. Data on each of these settings would have been informative, however the risk of having too few mammal passes within the limited data collection period to include each sensitivity setting in addition to the other variables was too great. I therefore set Bushnell CTs to ‘auto’ sensitivity as recommended by the manufacturer and the Acorn was set to medium sensitivity. The Acorn was used as a contrast to the Bushnell as its PIR sensor has an advertised 100° detection angle and 100° camera field-of-view, compared to an advertised 55° detection angle and 40° field-of-view for the Bushnell. At both sites, I fixed a data logger (Onset Hobo) 1.5m above the ground to record hourly air temperature, and in the otter enclosure pond I secured a data logger at 30cm depth to record hourly water temperature.

At both sites, I determined distances between each CT and features visible on the CCTV such as habitually used trails and trees in each CTs' field-of-view. CCTV footage was reviewed to identify passes of a single animal and create a chronological list of passes. I defined a 'pass' as a single animal moving across the central line of the CT's field-of-view, (see Hofmeester et al. 2017). As CTs targeted mammal runs, virtually all animals passed the central line. I included passes where the target species was considered the only potential stimulus for the CT PIR sensor (i.e. I excluded passes where extraneous stimuli were present), such as birds and rodents. Waving vegetation and direct sunlight would also have been seen as an extraneous stimuli, but these were not an issue during our study period because vegetation was sparse at the time of year of the study, and it was overcast and not windy. I also excluded passes where the animal was less than 1m from the CT, as the animals could potentially pass beneath the PIR sensor and/or field-of-view (Rowcliffe et al. 2011), also see section 2.3.2.

I cross-referenced passes on the CCTV footage against the CT footage using their respective time-stamps. It was noted that the Bushnell CTs set to still images lost time over the duration of the study, presumed to be due to the clock pausing on every trigger or photograph so the pattern of movement of each pass (i.e. distance from CT and direction of pass) on the CCTV was compared to the CT to ensure that both recordings were of the same pass. This enabled me to separately quantify Processes 2 and 3 (Figure 2-1) (i.e. distinguishing an animal passing but not triggering the CT from an animal triggering the CT but not registering in its footage). This process eliminated any false-triggers (i.e. where the CTs triggered but no otter had passed).

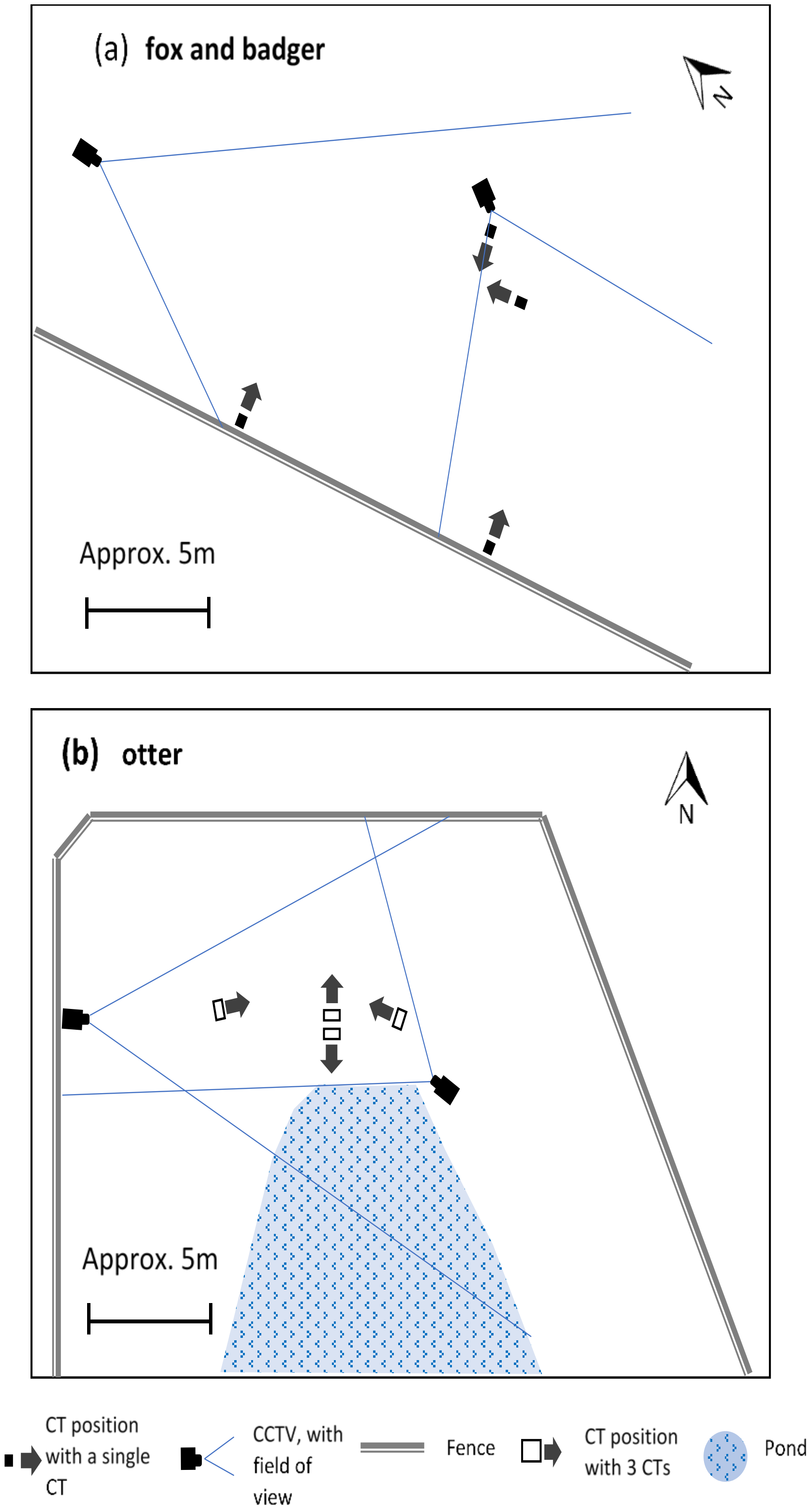


Figure 2-2 Schematic maps showing the positions of the camera-trap (CT) arrays and closed-circuit television (CCTV) at the study sites for (a) badger and fox, and (b) otter. Scales and relative positions are approximate and CTs and CCTVs are oversized. Arrows indicate direction CT stations faced

2.3.2 Testing of camera-traps

Before using both models of CT (i.e. the Bushnell Trophy CT and the Little Acorn 5310 WA), several tests were employed to determine whether the camera-traps were functioning as expected. On receipt of CTs the firmware was checked to ensure the latest version was installed on the CT. A mobile phone camera was used to view how many LEDs switched on when the camera-trap was triggered in a dark room. The mobile phone camera is sensitive to IR and the glowing LEDs could readily be checked. Both CT models included a setting called "test-mode", which allowed me to see when the CT had been triggered as a trigger caused a red LED to come on, on the front of the CT casing. This function may not be present on all CT models, but was useful in several tests. The CTs work on two parallel arrays of AA batteries. The connection between these two battery circuits was occasionally faulty leading to the camera-trap only being able to draw power from one of the battery circuits. This was tested by switching on the CT to "set-up" mode, then removing a single battery from the first array (i.e. closest to the programming screen). If the screen switched off due to lack of power, it meant that the second array was not properly connected. This test was then repeated to test the first array. Arrays of camera traps were set up in my house and allowed to run for several days and nights. The number of triggers were compared between the camera-traps to identify any units that were underperforming.

There is a blind spot between the base of the CT and the bottom of the field-of-view and/or PIR detection zone where animals can pass undetected (Apps and McNutt 2018b). Tests were undertaken to quantify this distance at different camera-trap heights so that passes through the blind spot (as observed on the CCTV) could be excluded. The distance this blind spot extends from the camera-trap increases with increased height of the camera-trap (Apps and McNutt 2018b). Setting the CT at a low height would decrease this blind-spot, but this benefit would be offset by increased vegetation density in front of the CT at greater distances. The height of the CT was a pragmatic compromise between the vegetation height and the shoulder height of the three focus species. To quantify the distance of the blind spot, a CT was set up at 27cm from the ground in 'test mode'. In test mode, a red light flashes on the front casing of the CT when the PIR is activated. A large piece of plastic was used to screen a person. The person moved their hand parallel with the ground 10 cm away from the front of the CT and approximately 17cm from the ground (i.e. the estimated height of an otter which was the shortest of the three focus species). This was repeated five times. The red light was observed to see if the PIR had been activated on each ‘pass’. This was repeated at increasing intervals of 10cm from the CT until the PIR reliably triggered. This was at 60cm from the CT for the Bushnell and 40cm or the Acorn. To measure the vertical field-of-view of the camera, the CT was set up at the same height of 27cm facing a wall at 60cm. A metal measuring tape was placed vertically in the centre of the field-of-view, flat against the wall. A hand was used to trigger the CT and take footage and the footage showed the vertical field-of-view. For the Bushnell, this was 17—39cm on video setting and 4—40cm on still, while the Acorn video was 0—56cm. The lowest edge of the field-of-view was at approximately the shoulder height of an otter, so the same procedure was repeated at 1m distance from the wall. The vertical field-of-view for the Bushnell in video mode was 10–47cm and still 7–50cm and the Acorn on video was 0—76cm. Passes at 1m of the CT were therefore considered the closest at which an otter could reliably trigger the PIR and be registered as an image, in the context of both CT models at 27cm high.

The horizontal dimensions of the detection zone of the camera-traps were not tested as they are not constant and vary under different conditions such as season and species (Hofmeester et al. 2017).

2.3.3 Variables recorded

I quantified trigger probability P(trigger|pass) with a binary variable of passes which either triggered the camera (1) or did not (0), regardless of whether its footage registered the animal. I also quantified registration probability P(registration|trigger) with a binary variable of passes which either triggered the camera and registered the animal (1), or triggered the camera but failed to register the animal (0).

As discussed, capture quality probability P(capture quality|registration) depends on a study’s objectives. In many studies of mammals, identifying presence of the species is not necessarily sufficient, but rather a good view of the head and body is needed to identify the age category/sex/breeding status of the individual (for instance, lactating females) (Sollmann and Kelly 2013; Findlay et al. 2017), or to observe individual natural markings (Karanth 1995; Silver et al. 2004). As all passes were of forward-moving animals, if the head could be seen in the first video frame or image then it was reasonable to expect that more of the animal would be captured in the following video footage or images providing that the CT was programmed to record subsequently via a burst of images or a video. The capture of head was therefore used as an indication of good capture quality. I quantified capture quality probability with a binary variable categorising good capture quality probability as capture of head only, head and body, or head body and tail (1), or poor capture quality probability when the head had already passed through the field-of-view (0).

From the CCTV footage and data loggers, a suite of animal and environmental variables were recorded for each pass (Table 2-1). The orientation of the animal pass to the CT was also recorded, using three categories. A lateral pass was when the animal passed exposing a complete side view, an anterior pass was when the animal approached the camera-trap presenting the head, shoulders and front legs and a posterior pass when the animal approached the CT from behind and walked away exposing its hind-quarters. Orientation was used to subset the data but was not used in models. I chose to record an animal's gait (i.e. walk, trot, run) to represent speed as gait was quickly identifiable whilst estimating ms-1 over such short distances would be prone to inaccuracies from perspective using CCTV footage and inconsistencies due to instances of the animal pausing. A walking animal is defined in this study as a slow-moving animal, with a smooth locomotion that lacks vertical movement (bounce). It always has two to three feet in contact with the ground. This contrasts with a running animal which has all four feet off the ground at intervals as part of the locomotion. The trot category was used to describe all intermediates between a run and a walk.

Running animals were subsequently combined with trotting animals as running animals were too infrequent to analyse separately, our variable GAIT therefore had two categories (walk/trot or run). I recorded whether there was any delay in the animal passing through the field-of-view as a result of the animal pausing to sniff, or scent mark (i.e. loitering). This was recorded as a binary variable LOIT. For otter, I also recorded whether the animal was dry after being in the holt and prior to immersion in water (from holt) or whether the animal had been immersed in water since leaving the holt (not from holt). This enabled me to subset the data to include passes where the otter was fully dry, or not fully dry. The time since the otter had been submersed in the water (i.e. TFW) was noted by watching the CCTV footage back from each pass to the time that the otter last emerged from the pond and subtracting this from the time of the pass as recorded on the CCTV clock. For fox and badger, I only used Bushnell CTs on video setting. For otter, I had stations of three CTs (Busnell video, Bushnell still images, Acorn video) together, to maximise data acquisition from each pass. I analysed data for each of the three CT models/settings separately so I could compare Bushnell video between fox/badger and otter, and because aspects of the three CT models/setting differ substantially in key elements such as detection zone and field-of-view, for otter.

Table 2-1 Data collected for each animal pass identified on CCTV. Response variables were recorded against the first frame of the CT video or the first still image from the burst of three. Explanatory variables described parameters of the pass as observed on CCTV

Response variables from CT recordings	**Badger/Fox**	**Otter**
TRIGGER: binary (1 = trigger / 0 = no trigger)	✓	✓
REGISTRATION: when trigger = 1. Binary (1 = animal registered / 0 = no animal registered)	✓	✓
CAPTURE QUALITY: when trigger = 1 and registration = 1. Binary (1 = good / 0 = poor)	✓	✓
Explanatory variables from CCTV footage		
DIST: perpendicular distance (m) between CT and animal, continuous	✓	✓
GAIT: binary (walk/trot or run)	✓	✓
LOIT: any pauses in animal’s progress when passes the CT such as sniffing or scent marking. Binary (LOIT/NO LOIT)	✓	✓
TFW: Time From Water (s), continuous		✓
WET.DRY: binary, DRY (i.e. from holt), and WET (passes where TFW≤10s)		✓
Explanatory variables from data loggers		
AIR: air temperature (°C), continuous	✓	✓
WATER: water temperature (°C), continuous		✓
ABSDIFF: the absolute difference between air and water temperatures (°C), continuous		✓
Random variable		
CAM.POS: The location of the CT within the study area, categorical	✓	✓

To understand how the otters’ IR footprint develops after exiting from water, I used a thermal imager (FLIR PAL65) to take thermal-images of otter on dry ground from the point of exiting water to 300s post-immersion. Seventeen images were taken, the land temperature ranged between 6-10°C and water 9.5 C. Mean temperature of the otter trunk and an equivalent area of ground adjacent to the otter were measured using FLIR

Tools software (v5.13.17214.2001). The absolute difference in temperature was plotted against time from water (Figure 2-3) and an exponential model was fitted to the data. Approximately a 2.7 °C difference between an animals emitted IR and the background IR is needed for a PIR sensor to initiate a trigger (Meek et al. 2012), although this will depend on the CT model and PIR sensitivity setting. Under these conditions, the fitted model predicts 32s to have elapsed before the temperature difference reaches a conservative 3°C.

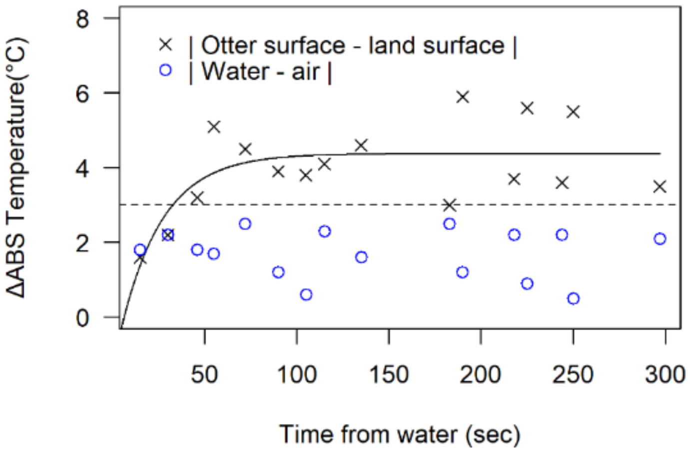


Figure 2-3 Absolute difference in temperature (°C) between an otter's trunk and surrounding land against time after being immersed in water illustrating how long since immersion it takes for the otter to emit enough heat (c. 3°C) for a passive infrared sensor to theoretically detect the otter. To describe the asymptotic relationship, I fitted an exponential model in the form $y = a(1-e^{-bx})+c$ where y is the temperature difference, x is the time since exiting water, and a, b and c are parameters estimated by the model. The absolute difference between air and water temperatures is also plotted, using temperature from data loggers.

2.3.4 Modelling trigger and registration probabilities

The aims of the analyses were to find which variables, or combinations of variables best explain the data, and to understand any trends, particularly the direction and strength of trends. I chose generalised linear mixed models (GLMMs) so that I could control for any effects of the individual camera-trap stations by inclusion of the camera-trap station as a random variable which reduces the number of parameter estimates and allows fitting with a binomial distribution. Absence of collinearity between variables was checked using the package "performance" (Ludecke et al. 2020).

I carried out modelling in R version 3.2.2 (RCore Team 2015) within R Studio (RStudioTeam 2015), fitting GLMMs using lme4 (Bates et al. 2015) and generating model comparison tables using MuMIn (Barton 2016). I used the package manipulate (Allaire 2014) to fit the exponential model in Figure 2-3.

I used GLMMs with a binomial distribution to investigate variation in the response variables P(trigger|pass) and P(registration|trigger) for each species and CT model. The CTs positions potentially had different local conditions. Therefore, I set CT position as a categorical random effect, and built a list of candidate models (see Appendix 1) containing combinations of appropriate variables in Table 2-1, including a null model in each.

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

I investigated whether immersion in water negatively affected trigger probability for otter, as suggested by (Lerone et al. 2015). First, I modelled trigger probability for dry otters after they had emerged from their holts and prior to entering water. This allowed me to compare dry otter to fox and badger. Then, I repeated the model comparison including a generated binary variable WET.DRY, to distinguish passes where the otter was fully ‘wet’ (≤ 10 s since exiting water) and passes where the otter was fully ‘dry’ (passes where FROM.HOLT = 1). Finally, using all passes where FROM.HOLT=0, I repeated the model comparison including TFW to test whether it was a significant variable, but it was not well supported. The models were ranked based upon their Aikaike Information Criterion (AIC). This is a numerical figure for each model which is a measure of relative model fit whilst also accounting for model complexity. The model with the lowest AIC is the best supported model given the model set. The delta AIC (Δ_{AIC}) is then calculated for each model in the candidate set by subtracting the AIC of the best model from the AIC from each individual model’s AIC. I used a threshold of $\Delta_{AIC} \leq 2$ to indicate models with “substantial support” (Burnham and Anderson 2004). For brevity I only include plots for the best supported model ($\Delta_{AIC} = 0$) in the main text, but other plots of all models with $\Delta_{AIC} \leq 2$ and parameter estimates for all models are provided (Appendix 1).

2.3.5 Quantifying detection in a 'worst-case scenario'

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

2.3.6 Latency between trigger and registration

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

2.4 Results

False-negatives were recorded at each stage of detection I studied (triggering, registering, capture quality), but the extent of false-negatives from each process varied between species, within species (e.g. wet vs dry otters), with CT mode (still vs video) and CT model (Acorn vs Bushnell) (Figure 2-4). For all scenarios, at least 20% of passes did not elicit a trigger despite the animal entering the putative detection area (Figure 2-4, white bars). For otters, badgers and foxes on videos, a substantial component of false-negatives occurred when the CT triggered but did not register the animal, while for stills (otters only) this occurred very infrequently (stippled bars). Based on our specific criteria of recording the animal's head, substantial data loss occurred due to poor capture quality regardless of whether stills or videos were used, although this varied widely between scenarios (light grey bars). There was substantial variation in the proportion of passes that registered images (combined dark and light grey bars) or images of sufficient quality (dark grey bars).

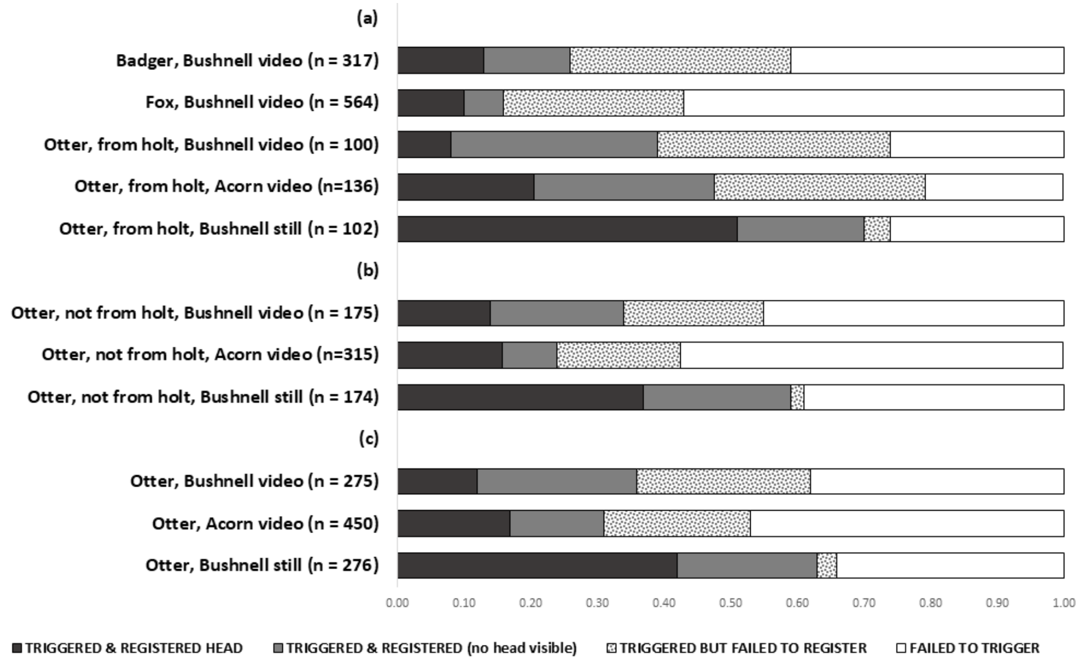


Figure 2-4 Success rate of Trigger, Trigger and Registration, and Trigger and Registration of head as a proportion of the number of passes for (a) fox and badger on video and otter from holt on video and still images (b) otter passes not from holt (c) all otter passes (passes from holt and not from holt)

2.4.1 Trigger probability P(trigger|pass)

For the terrestrial mammals and fully dry otters, model comparison results and plots of lowest AIC models are in Figure 2-5. DIST and GAIT influenced trigger probability for all species using the Bushnell CTs. DIST has a negative effect in each scenario, with a slower GAIT having greater trigger probability except for the interaction seen in badger where this was only true close to the CT. Trigger rate by the Acorn CT was influenced by AIR and DIST with trigger probability being better at the higher air temperature, but again decreasing with increased DIST.

Model	K	AIC	Δ_{AIC}	W_i
(a) Badger video, Bushnell (n = 249)				
GAIT * DIST	4	271.0	0.00	0.937
… 4 models…				
Null model	1	284.1	13.06	0.001
… 3 models…				
(b) Fox video, Bushnell (n = 454)				
DIST	2	567.0	0.00	0.401
GAIT +DIST	3	567.8	0.79	0.269
GAIT * DIST	4	568.6	1.72	0.178
AIR+DIST		568.9	1.94	0.152
…2 models…				
Null model	1	620.6	53.57	0.00
…2 models…				
(c) Dry otter video, from holt, Bushnell (n = 111)				
GAIT+log(DIST)	3	63.1	0.00	0.440
Log(DIST)	2	64.1	1.00	0.266
GAIT*log(DIST)	4	64.8	1.72	0.186
…4 models…				
Null model	1	108.7	45.60	0.00
…1 model…				
(d) Dry otter video, from holt, Acorn (n = 115)				
AIR+DIST	3	77.7	0.00	0.387
GAIT*DIST	4	78.4	0.68	0.275
DIST	2	78.7	0.93	0.243
...3 models...				
Null model	1	107.2	29.48	0.00
...2 models...				

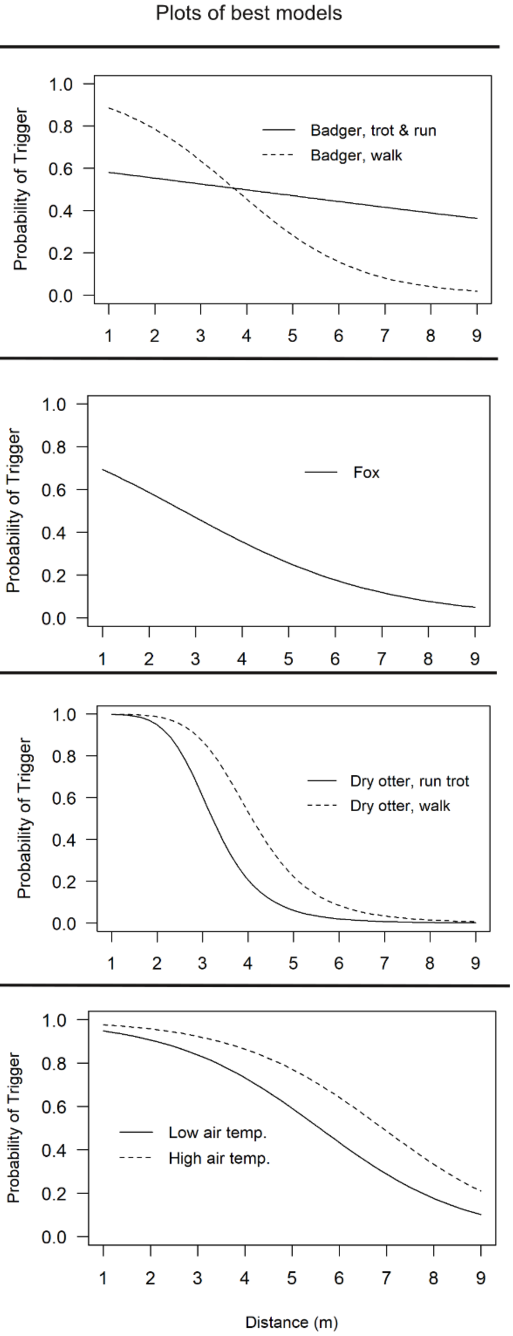
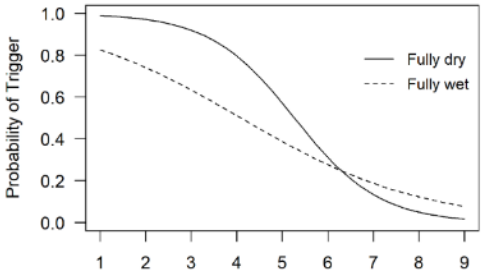


Figure 2-5 Model selection tables, and plots of the best supported model for Trigger Probability, P(trigger|pass), for (a) badger with Bushnell camera-trap (CT) on video setting (b) fox with Bushnell CT on video and (c) dry otter with Bushnell CT on video, and (d) dry otter with Acorn CT on video. Model variables are defined in Table 1. For brevity, only models with ΔAIC ≤ 2 and the null model are shown in the ranking tables. Full model results are included in Appendix I, Table A1.

Figure 2-6 shows model comparisons for trigger probability of the best supported models in which fully wet and fully dry otter were considered. With both CT models, DIST had a negative effect but the negative effect was reduced for dry otter compared to wet.

Model	K	AIC	Δ_{AIC}	W_i
(a) Coat wetness, Bushnell video (n=190)				
WET.DRY*DIST	4	161.3	0.00	0.606
WET.DRY+DIST	3	163.1	1.80	0.246
…11 models…				
Null model	1	233.3	72.03	0.00
… 1 model…				

Plots of best models



Model	K	AIC	Δ_{AIC}	W_i
(b) Coat wetness, Acorn video (n=193)				
WET.DRY+DIST	3	175.4	0.00	0.715
WET.DRY*DIST	4	177.2	1.84	0.285
…9 models				
Null	1	234.9	59.49	0.00
…3 models				

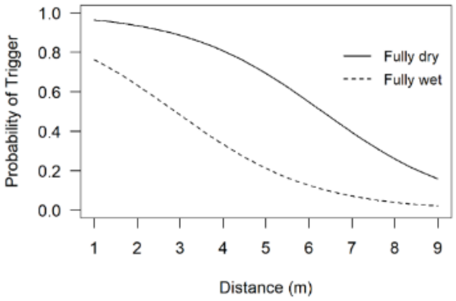


Figure 2-6 Model selection tables, and plots of the best supported model for Trigger Probability for otter, P (trigger|pass), including the variable WET.DRY, using (a) Bushnell video and (b) Acorn video. Model variables are defined in Table 2-1. For brevity, only models with ΔAIC ≤ 2 and the null model are shown in the ranking tables. Full model results are included in Appendix I, Table A2.

2.4.2 *Registration probability P(Registration|trigger)*

Registration probabilities for the Bushnell still images of otter were almost perfect (i.e. only 2-4% data was lost from cameras triggering but not registering), see Figure 2-4, so we did not model these. For videos, registration probability model comparisons are in

Figure 2-7. Because registration probability is conditional on the camera having triggered, I did not expect the thermal properties of the animal relative to the background to influence it, so I combined wet and dry otter passes for the analysis.

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

Model	K	AIC	Δ_{AIC}	W_i
a) Badger video (n=140)				
LOIT+GAIT+DIST	3	166.5	0.00	0.727
…5 models…				
Null model	1	184.3	17.8	0.00
…2 models…				
b) Fox video (n=199)				
LOIT+GAIT+DIST		224.0	0.00	0.513
LOIT		225.2	1.23	0.278
…4 models…				
Null model	1	231.4	10.42	0.003
…3 models…				
(c) Otter Bushnell video (n = 220)				
LOIT+GAIT+DIST		264.3	0.00	0.996
…4 models…				
Null model	1	308.5	44.23	0.00
…3 models…				
(d) Otter Acorn video (n = 201)				
LOIT+GAIT+DIST		225.9	0.00	0.906
…5 models…				
Null model	1	267.0	41.07	0.00
…2 models…				

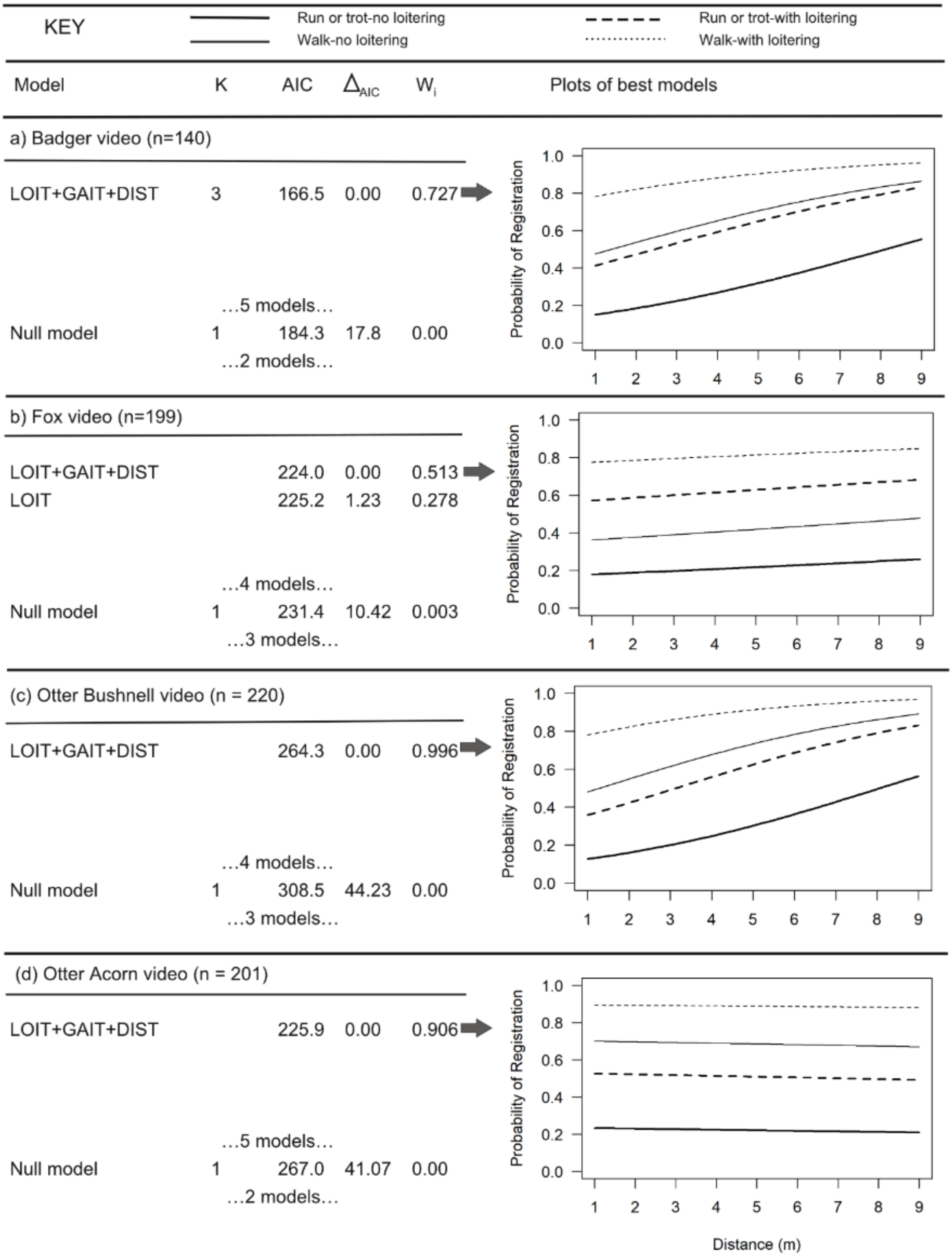


Figure 2-7 Model selection tables, and plots of best models for registration probability P (registration|trigger), for (a) badger, Bushnell video (b) fox, Bushnell video (c) otter (all passes), Bushnell video and, (d) otter (all passes), Acorn video. Only lateral passes were included (see text). Model variables are defined in Table 2-1. For brevity, only models with ΔAIC ≤ 2 and the null model are shown in the ranking tables. Full model results are included Appendix I, Table A3.

2.4.3 Capture quality probability

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

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

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

2.4.4 Detection in a 'worst-case scenario'

For 28 anterior passes of otters emerging from water at the CT station 2.5m from the pond, the percentage of triggers, registrations and overall capture probabilities are in Table 2-3.

Table 2-3 Summary of trigger, registration and overall capture probabilities for otter representing "worst case scenario", from camera-trap position facing water's edge at 2.5m recording anterior passes of otter emerging directly from water (n = 28).

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

2.5 Discussion

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

2.5.1 *PIR sensitivity caused loss of data at close distances*

Decreased capture with increased distance is well documented (Rowcliffe 2017; Randler and Kalb 2018), but our data demonstrate this occurs primarily because of reduction in triggering, not a reduction in registering of animals on footage. The PIR sensor receives long-wave infrared (IR) through an 8-14 µm filter. Atmospheric transmission of long-wave IR through air is good (Usamentiaga et al. 2014), therefore absorption (by atmospheric gases such as CO_2 and water vapour) of IR energy between the animal and PIR sensor is not thought to be of consequence (Welbourne et al. 2016). Other mechanisms are therefore needed to explain decreasing trigger probability with increased distance. I suggest that there are two ways that distance can affect the presentation of the animals IR footprint to the PIR sensor. The first relates to the loss of intensity of the animals emitted IR with increasing distance, as the energy per unit area from a point source decreases according to the inverse-square law (Papacosta and Linscheid 2014). The second is that the further away the animal is from the PIR, the more likely there are to be objects or vegetation between the animal and PIR sensor which could block the passage of IR and reduce capture rates (Hofmeester et al. 2017). Whilst distance will always have a predictable negative effect on trigger probability due to the loss of intensity of IR, this will be compounded by objects within the detection zone and lead to variation in the relationship between trigger probability and distance, depending on context, such as local vegetation density.

I set the Bushnell Trophy CTs to "auto" sensitivity and the Acorn CTs to "medium" sensitivity. A negative relationship between distance and trigger probability would be seen with different PIR sensitivity settings as increasing distance reduces the amount of IR reaching the PIR by the mechanisms described. The sensitivity of the PIR can be set by the user, and the choice of setting is a compromise between assumed higher detection on a high sensitivity setting with an unwanted increase in false-triggers (Rovero et al. 2013). The auto sensitivity setting on the Bushnell CTs responds to the temperature and increases sensitivity in higher temperatures. Detection by PIR is less effective where the difference in emitted IR from an animal to the background IR is small, such as in the tropics (Apps and McNutt 2018b). In such cases, the choice of PIR sensitivity to the highest setting is straight forward. However, in areas where there may be significant differences in temperature throughout a 24h period, the auto setting adjusts the sensitivity to balance capture probability with the probability of excessive false-triggers and this is likely to be the choice of practitioners, especially as it is recommended by the manufacturer. Quantifying the impact of different sensitivity settings on trigger probability would be a worthwhile extension of the work in this thesis.

The negative effect of distance is critical in CT studies that adopt the Random Encounter Model (REM) to estimate population densities when individuals cannot be identified (Rowcliffe and Carbone 2008). This has been an important development in density estimation using camera-traps because capture-recapture methods cannot be applied to species that are not individually identifiable. The REM or similar could be used for all species, therefore removing any potential error from misidentification of individuals. REMs require knowledge of the size of the detection zone of CTs (Rowcliffe et al. 2008).

However, because detection probability is variable within the detection zone, distance sampling has been integrated into REMs to estimate effective detection distances for species (i.e. the distance within which the number of animals not captured equals the number captured beyond) (Hofmeester et al. 2017). This relies upon “a shoulder of certain detectability up to a certain distance” from the camera-trap (Rowcliffe et al. 2011) (i.e. there is an assumed zone close to the camera with a 100% capture probability for a passing animal). However, I found that at close distances there was a substantial predicted rate of false-negatives due to trigger failure. Using the best supported models, the modelled trigger probability at 1 m distance from the CT for fox (all gaits) was 69% (i.e. there was a predicted 69% probability of the CT triggering for an otter passing 1 m from the camera); badger run/trot 58% (walk 88%); dry otter from holt with Bushnell CTs run/trot 74% (walk 93%). The REM approach is caveated with the assumption that PIR response must be reliable (Rowcliffe et al. 2011). Our trials with two frequently used models of camera-trap demonstrate important limitations in PIR sensitivity. Similar poor capture at close distance (1m) has also been found in a study of birds (mean of 60% across six size classes of bird and six CT models), where CTs were programmed to capture still images and high sensitivity (Randler and Kalb 2018). We suggest that imperfect triggering at close distances for small to medium homiotherms may be ubiquitous in CT technology and thus needs to be evaluated prior to distance sampling and other quantitative studies, with a CCTV control being a useful method.

2.5.2 Speed is important in Registration probability

Gait was an important variable affecting trigger probability for badger and dry otter, but less so for fox with a slower gait increasing trigger probability. I used gait to represent the relative speed of passes within each species, but in some species, there is also a difference in the vertical movement (i.e. bounce) as well as horizontal movement with different gaits. The bouncing gait of a trotting badger will interact with a larger proportion of its background, possibly creating a better signal to the PIR. This may lessen the effect of distance on trigger probability, as seen in the interaction of GAIT and DIST in Figure 2-5. There was a more consistent effect of gait on registration probability, in all cases slower passes are more likely to register in an image/video (Figure 2-7). Observations of running animals were rare in our study, and this has been noted in other mammal groups such as the Felidae (Anile and Devillard 2016), so speed may cause greater bias in multi-species surveys where species move at different speeds affecting both trigger and registration probability (Hofmeester et al. 2019).

2.5.3 Distance drives trigger and registration probability in opposite directions

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

A hypothetical scenario, illustrating a mechanism by which registration probability for a lateral pass is likely to increase with distance, and how this is likely to interact with animal speed, is shown in Figure 2-8. This interpretation presents a hypothesis that could be tested in future experiments.

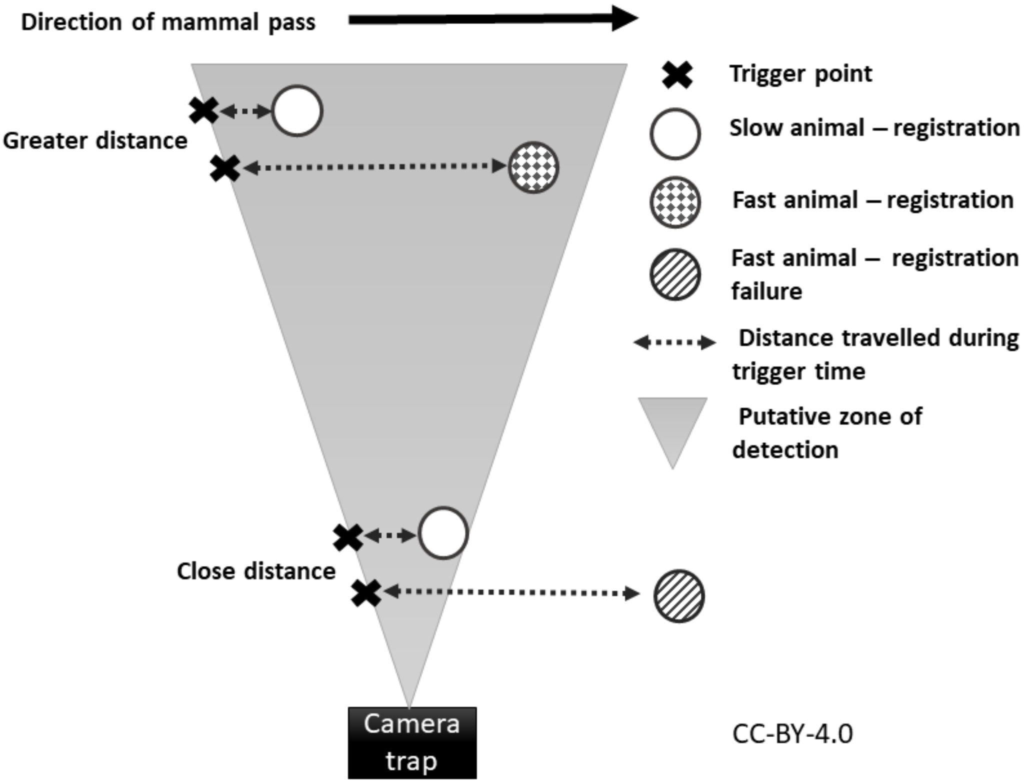


Figure 2-8 Hypothesised mechanism showing how distance to camera-trap (CT) can interact with animal speed to influence registration probability. Registration probability is positively affected by distance due to the larger area within the field of view at greater distances. Conversely, faster moving animals can completely pass through the small width of the field-of-view close to the CT before the camera takes an image

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

2.5.4 The choice between still image and video capture

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

Still capture is indicated for capture-recapture density studies where a key consideration is high quality images to distinguish pelage details, still capture also enables the use of Xenon white flash although white flash can impact behaviour (Gibeau and McTavish 2009). Still capture is also more efficient for faunal inventories and occupancy studies where data generated by videos is not usually required. Density studies using REM can use video, or a burst of still images to estimate average speed of an animal. Whilst there will be lost data from both settings due to trigger probability, the video setting is also likely to have reduced registration probability, unless the trigger speeds are comparable. Where data from video is required, for instance in behavioural studies, CTs should be aimed at areas with field-signs indicating activity that delays the passage of a passing animal, such as at dens, bait stations or scent marking sites.

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

2.5.5 Effects of immersion of otter on detection are short-lived

The trigger probability of dry otter passes on Bushnell videos broadly reflected those of the two terrestrial species, with distance and/or gait being important in all the best fitting models although the best supported model for the Acorn video CT included air temperature and distance. Our results corroborate observations that wet otters are poor in eliciting a PIR trigger (Lerone et al. 2015). However, time from exiting water was not an important variable in trigger success, indicating that other variables may impact on the rate of change in IR emitted after an otter has left water. Otter thermoregulation in cold water can result in reduced emission of infrared from an otter's body and tail, however the intensity and duration of swimming prior to exiting water can affect thermoregulation and hence the amount of IR emitted (Kuhn and Meyer 2009). These variables, and others, may confound any effect of time from exiting water on trigger success. When I set a CT facing water at 2.5m to record otter emerging from water, the trigger probabilities for Bushnell (video and still) and Acorn CTs were very poor (36–43%). The slower trigger speed for video led to poor registration probability of 40–63% (Table 2); the resulting capture of all passes on video setting (e.g. 14% for Acorn) is very poor. Within the limits of our study conditions and limited sample size, thermal imaging readings indicated that when an otter emerges from water, its surface temperature nearly matches water temperature (see Figure 2-3). It only takes a short period of time from immersion (≤1 min) for an otter to develop a thermal footprint with a 3°C difference from the background, 3°C being an approximate difference that would trigger a camera-trap PIR (Meek et al. 2012). This indicates that the relationship between water and land temperatures due to the influence of season, geographic location and circadian temperature changes has the potential to significantly affect trigger probability of animals after immersion in water. A greater difference between land and water temperatures would result in a higher trigger probability and a smaller difference in a lower trigger probability. Further study to include variation in water and land temperatures would be beneficial to investigate how this affects the time required from immersion to the animal having a thermal footprint sufficiently different from the background to trigger a PIR detector.

2.5.6 Understanding the stages of detectability will improve study design

CTs can be used for a range of study types, hence study design needs to consider CT model specifications, placement and settings (Rovero and Zimmermann 2016). Understanding how the animal, environment and equipment interact is important for all CT studies. Recognition of detection as a sequence of processes (Figure 2-1) enables each process to be considered independently when planning CT studies as the mechanisms for success in each process are different, for instance recognising potential causes for detectability heterogeneity between CT sites or species within a study. I demonstrate the high level of data loss (on both video and still setting) on medium sized animals due to poor triggering, even at close distances. This would need to be accounted for within population density analyses such as the REM when distance-sampling is used to estimate effective detection distances. Using CCTV as a control, the influences of different seasons, temperatures, humidity and vegetation structure could also be quantified.

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

I would recommend that the trigger speed of the chosen CT model and mode of recording is established, either from the manufacturer’s specification or via testing. Video trigger speeds are rarely specified by manufacturers as they are usually significantly slower than still.

2.6 Conclusions

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

Chapter 3 Developing an empirical approach to optimal camera-trap deployment at mammal resting sites: evidence from a longitudinal study of an otter *Lutra lutra* holt

The following chapter was published as:

Findlay MA, Briers RA, Diamond N, White PJC (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. doi: 10.1007/s10344-017-1143-0

The publication is included in Appendix III. It has been modified slightly for the thesis. Author contributions are as follows:

MAF undertook the fieldwork, first as part of a commercial consultancy contract and then for personal interest. MAF conducted the analysis with advice from PJCW and RAB. MAF wrote the manuscript with advice from PJCW, and PJCW and RAB contributed guidance and revisions. After peer-review, MAF responded to the reviewer's comments and prepared the revised manuscript which was accepted.

3.1 Abstract

Most studies of nocturnal mammals rely on indirect evidence (i.e. interpretation of signs left by the mammal) or invasive methods involving capture and tagging of individuals. Indirect methods are prone to error, while capture and tagging mammals have logistical and ethical considerations. Off-the-shelf camera-traps are perceived as an accessible, non-intrusive method for direct data gathering, having many benefits but also potential biases. Here, using a six-year camera-trap study of a Eurasian otter holt (den), I evaluate key parameters of study design. First I analyse patterns of holt use in relation to researcher visits to maintain the camera-traps. Then, using a dual camera-trap deployment I compare the success of data-capture from each camera-trap position in relation to the dual set-up. Finally, I provide analyses to optimise minimum survey effort and camera-trap programming. My findings indicate that otter presence and resting patterns were unaffected by the researcher visits. Results were significantly better using a close camera-trap emplacement than a distant. There was a higher frequency of otter activity at the holt during the natal and early rearing period which has implications for determining the minimum survey duration. Reducing video clip duration from 30 to 19 s would have included 95% of instances where sex could be identified and saved 35-40% of memory storage. Peaks of otter activity were related to sunrise and sunset, exclusion of diurnal hours would have missed 11% of registrations. Camera-trap studies would benefit by adopting a similar framework of analyses in the preliminary stages or during a trial period to inform subsequent methodological refinements.

3.2 Introduction

The study of terrestrial carnivores encompasses a great variety of direct and indirect monitoring methods, such as telemetry, capture-mark-recapture, distribution of field-signs, harvest reports and questionnaire surveys (Gese 2001). The development of remote trail cameras, or camera-traps opened new avenues of study and the twenty-first century marked a rapid proliferation in their use in ecological research (Rowcliffe and Carbone 2008). Camera-trap technology has been applied to biodiversity monitoring (Mugerwa et al. 2013; Tobler et al. 2015), estimating population size (Rowcliffe et al. 2008; Tobler et al. 2015) and behavioural observation (Brzeziński et al.

2014; Huang et al. 2014). There are, however, acknowledged potential sources of bias in camera trap studies including disturbance, detectability, sampling design and trapping effort which may affect the use of camera-traps as a research tool (Sollmann and Kelly 2013; Gužvica et al. 2014).

The ability of a camera-trap to detect and record its target has been shown to be affected by the mass of the target, the distance between the camera trap and the target, the speed the target moves at and the season (Rowcliffe et al. 2011). Differences in detectability have also been found between camera-trap models (Swann et al. 2004; Wellington et al. 2014). Imperfect detection by a single camera-trap has been improved by using two camera-traps in different configurations, e.g. where camera traps are set at different distances from the target (Kilshaw and MacDonald 2011), adjacent to each other (Glen et al. 2013) or at 90° to the target (Newey et al. 2015a). Most camera-traps use passive infra-red (PIR) motion detectors which monitor ambient infra-red radiation and are triggered by changes due to infra-red radiation emitted by a passing animal. The otter's adaptations to a semi-aquatic life such as fur structure and thermoregulation, may reduce their infra-red footprint when exiting water, thus reducing their visibility to PIR suggesting that they may not be suitable for PIR motion detectors (Lerone et al. 2015). When the efficacy of camera-traps were compared to scat surveys to quantify visitation rates by North American river otter *Lontra canadensis* to scat sites, the camera-traps produced fewer false-negatives than presence indicated by field-signs (Day et al. 2016). However, that study found a relationship between scat counts and the number of otter registrations on the CT and concluded that scat counts could be used to determine the intensity of use of a spraint site. In addition to investigating presence of otter at spraint sites, camera-traps have been used to assist field-sign interpretation in areas where several otter species co-exist but have similar spoor (Kanchanasaka 2001).

Camera trapping has been perceived as a non-intrusive "hands-off" method of direct observation (Rowcliffe et al. 2008; Adamič and Smole 2011). However, evidence is emerging that challenges this assumption: camera-trap shyness has been exhibited by tiger *Panthera tigris* (Wegge et al. 2004) and a startle reflex has been observed in the grey wolf *Canis lupus* (Gibeau and McTavish 2009). Behavioural responses to camera-traps vary between species, and between individuals within species (Meek et al. 2016).

Suggested sources of disturbance include the deposition of scent from ecologists undertaking maintenance visits (Munoz et al. 2014) and also noise (mechanical and ultrasonic) and infra-red illumination emitted by the camera-traps (Meek et al. 2014b). Potential bias from observation-effects should also therefore be considered in camera-trap studies.

Camera trapping is time-efficient in the field but analysis time can be onerous due to capture of non-target species and superfluous triggering caused by extraneous stimuli. In conservation and research, resources are inevitably limited; considering methodology efficiencies is important in terms of resources saved against any impact on data quantity or quality.

When deploying camera-traps at den sites, key considerations therefore include: (A) potential bias from disturbance, (B) the optimal number and placement of camera-traps, (C) study duration, and (D) the optimal camera-trap settings (e.g. clip duration, hours of operation/duty time). This study presents an empirical approach to address these using a six-year study of the holt of a semi-aquatic mammal, Eurasian otter *Lutra lutra*.

Firstly (A), I investigate any effect on otter activity levels caused by regular visits by the two researchers to maintain the camera-traps. I hypothesise that if researcher visits caused disturbance to otters using the holt, a positive relationship between frequency of resting or scent-marking behaviours and number of days elapsed since the maintenance visit would be expected.

Secondly (B), I investigate how the position of a camera-trap in relation to the recording area can affect the amount and type of data recorded. I hypothesise that data gain would improve using dual camera-traps compared with one camera-trap and that camera-trap position relative to the holt would affect both the probability of capturing an event and also the ability to record more specific observations such as sex and behaviour.

Thirdly (C), I investigate optimisation of study duration by quantifying the minimum number of days camera-traps would need to be employed to observe specific activity types which would contribute to defining the Minimum Survey Duration (MSD).

Finally (D), I examine whether camera-trap settings could be informed by an analysis of optimal video clip duration, and of duty time (time during the daily cycle when camera-traps are armed) in relation to parameters which would be commonly recorded.

Our approach provides a framework whereby camera-trap studies in other locations or for other species could be optimised from the analysis of pilot study data. While I do not aim to define specific deployment and programming criteria for otter holt camera-trap studies, our results provide a comparison to be used by other studies.

3.3 Methods

3.3.1 Study species and context

The Eurasian otter, (hereafter “otter”), is on Annex IV of the Habitats Directive (Council Directive 92/43/ECC) which affords it strict protection. Article 12 of the Directive frames protection in terms of the species’ wider habitat and also in relation to a species’ breeding and resting sites. With wide-ranging species such as otter, the actual place of rest is considered protected (EU 2007) and the Directive states that such sites must be “clearly perceptible” or “perfectly known and identified as such” (European Commission 1992). It is therefore important that breeding and resting sites can reliably be identified for the purpose of Environmental Impact Assessment and derogation licensing. Camera-traps have been used to confirm the use of structures as dens for other species such as the Asiatic black bear *Ursus thibetanus gedrosianusas* (Fahimi et al. 2011) as well as examining circadian activity of neotropical otter *Lontra longicaudis* at holts (Rheingantz et al. 2016). For species with unpredictable denning and breeding habits such as otter, camera-trapping offers an accessible monitoring method to complement traditional field-evidence surveys.

3.3.2 Study Holt

The study holt is in southern Scotland at a latitude of 56° 6′ 26″ N and is at an altitude of 125 m AMSL. The holt is adjacent to a small watercourse 3 - 4 m across in a secluded and undisturbed valley with near-continuous cover from scrub and thickets of bracken *Pteridium aquilinum.* It is 600 m downstream from a eutrophic loch, formerly a mixed fishery which is still fished informally and used for dog walking. Therefore, the holt and its immediate environs are undisturbed, but recreational disturbance is present around prey-rich habitat relatively close by. The holt is approximately 20 m from water and did not flood during the study period. The structure is a partially blocked drift mine with a tunnel (cross-section approximately 34 cm high and 140 cm wide) in rock which narrows and divides into two smaller tunnels after approximately 6 m.

3.3.3 Sampling period and summary of holt use

The study was undertaken between December 2009 and September 2015. Of the 2,120 potential camera trap days, cameras were operative on 1,720 (81%). A large gap in recording in 2011 was due to stolen camera-traps; to avoid further loss of equipment, monitoring ceased for approximately six months which also gave time to install more secure housing. Other gaps were due to battery depletion and delays in procuring replacement of defunct units. Maintenance visits during periods of continuous monitoring were on average every 15.2 (± SD 6.6) days, with approximately 15 min at the study site per visit. The same two researchers shared the maintenance visits throughout the study period; usually just one researcher attended at each visit according to availability. Researcher visits avoided peak activity times of dawn and dusk.

The holt was assigned one of a set of mutually exclusive functions (pre-natal, natal, early rearing, mid rearing, late rearing and non-breeding) according to the status and/or absence of a breeding female (Figure 3-1). The natal period, before emergence of the cubs, was taken as the 10 weeks preceding the first record of small cubs (Durbin 1996a; Kruuk 2006a) provided that there had been near-daily activity of adult otter recorded for at least 8 weeks. The early rearing period was defined as 60 days following the first day of emergence, mid rearing as 60 days following the end of early rearing and late rearing as 60 days following the end of mid rearing. At the end of the late rearing period the cubs would be at least eight months old, difficult to distinguish from the adult female and approaching dispersal (Jenkins 1980; Kruuk 2006a). The prenatal period was defined as 30 days before the estimated birth date, which is approximately the second half of the 63 day gestation period (Roos et al. 2015). Atypical activity was recorded during the single pre-natal period recorded (Nov-Dec 2011) when a female, a sub-adult male thought to be her cub from the last litter, and an adult male frequently rested in the holt as single otters, dyads or triads. Non-breeding was defined as none of the above. There was a minimum of two different breeding females during the study period: for the first two winters the holt was used for birthing (natal), possibly by the same female, subsequently in the winters of 2011-12, 2012-13 and 2013-14 a female with a distinctive broken/malformed tail used the holt for rearing but not birthing.

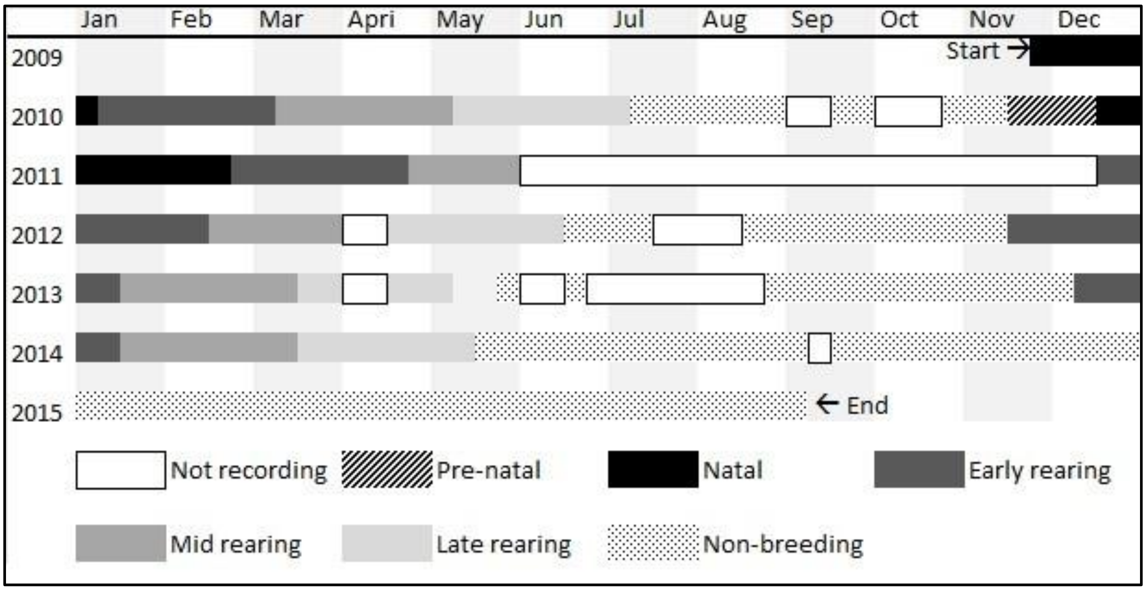


Figure 3-1 Timeline of holt function as defined by the status of the breeding female throughout study period (November 2009 – September 2015) and times when camera traps were not recording. Holt function is defined in the text

3.3.4 *Camera trap deployment and set up*

Over the study, two camera-trap positions were used, “close” and “distant” (Figure 3-2). The topography around the holt entrance was irregular and there were two clear otter runs into the holt. Tall summer vegetation and potential theft of the camera-traps had to be considered. A close camera-trap was positioned at 1.6 m from the centre of the holt entrance to enable the complete width of the holt to be in the field-of-view, and for the centra of the holt entrance to be at the centre of the field-of-view. The camera-trap was at a height of 40cm and tilted slightly downwards to reduce the blind spot immediately below. The distant position was 4.2m from the holt and was slightly elevated to avoid conflict with the runs and to gain camouflage from a rose bush. This was set at 30cm height to overcome vegetation and again was aimed to capture both of the otter runs and also the holt entrance which necessitated a slight downwards tile of the camera-trap. No bait or lure was used at any time.

The time-scale of the study resulted in two different camera-trap models being used which had different programming capabilities. Initially, a Moultrie I40 was deployed in the close position in December 2009. This model had an IR frequency < 850nm and was programmed to record the maximum length of video possible (5 s) with the minimum programmable rearm time between videos of 1 min. A second camera-trap was added in November 2010 in the distant position to create the dual camera-trap deployment. The second camera-trap was a Uway Night Trakker 50B (IR frequency 950nm). This had better programming flexibility and so was set to record videos of 30s with the minimum of 6s to re-arm between videos. The close camera-trap was replaced by a Uway in February 2011. The sensitivity of the PIR detector could not be altered on the Moultrie I40 or the Uway NT50b.

The holt was in a linear hollow which limited the extent of the detection and recording areas and also naturally contained otter activity.

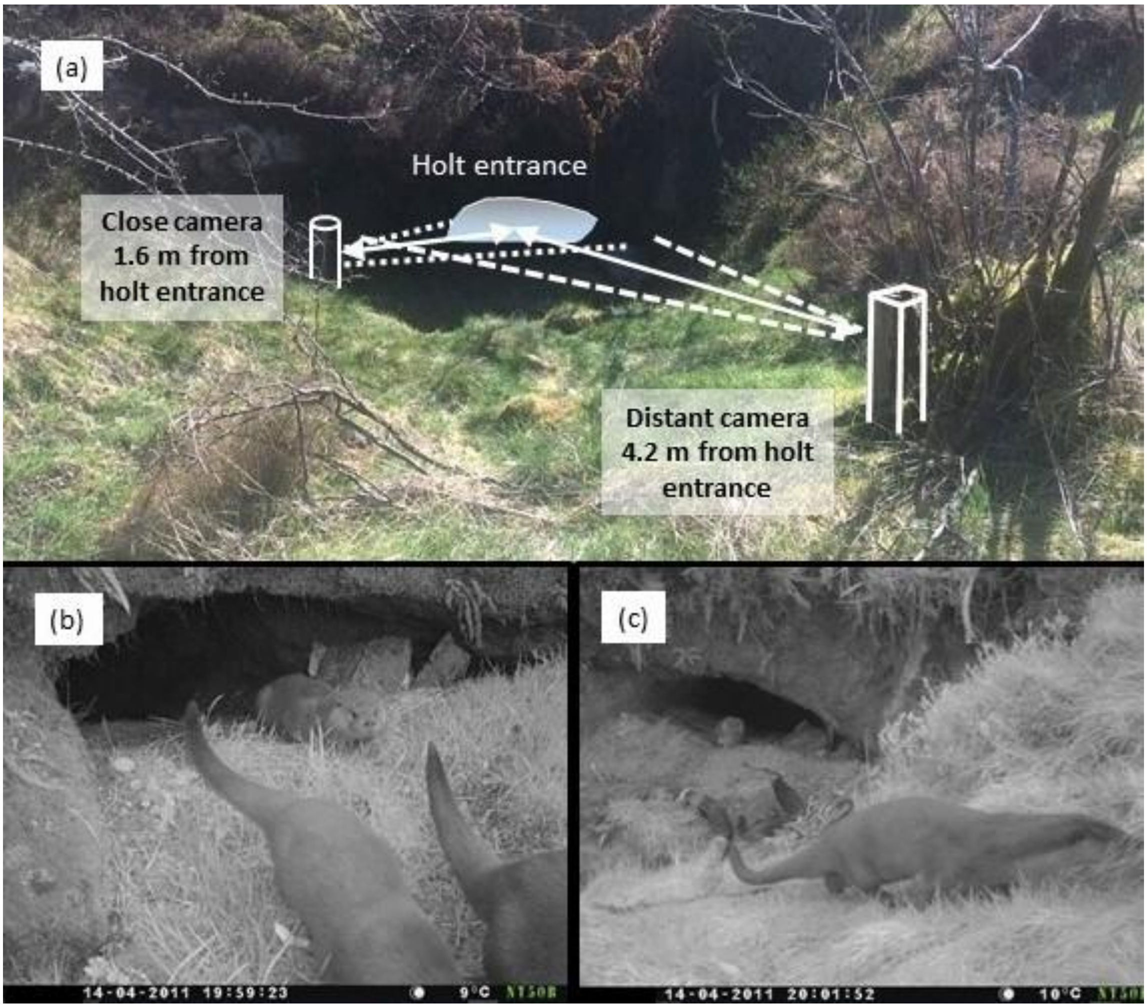


Figure 3-2 Diagram illustrating camera-trap positions and approximate fields of view: (a) Camera-traps were deployed in a modified plastic drain pipe (close camera) and wooden housing (distant camera) which emulated an old fence post for camouflage. The height and angle of the camera-traps were consequently consistent each time they were reset; (b) field-of-view of close camera-trap; (c) field-of-view of distant camera-trap

3.3.5 Filtering videos and extraction of data

The date, time (GMT), number of otters and movement in or out of the holt were recorded, as was sex where possible. Sex was identified using primary characteristics (presence of scrotum, presence of nipples, source and direction of urine stream) and/or secondary characteristics (size and body shape). Selected behaviours including scent-marking (spraint and urine), vocalisation, play, grooming, loafing and bedding collection were recorded. Video clips from both cameras were cross referenced using the date and time to compile a database of “events”. An event was 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. The event record contained the combined data gained from both camera traps.

Time spent in the holt was calculated where an otter was observed both entering and leaving, termed a ‘paired event’. On occasions, a group of otters would use the holt but entered and exited individually at different times. In such cases, the time in the holt of individual otters could not be tracked and the minimum time spent in the holt was calculated from the last entry time to the first exit time (such occurrences accounted for 7% [36/492] of paired events). A bimodal frequency distribution of time spent in the holt indicated two natural categories of rest type: “visits” of 15 min or less (n=305), or “rests” of greater than 15 min (n=492) (Figure 3-3).

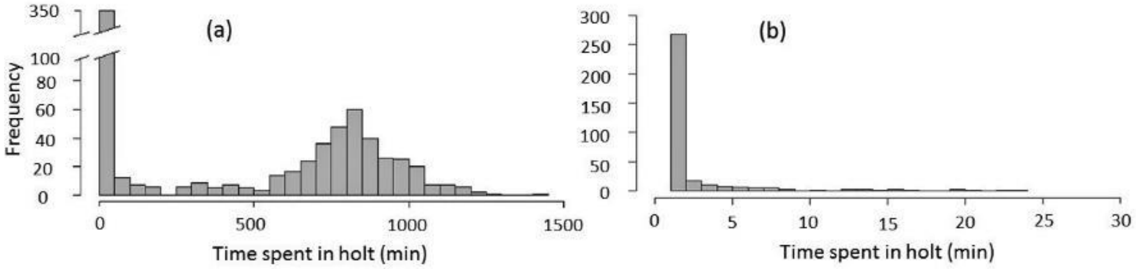


Figure 3-3 Frequency distributions of time spent in holt for paired events; (a) bimodal distribution of time spent in holt (n = 797), and (b) detail of the distribution in the first 30 min only (n = 425)

Thermal imaging has shown that wet otters can have a limited heat footprint due to their highly insulating fur (Kuhn and Meyer 2009). Single events of an otter exiting the holt at dusk with a dry coat without a corresponding record of it entering the holt were attributed to detection failure of the camera-traps of a wet otter upon entry. These events were excluded from the analysis of time spent in the holt but were included as a rest in further analysis (17% of all rests) since it was assumed that to become dry the otter would have to have been in the holt for at least 15 min.

3.3.6 Analysis

Statistics were carried out in R version 3.2.2 (RCore Team 2015) within R Studio (RStudioTeam 2015). Fitting of generalised linear mixed models used packages lme4 (Bates et al. 2015). A function to calculate sunrise and sunset was written using the packages rgeos (Bivand and Rundel 2016) and maptools (Bivand and Lewin-Koh 2016). I used the manipulate package (Allaire 2014) to fit the first apparent in frame models and the package lubridate (Grolemund and Hadley 2011) to facilitate use of dates and times.

3.3.6.1 A. Potential bias from disturbance

If otter activity was influenced by the researchers' camera-trap maintenance visits, there would be a relationship between key otter behaviours such as resting and scent-marking and the number of days elapsed since a researcher visit. Additionally, it was hypothesised that propensity to disturbance might be influenced by the current function of the holt and that any disturbance would potentially be greatest during the natal and early rearing periods when cubs were small. Thus, generalised linear models (GLM) with binomial error distributions were constructed with the probability of rests (i.e. > 15 minutes in duration) occurring on any day as the binary response variable (1 = rest occurred, 0 = no rest occurred). The date of the rest was recorded as the date of entry to the holt.

Three explanatory variables, were generated: (i) a binary variable indicating the holt function at the time of that rest as either 'breeding' (pre-natal, natal, and early, mid and late rearing) or 'non-breeding', (ii) a binary variable indicating the holt function at the time of that rest as either 'natal or early breeding' or 'all other functions' (non-breeding, pre-natal, mid and late rearing), and (iii) a continuous variable indicating the number of days elapsed between the last researcher visit and the rest (the date of the rest was recorded as the date of entry to the holt). I then tested two models: one containing the interaction between (i) and (iii), and one containing the interaction between (ii) and (iii). For each model if no interaction was found, the interaction was removed and the main effects were tested.

I used a likelihood ratio test with the X^2 distribution to compare models with and without the interaction term. If the test was not significant, I removed the interaction terms and tested the main effects within the non-interactive model.

Similarly, any relationships between the frequency of scent-marking at the holt and days elapsed since maintenance visit were tested for; the response variable described whether scent-marking was detected on a particular day (1 = yes, 0 = no). Season was also included as a categorical explanatory variable (four levels: spring, summer, autumn, winter) as sprainting on land has been shown to be affected by season (Yoxon and Yoxon 2014). I tested whether the probability of scent-marking was related to an interaction between season and days elapsed since researcher visit. Again, I used a likelihood ratio test with the X^2 distribution to compare models with and without the interaction term, and then tested the main effects in the non-interactive model if the test was not significant.

3.3.6.2 B. The optimal number and placement of camera-traps

The probabilities of data capture by each of the individual camera-traps were compared with the combined data gained from both camera-traps. The dual camera-trap setup would always capture at least as much data as a scenario where only one of the camera-traps was operational. Thus, I could examine the efficiency of each camera-trap position relative to each other and relative to the dual setup as a baseline, although not relative to perfect detection. This analysis can be conceptualised as the hypothetical removal of each camera in turn to retrospectively examine what the impact on our data would have been had I only had either the close or distant camera in place, thus comparing both cameras to the dual setup, and both cameras to each other. I examined the relative performance of both camera locations using three criteria: (i) count of otters, (ii) detection of sex of adult otter using primary characteristics (note that in the sample there were no events including more than one adult), and (iii) detection of selected behaviours (Table 3-1). Behaviour was recorded as the count of different behaviours observed; this was applied to both single otters and groups.

Table 3-1 Descriptions of behaviour categories

Behaviour category	Description
Vocalisation	A variety of calls emitted, ranging from a hiss to a short whistle.
Play	Observed in cubs and young otters especially between siblings but occasionally by single otters. Includes practice and development of any skills, common examples include fighting, climbing up rock face behind holt and bedding collection (i.e. pulling at vegetation)
Scent marking	Deposition of a small amount of faecal matter or urination
Bedding collection	A full capture would be an otter exiting the holt and tearing up vegetation with its mouth and returning to holt carrying bedding in mouth. This behaviour is normally undertaken at run with the otters head held characteristically high. Bedding collection is often recorded over several video clips, comprising otter running out of holt and leaving field of view, sound of rustling vegetation and otter running into holt with bedding. The otter may do this just once, or numerous times in succession.
Groom/roll	Otter licking fur and/or extended periods of scratching or lies down and rolls on back or rubs torso on ground
Loafing	Otter lying down, stretched out on back or on stomach and with little to no movement. In a relaxed state, occasionally shutting eyes

A random sub-sample of 200 events was selected when both Uway camera-traps were in operation (i.e. post February 2011). These criteria required me to carefully watch footage, often repeatedly, so from the large total of 2301 events, I randomly subsampled 200 (9%) events to provide a representative sample. Each event was given a numerical categorical identifier. Microsoft Excel was used to generate random numbers and events were selected using these numerical identifiers. Where the event was paired, the individual pass (in or out of the holt) was randomly selected by flipping a coin. The analysis included instances when one camera-trap failed to trigger, or one camera-trap triggered but did not record otter. For each pass of otter the selected criteria (count, detection of sex using primary characteristics, behaviours) were recorded for each camera-trap.

Generalised linear mixed models (GLMM) with binomial error distributions were constructed to investigate effects of camera-trap position and group size on the probability of capturing these three criteria. I hypothesised that the relative efficiency of each position could interact with group size, because a large group size may be a greater trigger stimulus than a single otter and therefore may increase detectability over longer distances. The categorical identifier was always included as a random effect to account for non-independence of the two camera-positions within each event. As competing models were nested, I used backwards stepwise selection to select the best model (Crawley 2005, pp. 104–105). This approach starts with the most complex model and compares it against a model with one less term. I used a likelihood ratio test with the X^2 distribution to compare models with and without the interaction term. If the test was not significant, I removed the interaction terms and tested a model just containing the main effects.

The first model used probability of detecting an otter as the response variable. The measure of success for each camera-trap in detecting an otter was represented by a dual vector comprising the number of otters seen on the single camera-trap (binomial numerator), and the number observed by the dual camera-traps (binomial denominator).

A second GLMM was constructed using the ability to determine sex as the response variable (1 = sex identified, 0 = sex not identified). Finally, this was repeated using observation of behaviour as a response variable, represented by a dual vector of the numbers of behaviours observed on a single camera-trap (binomial numerator) and the number of behaviours observed on the dual camera-trap system (binomial denominator). Again, an interaction between camera-trap position and number of otters on the dual system was tested for, and if this was not significant the interaction term was removed to test the significance of the main effects within the non-interactive model.

Within the subsample of 200 random passes, redundancy of the two camera-traps positions in the dual camera setup was assessed for each pass by determining whether a particular data type was recorded by (a) both camera-traps, (b) only the close camera-trap or (c) only the distant camera-trap. The higher the percentage of events that fall into (a), the more redundancy there is in the dual camera set-up. The data types considered were (i) presence of otter(s) (yes/no); (ii) count of otters; (iii) observation of behaviour (yes/no); and, (iv) determination of sex (yes/no). For (ii) I took the count as the minimum number of otters seen on the dual camera-trap setup.

3.3.6.3 C. Study duration

Given the status of otter as a European Protected Species (European Commission 1992), there is a requirement to ascertain whether or not a structure is used for resting but there are no explicit criteria for identifying an otter resting-site. Based on the distribution of duration of time spent at the holt three hierarchical categories of otter use of the holt per study day were generated: absence of otter, any presence of otter (all registrations), and a rest by an otter (a stay within the holt of > 15 minutes). The last two categories broadly align with two potential aims of a camera-trap study at a holt (i.e. either to (a) simply determine presence of otter at a site, or (b) to determine whether a site can be defined as a 'resting site'). The number of days between a specified event type (i.e. presence, or rest) would inform the minimum study duration required for that specific aim.

For each period of holt function (Figure 3-1) the intervals (days) between consecutive instances of the same activity-type (presence or rest) were calculated. If the interval spanned more than one holt function, such as the last rest in the early rearing period of 2010 to the first rest in the early rearing period of 2011, then it was excluded.

A generalised linear model (GLM) was used as the response variable comprised count data, so a GLM with Poisson error distributions was constructed with the number of days between successive visits as the response variable, and holt function as the explanatory variable. Over dispersion was tested using the Ben Bolker function and if over-dispersed an alternative error distribution would be tried e.g. quasi-poisson. I repeated this using the number of days between successive otter rests as the response variable. A likelihood ratio test with a X^2 distribution was used to assess model significance.

I calculated the 90th and 95th percentiles of intervals between events (separately for presence and rests) as a contributor to minimum survey duration which represents a 90-95% probability I would record one of each activity-type if our study was at least that long. Because holt function significantly influenced the intervals between events for both presence and rests, I calculated separate percentiles for each holt function (natal, early rearing, mid rearing, late rearing and non-breeding).

3.3.6.4 D. The optimal camera-trap settings: clip duration and duty time

Setting a camera-trap to record longer video clips may increase data gain, but results in greater battery depletion and memory storage each time a camera triggers (often by non-target species or false-triggers), as well as longer time required to review the clips. Thus selection of the duration of video clips represents a trade-off that ecologists have to make for each study. Reducing clip duration without losing significant data has the potential to increase efficiency of camera-trapping studies.

I specified a set of three observable criteria that ecologists are likely to record using camera-trap footage: (1) determining sex of an otter using primary sexual characteristics only or (2) both primary and secondary sexual characteristics (primary characteristics plus body-shape), and (3) scent-marking activity (sprainting, urination). Using events recorded by the dual camera-trap set up with two Uway camera-traps I extracted all events containing the desired criteria (scent-marking n = 274, primary sexual characteristics n = 373, primary and secondary sexual characteristics n = 171). Some otters in this study had characteristic tail abnormalities which identified them as individuals. To avoid bias from individuals being recognised and influencing observations of sex, these were omitted from the subsampling for observation of primary sexual characteristics (reduction of n = 373 to 123). Excluding the period when the Moultrie camera-trap was operating, I randomly selected and rewatched 60 events from each subset to provide a representative sample. For each event, the data from either the close or distant camera-trap was randomly selected, as was the individual pass if it was a paired event (either going in or coming out of the holt). For each pass I observed a maximum of 30 s of video and recorded the time to the nearest second when each observable criteria was first apparent in frame (hereafter ‘FAF time’).

For each criteria, the FAF times were ranked in ascending order. The rank of each data point was then divided by the sample size for that criteria to form a cumulative proportion. The cumulative proportion (y-axis) was plotted against the FAF (x-axis) for each pass. To describe the asymptotic relationship that was apparent for each criteria, I fitted an exponential model of the form $y = a.(1\text{-}e^{-b.x}) + c$ where y is the predicted cumulative proportion of that observable criteria that would have been recorded given a hypothetical clip duration (s) of x, and a, b and c are parameters estimated by the model. There is a short delay between a subject triggering a PIR detector and the camera-trap initiating recording. A recorded FAF time of zero can actually represent a range of true FAF times within that delay range. As such, the plotted cumulative distributions appeared truncated at t = 0. To avoid truncation influencing model fit, values of FAF = 0 were excluded from the model.

The fitted models were used to predict the minimum clip duration that would be required to record 95% of passes containing each observable criteria since I considered that 5% data loss would be acceptable if it could result in a proportionally greater reduction in superfluous video, battery depletion or memory depletion.

Many camera-trap models have the ability for duty time to be programmed (i.e. daily periods of time when the camera-trap is active or inactive). They are prone to being triggered by precipitation, strong light conditions or vegetation moving in the wind (Swann et al. 2004), termed 'false-triggers'. Runs of false-triggers were experienced almost exclusively during the daytime depleting the limited supply of memory storage capacity and increasing analysis time. Efficiency in analysis time would be improved if false-triggers could be substantially reduced by the camera-trap being in 'sleep-mode' during some, or all of the day if it could be demonstrated that this would not lead to a significant loss of data. In describing mammal activity in relation to sunrise and sunset, four activity periods have been described (Lucherini et al. 2009); (a) day; (b) night; (c) dawn (one hour before sunrise to one hour after), and; (d) dusk (one hour before sunset to one hour after). Otters are predominantly nocturnal (Green et al. 1984) but they can be active during the day. For each otter registration, the times of the closest sunset and sunrise were back-calculated using the date and time in conjunction with the holt's latitude and longitude. The time of each registration was then compared to the time of the closest sunrise and sunset and assigned to whichever one it was closest to. I then plotted the distribution of hours relative to sunrise and sunset for each registration and calculated the proportion of registrations that occurred in the four activity periods (day, night, dawn, dusk). This was repeated for registrations within each holt function category.

3.4 Results

3.4.1 A. Potential bias from disturbance

The GLM which tested for any effect on the probability of a rest during periods when the holt function was breeding or non-breeding and days since maintenance found no significant interaction (X^2 = 1.16, df = 1, p = 0.281). When the interaction term was removed, there was no significant effect of holt function and days since maintenance check on the probability of a rest (X^2 = 0.859, df = 1, p = 0.354). Similarly, the GLM which defined the holt function as early breeding (natal and early rearing periods) or not early breeding, found no significant interaction between holt function and days elapsed since maintenance visit on the probability of use of the site for a rest (X^2 = 0.65, df = 1, p = 0.418). When the interaction term was removed, there was no significant effect of holt function and days since maintenance check on the probability of use of the site for a rest (X^2 = 0.22, df = 1, p = 0.637).

The GLM using the probability of scent-marking as the response variable found no significant interaction between the season and days elapsed since maintenance check (X^2 = 6.84, df = 3 p = 0.077). When the interaction term was removed, the probability of scent-marking on a given day was not significantly related to days elapsed since maintenance check (X^2 = 0.57, df = 1, p = 0.520).

3.4.2 B. The optimal number and placement of camera-traps

The GLMM investigating effects on the probability of detecting an otter found no significant interaction between camera-trap position and group size (X^2 = 0.04, df = 1, p = 0.852). When the interaction term was removed, the probability of detecting an otter was significantly related to camera-trap position and group size (X^2 = 25.86, df = 1, p <0.001) (Figure 3-4a). When investigating the effects on the probability of detecting the sex of an adult otter, no significant interaction was found between camera-trap position and group size (X^2 = 1.80, df = 1, p = 0.179). Removal of the interaction term resulted in a significant effect of camera-trap position and group size (X^2 = 21.96, df = 1, p <0.001) (Figure 3-4b). The GLMM investigating effects on the probability of observing behaviour found no interaction between group size and camera-trap position (X^2 = 0.52, df = 1, p = 0.469) and when the interaction term was removed, there was no significant difference from the camera-trap position and group size (X^2 = 0.04, df = 1, p = 0.842), however there was a significant effect of camera-trap position (X^2 = 28.07, df = 1, p <

0.001). The probability of the close camera-trap recording behaviours was 0.81 (± 0.04 SE) substantially greater than for the distant camera-trap (0.47 [± 0.08 SE]).

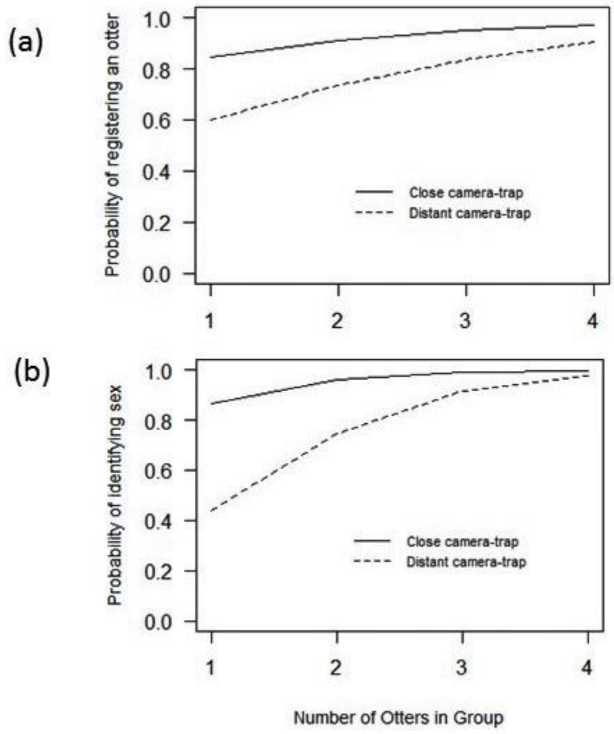


Figure 3-4 The probability of data capture was different between the two camera-trap positions when considering (a) the probability of detecting an otter; and (b) the ability to sex the adult otter

The close position substantially out-performed the distant camera-trap both in terms of registering presence, count of otters and facilitating the identification of otter sex (Figure 3-5) and also recording behaviour. There was the highest degree of redundancy between cameras when recording behaviours, when 91% of all events where behaviours were recorded by both cameras. However there was substantially less redundancy between cameras for presence (57%), count (48%) and sexing (52%).

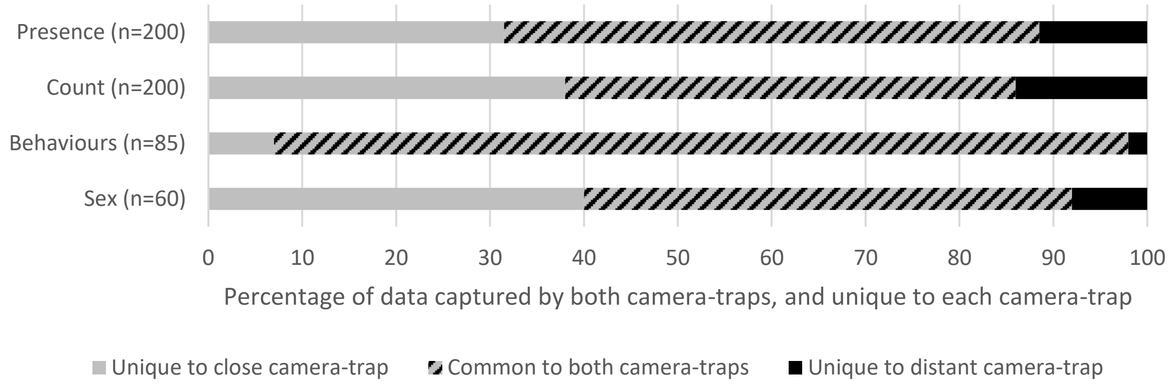


Figure 3-5 Comparison of the uniqueness of data capture between the two camera-trap positions in a random sample of 200 events. Pale grey indicates the proportion of events where only the close camera-trap recorded data in each category (Presence, Count, Behaviours, Sex) which was unique and black indicates the proportion of events where only the distant camera-trap recorded data in each category. The hatched area represents the proportion of events where both camera-traps recorded the same data in each category

3.4.3 C. Study duration

There was a significant effect of holt function on days between consecutive records of otter presence (X^2 = 195.35, df = 5, p < 0.001). There was also a significant effect of holt function on days between consecutive records of otter rest (X^2 = 158.47, df = 5, p < 0.001).

The number of days between consecutive records of otter presence at the holt increases with decreasing breeding status relative to the natal period (Figure 3-6), this is more pronounced with resting patterns than presence.

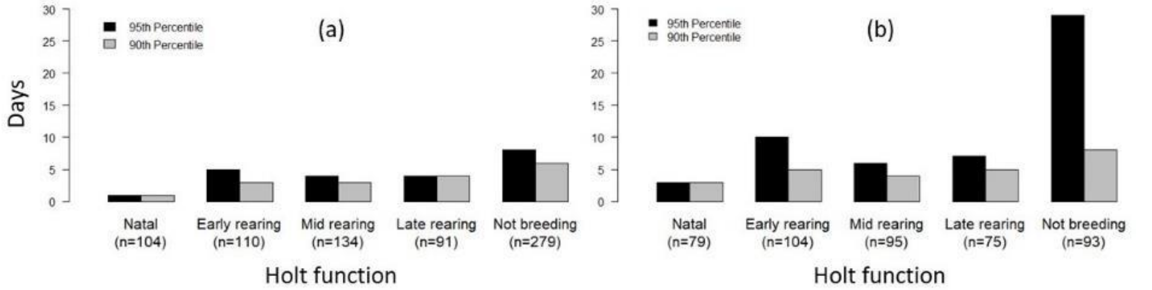


Figure 3-6 95% and 90% percentiles of intervals in days between consecutive rest types for each holt function excluding prenatal as sample was too small; (a) for presence of otter at holt and; (b) for a rest of over 15 min

3.4.4 D. Optimal camera-trap settings

3.4.4.1 Clip duration

The 95th percentile for sexing otters using primary characteristics only was 22s, for sexing otters using a combination of primary and secondary characteristics was 19s and for recording scent-marking behaviour was 24s(Figure 3-7).

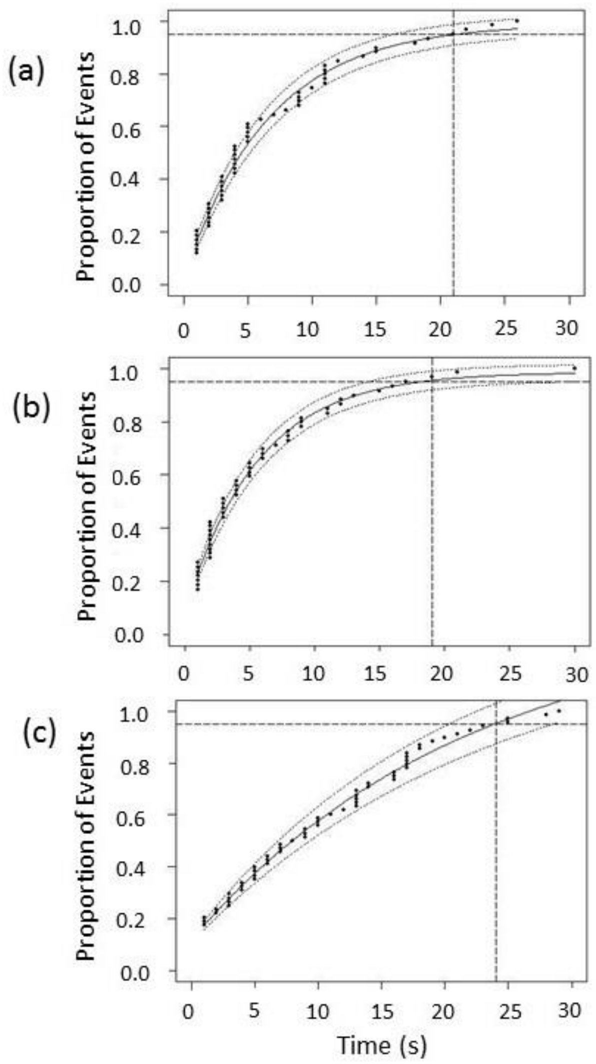


Figure 3-7 Minimum clip durations illustrating 95th percentile for three types of observation: (a) for sexing otters using primary characteristics only; (b) for sexing otters using a combination of primary and secondary characteristics and; (c) for recording scent-marking behaviour. (Solid line: fitted model, dotted lines: standard errors of the relationship, dashed lines: 95^{th} percentile readings)

3.4.4.2 Duty time

Frequency of registrations peaked approximately two hours before sunrise and two hours after sunset (Figure 3-8). Nocturnal activity accounted for 81% (n = 2,301) of all registrations. Inclusion of dawn and dusk periods increases the proportion of registrations to 89%. However, when the holt was functioning as a natal holt, 86% of registrations were nocturnal and 100% of registrations occurred in the nocturnal and dawn and dusk periods (i.e. there was no diurnal activity). There was a slight increase in diurnal activity during the early rearing period (nocturnal: 86%, nocturnal, dawn and dusk: 93%). Diurnal activity increased during late rearing and non-breeding status too (late rearing nocturnal: 64%, nocturnal, dawn and dusk: 81%; non-breeding nocturnal: 78%, nocturnal, dawn and dusk: 87%).

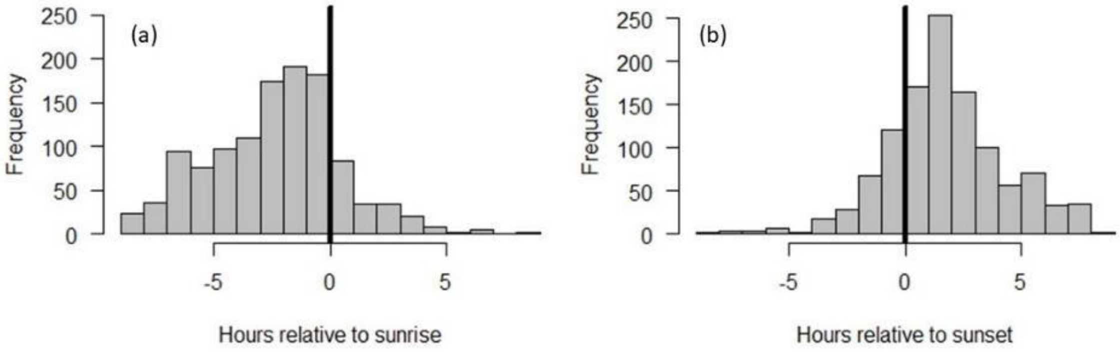


Figure 3-8 Histogams of otter registrations at the holt in relation to hours around; (a) sunrise and; (b) sunset. Each registration is included within a single histogram depending on whether it was closer to (a) sunrise or (b) sunset

3.5 Discussion

Before interpreting the results from any camera trap study, potential sources of observer bias must be considered. There are two primary potential causes of observer bias in our study arising from the fieldwork affecting the otters: (i) regular maintenance visits and (ii) any effect from the camera-traps themselves. I did not find any effect of maintenance visit on the probability of resting or scent-marking at the study site and this was unaffected by the breeding status of the holt.

The maintenance visits at the study site were, on average, two weeks apart and did not include scent masking, so the deposition of human scent at this interval does not appear to have affected otters’ use of the holt. There may be a threshold of shorter intervals between maintenance visits which would cause disturbance and affect patterns of activity, and future studies might be able to quantify this. Over such a long-term study, there may have been habituation to the visits which were by the same researchers throughout the study period. Additionally, the sleeping chambers of the holt are at least

6 m from the entrance so disturbance at the entrance to the tunnel may not be critical given the size and security of the structure.

As such, further investigation using different types of structure in areas of higher/lower ambient disturbance levels (e.g. urban vs. rural sites) may be required to assess impacts of disturbance and habituation. Behavioural reactions to the camera-traps were not quantified in this study, although no adverse reactions to the close camera-trap were observed on the distant camera-trap. Studies on predatory species found that animals could readily detect camera-traps (Meek et al. 2014b) with some nocturnal predators, such as felid species being particularly sensitive. Individuals of some species have been observed exhibiting adverse reactions such as backing away (Meek et al. 2016), and this could potentially affect detectability. However, neotropical otters continued to use holts after camera-traps were deployed facing the holts, and this was observed in both areas of the study (Rheingantz et al. 2016), also giant otter *Pteronura brasiliensis* were almost indifferent to camera-traps placed at the edge of latrine sites (Pickles et al. 2011) suggesting that this otter species may not be sensitive to camera-traps. For these reasons, the unaffected activity patterns may not necessarily be applicable at other sites, but the lack of any change in activity indicates that observer effect need not be considered in our subsequent analyses.

In addition to bias resulting from any effects of the equipment or maintenance visits on the otter’s activity, observer bias could also have arisen when watching and documenting videos. The number of species of mesocarnivore encountered was limited to five (otter, badger, mink, fox and pine marten). These could readily be told apart even on poor quality videos due to size, shape (especially tail shape and length) and vocalisations. Identification of sex was considered to have most risk of observer bias as size and proportions of the head and shoulders can be used to pick out male otters, criteria which are somewhat subjective in interpretation. To overcome this, the identification of sex was coupled with a second variable to indicate if the identification was based upon primary (i.e. immutable) characteristics such as presence of scrotum or nipples, or secondary characteristics which requires experience and expert judgement to assess body proportions (see section 3.3.5). Instances where the identification of sex was not possible were expected and allowed for in the data. If a similar study was undertaken with multiple people, then inter-observer reliability between observers could be tested using the Cohen's Kappa statistic (McCarthy et al. 2018).

Very poor detectability of otter by PIR triggered camera-traps led researchers to question whether such camera-traps are appropriate for semi-aquatic species and whether active triggers would be more effective (Lerone et al. 2015). Our study illustrates that PIR camera-traps can successfully be used to study otter (see also Rheingantz *et al.*, 2016), but differences in deployment can cause variation in detectability. In the comparison of data capture between the dual set up and individual camera-traps, the close position provided the most information, both in terms of detecting otter and the ability to identify sex. With perfect detection, I would have observed one otter entering the holt for every otter exiting the holt (i.e. every event would be paired), but this only occurred in 61% (1,610 of 2,639) of events where holt entry/emergence occurred. Single events were thought to be due to missed registrations either when the otter did not trigger the PIR, where the PIR was triggered but the otter was not recorded possibly if the otter was moving quickly, or if an otter passed during the time when the camera-trap re-armed between videos. The high proportion of missing passes and the poorer detectability of the distant camera-trap are notable, although probability of detection has previously been shown to be affected by distance (Rowcliffe et al. 2011; Howe et al. 2017). A greater source of bias would have been experienced if only the distant camera had been used; this large discrepancy suggests a cause for concern when management/derogation licensing decisions are made based on camera-trap monitoring.

Setting the distance between the camera-trap and the holt is a compromise. Increased distance gives a better overview of the den area and has a perceived, though not evidenced, potential reduction in disturbance, but has a negative effect on detection probability. The sensitivity of the target species to disturbance coupled with the individual characteristics of the den structure and the species' effects on detection therefore all need to be balanced and understood when setting camera-traps at den sites. Detection improved when family groups used the holt which indicates distance to the target may be more critical for solitary species than species living in a social group. A group of otters will present as a larger stimulus for PIR. This may have been a contributing factor in the success of other camera-trap studies of otter species which live in groups (Pickles et al. 2011; Day et al. 2016; Rheingantz et al. 2016) and the poor PIR detection reported for the Eurasian otter (Lerone et al. 2015) which is often solitary.

If a close camera-trap is deployed, the addition of a second camera-trap should offer significant data gain or have other tangible benefits to justify the capital cost and substantial increase in analysis time. In this case study, the distant camera-trap offered little extra gain of data (Figure 3-5) and its loss would have been acceptable in light of this and also its limitations as a back-up if the close camera-trap failed. However, a second camera-trap placed on the other side of the holt may have reduced the amount of missing passes.

False-triggers are a drain on power and memory storage. Duty time can be set on many models; a dormant camera-trap during the daytime for a nocturnal species would likely increase the longevity of a camera-trap in the field and reduce the likelihood of battery or memory depletion before maintenance visits. Otter activity at the holt was concentrated between one hour before dusk to one hour after sunrise, with 89% of all registrations occurring in this period and 100% of registrations when the holt was in the natal or early rearing phase. This conforms with studies on activity from radio telemetry where emergence occurred just after sunset and retirement was related to sunrise, but some diurnal activity was also recorded (Green et al. 1984). If duty times were set so that the camera-trap recorded from one hour before sunset and finished at one hour after sunrise, the loss of data (11%) in this study would have been considered acceptable in context with the considerable time it took to filter daytime footage and compile the events database, and likely would have reduced instances of battery or memory depletion. However, it has been suggested that resource partitioning may occur in areas of high density with single otters foraging in areas during the daytime and families of otter using the same area during the night (Jenkins 1980). It has also been demonstrated that the circadian activity of neotropical otter varies between regions (Rheingantz et al. 2016). Caution is therefore needed before restricting the duty time of camera-traps even for perceived nocturnal species without knowledge of the study population, and our approach could be used on a set of pilot data before setting any restrictions on recording.

The frequency of resting at the holt was significantly related to the holt function. To determine the current function of the holt, the minimum study duration should consider the number of days between desired events, such as rests, with an additional period of habituation likely to be determined by the type of structure. This study of a very busy and secure holt in rich habitat indicates a minimum of twenty-eight days to have a 95% probability of recording at least one rest regardless of holt function, which would be unlikely to be known when initiating a study. A period of habituation also needs to be factored in. A minimum of 28 days would have been long enough to detect a more significant function such as cub-rearing or birthing (natal) if the holt currently had that function. If the aim is to determine breeding, the monitoring should coincide with any known local breeding season, although this varies considerably across the species' geographic range: summer on Skye in Scotland (Yoxon and Yoxon 1990), spring in southern Sweden (Erlinge 1967), locality-specific seasons in the Mediterranean (Ruiz-Olmo et al. 2002) and aseasonal in England and Wales (Chadwick and Sherrard-Smith 2010). A female is unlikely to give birth more frequently than once per year giving a window of opportunity for recording natal behaviour of 9-10 weeks out of 52. Where no breeding season is known, sampling through the year would be required if determining the status of a structure is a requirement for Environmental Impact Assessment or other assessments, however fidelity to natal holts is not guaranteed leaving some residual uncertainty.

Long video clips will fill up memory space, drain batteries and increase analysis time. In the analyses for optimising clip duration, a survey simply for presence of otter would require the shortest clip duration, and it could be argued that still images would be more appropriate. To gain additional data such as identification of sex and recording scent-marking behaviour, a balance needs to be found between analysis time and data gain. If video clips had been reduced to 19 seconds (the 95th percentile of the FAF analysis) from 30, to facilitate sexing of otter using both primary and secondary characteristics, then this would proportionately have reduced memory storage by 35 - 40 % (11/30 s) and reduced power consumption, which would have the benefit of extending the number of days that the camera-trap could run untended. It would also have reduced video analysis time and so, on balance, the loss of the 5% of instances where the sex can be determined against the reduction of analysis time and greater field longevity of the camera-trap would have been an acceptable trade-off. The FAF approach could therefore be applied to optimise settings for specific data collection; a trial period would enable the most efficient video duration to be estimated.

3.5.1 Recommendations

The study holt was a well-used otter breeding structure in rich habitat, and so there are limitations to the generality of the findings across all possible otter structures that practitioners may monitor. However, these results do present some general considerations for camera-trapping otters and other species of semi-aquatic and terrestrial mammals, as well as presenting a framework whereby efficiency and efficacy of camera-trapping can be investigated and improved via the analyses of prior data collected. At den sites, I recommend analyses to assess any observer effect. If more than one camera-trap is used on the same target area, the effect of distance on detectability should be considered, which could result in two close camera-traps. However, data redundancy should be evaluated, and a high level of redundancy may indicate that one camera-trap could be removed or could be run as a back-up. Any local variation in activity should be taken into account when determining duty time and minimum survey duration; factors such as breeding status should also be considered. An adaptive approach, whereby data is evaluated in the early stages of a study and appropriate modifications made to study design, could improve both data quality and use of resources.

There are many potential biases within camera-trapping studies and further research is required to understand how environmental, spatial and animal-based factors interact to influence the detection probability of animals to camera-traps. These may vary between taxa or functional groups (e.g. semi-aquatic versus terrestrial mammal species), between solitary and social species and between habitats or environments, and so a one-size fits all approach is unlikely to be appropriate.

Chapter 4 Camera-traps as a tool to identify resting sites: a catchment scale study

4.1 Abstract

Camera-traps are a potential tool to identify otter resting sites. This study aims to contribute to an evidence-based method so this potential can be realised. Twenty-six structures indicated to be otter resting sites from field-signs (i.e. spraints, footprints etc.) were identified across the River Tweed catchment in southern Scotland. Each of these structures was monitored using camera-traps for approximately a year. From the camera-trap videos collected, patterns of resting and behaviour associated with resting were identified. Rests, where an otter spent at least 15min in the structure, were observed at six sites. There was a strong seasonal bias in rest events at these six sites; at least 95% of rests occurred in winter and spring and all structures were repeatedly used within each winter-spring period and in successive winter-spring periods. All six structures were used for nocturnal and diurnal rests and by single and groups of otter. Latrine behaviour and bedding collection were found to be good behavioural indicators of resting. Simulations of the data found that two sampling periods of 35 days each, one period in winter and one period in spring (i.e. a total of 70 days) would have had a 95% or greater probability of detecting a rest at all sites. This was more efficient than a single camera-trapping period which would have required 108 days to achieve the same outcome. This study indicates that camera-traps are an effective tool for identifying otter resting sites. Activity patterns, specifically the duration of time an otter spends in a structure, and behavioural indicators can be used to identify resting sites. The study found that survey effort could be refined by targeting the seasons when resting is most likely to occur at structures, and the sampling effort found in this study can be used as a guide for further studies.

4.2 Introduction

The strict protection of otter necessitates the protection of individual places where otters rest (see Section 1.1.4.1). Radiotracking studies which sampled daily positions, found that approximately a third of resting sites were used once during the radio-tracking contact time. “Resting sites” is the generic term encompassing all sites where an otter is inactive, including the term holt which is specific to enclosed structures used for resting such as burrows, or couches which are unenclosed areas used for resting such as in dense vegetation. One study followed three animals for 22, 36 and 98 days in Perthshire, Scotland (Green et al. 1984) and the other followed four animals for 47, 54, 56 and 187 days (Isabel and Freire 2011). There would be negligible probability of finding and/or identifying such infrequently used sites without radiotracking (i.e. using field-signs). The Habitat Regulations extends the protection of resting places to periods when they are unoccupied. This is clarified by EU guidance which states that the ecological functionality of resting and breeding places of otter and all other European Protected Species should be maintained with the condition that there is “*a reasonably high probability that the species concerned will return to these sites and places*” (EU 2007, p. 41). Therefore, the focus for consultants’ surveys is to identify the sites where there is habitual use.

To identify a resting site solely from CT observations at a site, an expectation of activity types and patterns is required for context. Radiotracking studies detect an animal’s spatial positions, so resting is deduced when the animal is stationary, particularly during the daytime (Green et al. 1984; Isabel and Freire 2011). As CTs do not monitor the otter itself when it is resting out of view in an enclosed structure, a different approach to defining a rest is necessary, such as a threshold of time the otter spends within the structure. Resting must therefore be ascertained from activity patterns at a site. However, it is possible that certain behaviours may also be so strongly associated with resting that they could be diagnostic; these may be identifiable using CTs.

Radio-tracking studies have examined aspects of resting site selection and use (Rosoux and Libois 1996; Isabel and Freire 2011; Weinberger et al. 2019). The findings of these studies are mainly framed in term of spatial movements. Green et al. (1984) found that otters rarely change resting sites during the daytime, and this has been corroborated

(Rosoux and Libois 1996). Green et al. (1984) also found that otters are active in bursts through the night, with intervening rests. Locating resting sites at night using radio telemetry can lead to disturbance (Isabel and Freire 2011), and studies on resting sites therefore focus on diurnal sites (Weinberger et al. 2019). The use of holts for resting was found to be more frequent than couches in the seasons when vegetation is at a minimum, possibly due to a lack of visual cover as this was observed more in areas which had higher disturbance (Weinberger et al. 2019).

Some studies in the UK suggest a seasonal bias in otter births, peaks were found in early winter to spring on the Severn catchment (Mason and Macdonald 1987a) and also in Perthshire (Green et al. 1984). Radio-tracking studies also infer that females rear their young in small, calm watercourses, and use smaller core ranges (Green et al. 1984; Ruiz-Olmo et al. 2007). Winter-spring breeding with its associated reduction in range of the female and cubs, and selection of smaller watercourses, suggest that activity on smaller watercourses would be greater within the winter-spring period.

There is little information on whether resting sites are shared by adult otters, either at the same time or at different times. The CT footage for the long-term study site showed an adult male, a sub-adult male, breeding female and two cubs simultaneously resting in the holt structure several times. Female otters are assumed to rest with their cubs at least when the cubs are young so sharing of a resting site by a female and dependant cubs would be expected as a minimum. A radiotracking study in Portugal (Quaglietta et al. 2014) followed 16 otters to investigate socio-spatial organisation. In the animals that they were tracking, they found a significantly greater number of otters resting together simultaneously than predicted. They also found additional instances of simultaneous shared resting of tagged and untagged animals. These simultaneous shared rests were in an area where there was an abundance of resting sites, suggesting that the behaviour was by choice.

Ideally, any observations relating to resting activity or resting behaviour could be used as diagnostic indicators to distinguish between sites used for resting, and those which are not. However, in order to reject a site being a resting site, there needs to be a sampling protocol which gives an acceptable level of certainty that those indicators would be recorded during the sampling period if the site is a resting site.

4.2.1 Aims and objectives

The overarching aim of this chapter is to provide an initial analysis of seasonal and diurnal otter activity that can be used to inform camera-trapping protocols of otter resting sites. I analyse resting and non-resting activity recorded on camera-traps from 26 structures which have potential as otter resting sites across the River Tweed catchment in the UK.

I hypothesise that there will be patterns in resting events, specifically that (i) nocturnal rests will be shorter than diurnal rests; otter is a nocturnal species and likely to spend most of the dark hours foraging, with short rests, (ii) there will be a difference in resting duration between groups of otters and single otters due to different energy needs, and (iii) there will be more use of structures for resting in winter due to a greater need for shelter.

I hypothesise that there will be more otter activity on smaller watercourses in winter and spring than summer and autumn due to winter and spring peaks in breeding, and preference of smaller watercourses for cub rearing.

As there are no guidelines on camera-trapping survey effort to determine a resting site, I aim to calculate the minimum duration of camera-trap days required to detect a resting event with a reasonable level of certainty, and to identify any behavioural indicators of a resting site.

4.3 Methods

4.3.1 Study catchment

The River Tweed catchment spans the Scottish Borders in the south of Scotland and North Northumberland in England. Its headwaters rise in the Lowther Hills in Peebleshire, the highest point in the catchment being at 850m AMSL; it flows generally eastwards into the North Sea at Berwick-upon-Tweed. The catchment is approximately 4,335km^2 (SEPA 2015) and has a variety of river types from small, oligotrophic tributaries in the upper catchment, to the eutrophic reaches of the lower Tweed. The whole river and its tributaries are designated as a Special Area of Conservation (SAC) under the Habitats Regulations (see Section 1.1.4.1) which is the highest level of protection afforded to a site in the UK. Otter is one of the qualifying interests of the River Tweed SAC. For SACs, there is a duty to report to Europe on the populations of qualifying species every six year. The last assessment for otter was in 2011, and it was judged to be in Favourable Conservation Status (Scottish Government 2020).

4.3.2 Spatial arrangement of study sites

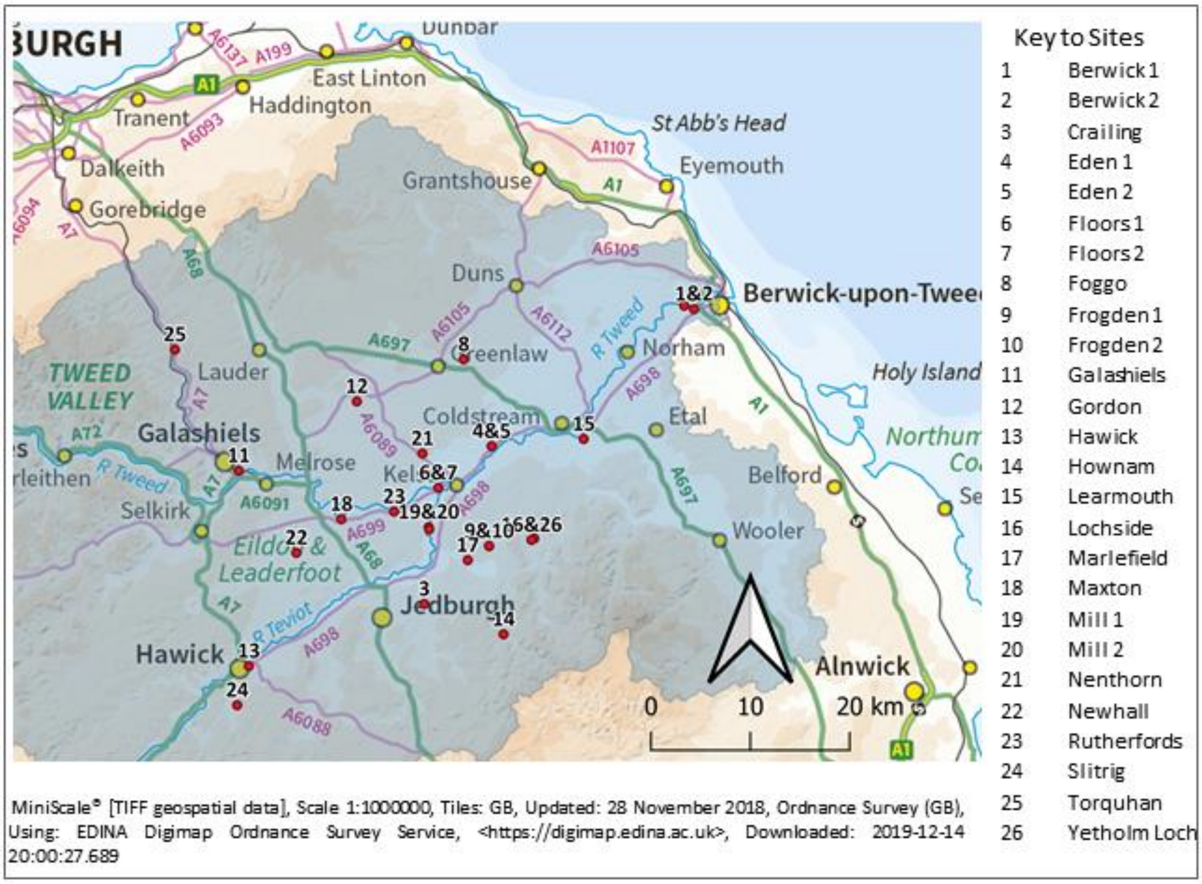
Individual monitoring sites in this study were spatially arranged for independence of data such that sites running concurrently were likely to be in different home-ranges. The minimum distance between sites being monitored at the same time (i.e. concurrently) was based on the approximate size of a females' range, according to common practice (Ferdia et al. 2011), although sites could be closer together if non-concurrent. Ranging data from radio-tracking studies (Table 4-1,) was used as a guide to variation in home-range size. Spatial independence of study sites was based upon a minimum of 20 km via watercourses in oligotrophic systems (i.e. low nutrient status) and 8 km between sites in mesotrophic (i.e. medium nutrient status) or eutrophic systems (i.e. high nutrient status). Green *et al*. (1984) noted that range boundaries were often at confluences or other prominent features, so major confluences were therefore considered as offering likely separation of home ranges. Where potential monitoring sites were found in proximity (i.e. likely to be within the same home-range), the sites were included but were monitored in different years. Since the study design, a more recent radio-tracking study in Southern Portugal found a mean female home-range of 11.2km (n = 5) (Quaglietta et al. 2015) which is within the range of those in earlier studies cited in Table 4-1.

Table 4-1 Size of otter ranges from radio tracking data. Sizes are given in km units as otters have approximately linear ranges

Source	Sex	Total range	Region and Habitat	Notes
Green et al. 1984	Female	16km 22km	River Earn (upper Tay catchment), Scotland. Oligotrophic river system	Female range unrelated to river width
	Male	39km		
Durbin 1996b	Female	24km	River Don, Scotland. Oligotrophic river system	
	Male	50km 84km		
Néill et al. 2009	Female	7.5km (SD1.5km) n=7	Ireland. Mesotrophic river system	Female home range inversely related to river width in rivers less than 15m wide.
	Male	7—19km n=5		
Georgiev 2007	Female	8.5km of linear watercourse, 2.2km of water body	Bulgaria. Mostly through field systems and including an area of canal so likely to be mesotrophic.	

4.3.3 Selection of study sites

Potential study sites were found by walking watercourses and adjacent habitat to locate suitable structures. Structures were assessed using the same approach as a field ecologist would to identify structures potentially used for resting by otters. Structures could be enclosed or semi-enclosed with any entrance to a tunnel or chamber being at least 10cm at the narrowest point. Potential resting sites were identified by the presence of field-signs e.g. spraint, footprints and forms (shallow depressions approximately 50—60cm diameter). Structures were excluded where there was an elevated risk of equipment theft, submersion of CTs during moderate river-level rises, or where access permission could not be secured or where there were safety considerations for return visits to change the CT batteries. Finding new study sites was an ongoing task, so that as some study sites were completed, suitable replacements had been identified. Sites used within the study are presented in Figure 4-1.



MiniScale® [TIFF geospatial data], Scale 1:1000000, Tiles: GB, Updated: 28 November 2018, Ordnance Survey (GB), Using: EDINA Digimap Ordnance Survey Service, <https://digimap.edina.ac.uk>, Downloaded: 2019-12-14 20:00:27.689

Figure 4-1 Location of study sites in the River Tweed catchment (shaded blue). Sites close to each other were not run concurrently.

4.3.4 Camera-trap deployment and settings

Camera-trap set up was necessarily bespoke at each site due to varying topography and surrounding vegetation. The analysis of data from the long-term study site (see Chapter 3), and detectability trials using CCTV (see Chapter 2) indicated that CT set-up should include at least one close CT within 2 m of the structure entrance, set parallel to the ground at approximately 20-30cm high. The ideal height for maximum detection is just below shoulder height (Apps and McNutt 2018b) so that the body of the animal is in the centre of the detection zone. I estimated the shoulder height of otter to be 17-25cm, but this height was considered too prone to interference from vegetation so the CTs were set slightly higher than this. The main area of interest (i.e. the structure entrance) was roughly central to the field-of-view, whilst ensuring that runs remained unimpeded. The challenging topography on many watercourse banks often precluded a “standard” set-up, in these cases distance to the structure entrance and maintaining unimpeded runs were prioritised.

Camera-trap deployment is classified into three broad categories: (1) trio CTs: three CTs when a structure had more than one entrance (n = 2), (2) dual CTs: most structures used a dual CT set up with two CTs set either at different angles or distances from the entrance (n = 22), and (3) single CT: where available space did not facilitate two CTs e.g. at Frogden2 which was 1m up a tree (Figure 4-2d), a single CT was deployed (n = 2). When a single CT was deployed, it was invariably close, at approximately 1m from the entrance.

Bushnell Trophy cams, models 119678, 119676 and 119776 were used which have low-glow LEDs that illuminate at 850nm to avoid visible light disturbing any otters. The covert illumination was also virtually invisible to humans, lessening the chance of them being detected and stolen. During the four years of data collection, some CTs became faulty and were replaced with new CTs. On occasions, these had to be newer models due to the manufacturer releasing different models. This resulted in three models being used. Metal security boxes were used to house CTs where possible, either attached to a tree if one was available in the right position, or to a wooden stake. At most sites, the camera-traps were locked into the housing. Hard fixings also ensured consistency of the field of view and detection zone of the CT between each change of CT. To avoid theft, CT housing often emulated features in the locality to avoid attracting attention. Examples of fixings include a tall wooden box emulating a fence post with a cut out section to house the camera-trap (Figure 4-2 b & f) and a section of round plastic pipe with a cut out section (Figure 4-2c).

Figure 4-2 Examples of different camera-trap (CT) deployments in this study with CTs indicated by arrows, (a) dual deployment on stakes on flat ground (Learmouth), (b) dual deployment on flat ground with CTs concealed in wooden posts (Torquhan), (c) single CT in drain pipe (Frogden 1), (d) single CT in security case (Frogden 2), (e) two CTs of a three CT deployment, one set high to cover otters climbing tree to entrance and one set low down to cover runs to entrance at ground level (Gordon), (f) dual system on steep bank with two close CTs covering structure entrance from different angles (Hownam), (g) dual system with CTs suspended on wooden arms to avoid submersion in water and enable maintenance from bank top when water-level was high (Eden 2) and, (h) wooden mounting board for CT to facilitate view of structure (Yetholm Loch).

At approximately three-week intervals (median = 21d, IQR = 16—26d), each CT was replaced with one with fresh batteries and an empty SD card from a pool of CTs. The decision to visit each site at three weekly intervals balanced several considerations. High milliampere hours rechargeable batteries (2,900 mAh) were used in the CTs due to the number of sites and longevity of study; battery depletion was therefore a concern and three weeks was thought to run a low risk of battery depletion. Analyses at the long-term study site (Chapter 3) found no effect of disturbance with two-week maintenance visits (see Section 3.4.1), and so three-week intervals suggested no measurable impact. Finally, field-signs (e.g. spraint counts) was recorded at each CT maintenance visit and three weeks was considered sufficient for field-signs to change between visits (this is discussed further in Chapter 5). Visits to sites to change CTs and collect field-sign data (discussed below), are hereafter called “maintenance visits”. High river conditions shortened the interval between maintenance visits in order to retrieve CTs, and at some sites, lengthening the interval as the water was too deep to access the CT emplacements.

CT time was programmed to Greenwich Mean Time. Times on CTs per site were synchronised as best as possible, however the time could not be set more precisely than to the minute. The CTs were programmed to record 20s video (as per the findings in Section 3.3.6.4), with accompanying audio, with the minimal re-arming time of 1s. Video was used as it collects more data in terms of sexing otter, vocalisations and scent marking behaviour, the longer trigger time of video capture was compensated for as the sites were used for scent marking, thus increasing the time of the animal in front of the CT (see Section 2.5.3). The PIR sensitivity 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 aim was to monitor each site for approximately a year, although monitoring at some sites was curtailed for short periods due to heavy rain and associated spates/floods. The monitoring period for sites identified as resting sites were extended for over a year to obtain more data on activity patterns. Monitoring ceased prematurely at Lochside and Newhall when the structures were destroyed by severe storms and monitoring ceased early at Foggo due to frequent threats of submersion due to closeness of the CTs to the water. The footage from retrieved CTs was reviewed briefly to assess how the CT had performed and if any faults were indicated with the CT unit.

The research was covered by licenses to disturb otters at resting sites, in Scotland (issued by Scottish Natural Heritage) 68572 and in England (issued by Natural England) 2016-26206-SCI-SCI.

4.3.5 Summary of study sites

The study sites include a range of structure types and are on a range of river sizes and positions in the catchment (Table 4-2). Open structures could be fully examined with a torch when initially found, but closed structures could not. The mean width of the water-course was calculated using QGIS v 3.8.2 - Zanzibar (QGIS Development Team 2018) from OS VectorMap digital maps using GIS from three measurements, at the location of the structure being monitored, 100 m upstream and 100 m downstream. The Strahler stream order is a measure of stream order based upon the number of divisions between the headwaters and where the river enters the sea (Strahler 1957). A headwater stream is allocated as a one, as would a spring fed stream further down the catchment. The lowest reach of the River Tweed is allocated a ten, therefore all values lie between one and ten.

Table 4-2 Summary of the main properties of the study sites. Mean width refers to the width of the watercourse at the structure (see text). Locations of sites are shown in Figure 4-1

SITE	STRUCTURE TYPE	OPEN OR CLOSED STRUCTURE	MEAN WIDTH (m)	STRAHLER INDEX
Berwick 1	Ledge	OPEN	100	10
Berwick 2	Burrow	CLOSED	103	10
Crailing	Erosion behind roots	CLOSED	7	7
Eden 1	Burrow	CLOSED	7	8
Eden 2	Erosion feature	OPEN	7	8
Floors 1	Burrow	CLOSED	66	9
Floors 2	Erosion feature	OPEN	76	9
Foggo	Erosion feature	OPEN	8	8
Frogden 1	Hollow tree	CLOSED	4	6
Frogden 2	Hollow tree	CLOSED	4	6
Galashiels	Burrow	CLOSED	16	8
Gordon	Hollow tree	OPEN	2	2
Hawick	Burrow	CLOSED	19	8
Hownam	Hollow tree	CLOSED	6	7
Learmouth	Hollow tree	CLOSED	2	3
Lochside(Eggs)	Hollow tree	CLOSED	2	5
Marlefield	Epicormic growth	CLOSED	11	7
Maxton	Rock/earth burrow	CLOSED	53	9
Mill1	Derelict building	CLOSED	52	9
Mill2	Burrow	CLOSED	54	9
Nenthorn	Hollow tree	CLOSED	6	8
Newhall	Burrow	CLOSED	10	7
Rutherford	Burrow	CLOSED	44	9
Slitrig	Erosion feature	OPEN	12	7
Torqhan	Hollow tree	CLOSED	9	7
Yetholm Loch	Burrow	CLOSED	4	3

4.3.6 Recording activity data from footage

Video sorting and data extraction from the videos for each site commenced after monitoring of that site had been completed, to avoid any unintended bias from video observations of sprainting (see below) affecting field-sign data collection (analysed in Chapter 5).

The videos from each camera trap were watched from each period between maintenance visits per site, and sorted into four folders (1) otter, (2) badger and mink,

(3) first and last video and, (4) bycatch (non-target species e.g. birds and rodents) and false-triggers (footage with no faunal observations). If the camera-trap failed to record for the full duration of the monitoring period due to excessive triggering depleting the batteries, the date of the last video was recorded to provide a record of days working in the field for each camera-trap position. The selected mammal videos were watched in full and a sequential list of activity, the "Events List" was produced from the combined data of all CTs at the site in the same way as for the longitudinal study (see Section 3.3.5).

An event was a unit of activity pertaining to an individual otter. Some events contained observations of an entry into the structure and subsequent exit, whether a short while or several hours later. These are termed "paired events" as in this example at Hownam: https://tinyurl.com/uk3gtsw & https://tinyurl.com/v26w3aa (also see video descriptions within links). "Single events" are when the time 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. Often, the otter would not enter the structure, but only interacted with the area at the entrance, these were recorded as a "pass" , as in this example at Mill1: https://tinyurl.com/ttubrs4 (i.e. the otters "passed" the site without entering). Trigger probability can be reduced when an otter has exited the water (see section 2.4.4). To test if this is affected by season, which would indicate an effect of temperature, the distribution of event types (i.e. paired or single-entry or single-exit) in summer and winter were tested for independence using the Chi squared test. Summer and winter were used as they would have the greatest difference in temperature. The null hypothesis being tested was that that season (i.e. winter and summer) does not significantly affect the type of event.

For each event, three main types of data were recorded: (1) the temporal details of the observation and the interaction with the structure (i.e. the date and time and whether the otter entered the structure or not), (2) details of the individual otter where possible (i.e. sex, age etc.), and (3) behavioural observations (see Table 4-3).

Finally, a calendar of activity was derived from the Events List, this summarised key observations for every day within the period that each site was active and comprised the variables in Table 4-4. This also included variables about the structure type, river width and position in the catchment.

Table 4-3 Variables derived from the activity recorded at each site, and included within the "Events List" datasheet

Variable and type of data	Levels/Units	Descriptions
SITE, categorical	26 levels	Name of site
EVENT TYPE, categorical	PAIRED	An event where the same otter is recorded entering and exiting the structure
	SINGLE	An event where the otter is either observed entering, or exiting the structure
TIME IN STRUCTURE, continuous	Minutes	Minutes calculated between entry to holt and exit from holt, rounded to nearest minute.
REST, categorical	1	Rest (TIME IN STRUCTURE ≥ 15 mins)
	0	No rest (TIME IN STRUCTURE < 15 mins)
SUNRISE, time	Date & time	Date and time of sunrise on day of entry to structure (calculated using function in R)
SUNSET, time	Date & time	Date and time of sunset on day of entry to structure (calculated using function in R)
MID, time	Date & time	Time and date of the mid-point between the entry and exit of each paired rest
NOCT.DI, categorical	Nocturnal	When mid-point of rest lies between sunset and sunrise
	Diurnal	When mid-point of rest lies between sunrise and sunset.
UNIQUE REST, categorical		A group of three otters was recorded as three separate observations. This variable enabled each day to be allocated as a rest day, or not.
	1	Rests by single otters and the first registration of a group of otters
	0	Second and subsequent otters resting in a group

Table 4-4 Variables used within a calendar of events datasheet which summarises otter activity per camera-trap day

Variable and type of data	Levels/Types	Descriptions
SITE, categorical	26 levels	Names of sites
No. EVENTS, integer	Count	Number of observations of otter at that site on that date
PRESENCE, categorical	O	Otter recorded
	NO	Otter not recorded
	GAP	No CTs set up due to impending spates
	CAMS.DEFUNCT	No CTs running as batteries depleted, or other malfunctions
ORDINAL DATE, integer	Integer	Sequence of numbers denoting day of year, Jan 1st =1, Jan 2nd = 2 etc.
YEAR	-	Year of observation
SEASON, categorical	WINTER SPRING SUMMER AUTUMN	December, January, February March, April, May June, July, August September, October, November
STRAHLER, integer	Range of 1-10	Number derived from GIS to describe position of site within catchment (stream order)
MEAN WIDTH, integer	Continuous	Mean width of river (m), from width at study site and 100 m up and downstream. Measured using GIS.
RESTING SITE, categorical	1 0	Resting site (see Section 0 for definition) Not a resting site
REST, categorical	1 0	Rest observed that day (see Section 0 for definition) No rests observed that day
STRUCTURE, categorical	 OPEN CLOSED	Description of structure: Unenclosed e.g. a ledge, Enclosed e.g. hollow tree

4.4 Analyses

4.4.1 Are there differences in the patterns of otter registrations at resting and non-resting sites

Using paired events, the duration of time the otter spent within the structure was calculated. A site was classified as a resting site if one or more paired events recorded an otter inside the structure for ≥15min. Sites where this was not observed were classified as non-resting sites (see Sections 3.3.5 for further details). Two sites, Marlefield and Mill2 could not be identified as resting or non-resting sites using this approach and are therefore excluded. Sites identified as resting sites are Crailing, Frogden1, Frogden2, Gordon, Learmouth and Torquhan.

The number of otter observations recorded by the CTs at each site per day was used as a response variable. As individual otters cannot be distinguished from each other, the count may represent one, or more than one individual. Days where the CTs were not functioning for any reason were excluded.

Variables hypothesised as potentially affecting patterns of activity were mean width of river, Strahler index, whether the site was a resting site or a non-resting site (i.e. where an otter had not been observed inhabiting the structure for 15min or longer), the type of structure (open or closed), season and month.

Mean width and Strahler index were highly correlated ($r_s = 0.90$, $p < 0.001$); mean width was selected for inclusion in the models as it was a direct measurement. Additionally, the six resting sites (identification based upon paired events) were all on narrow watercourses (Figure 4-3). However, as both these variables were of interest they were included in competing models, but not within the same model.

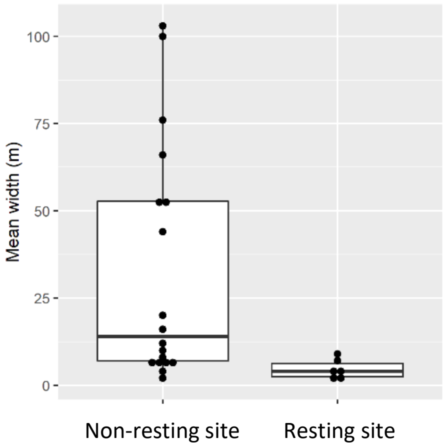


Figure 4-3 Distribution of the mean width of the river for non-resting sites (n=18) and resting sites (n= 6) identified in this study. Two sites (Marlefield and Mill2 are excluded due to uncertainties over their status as resting sites or not)

There was a high proportion of zeros in the data (73% of observations, n = 8075) (Figure 4-4) (i.e. days when no otter activity was observed at a given site [across all sites, resting sites and non-resting sites]), which indicated that a zero-inflated or hurdle model might be necessary.

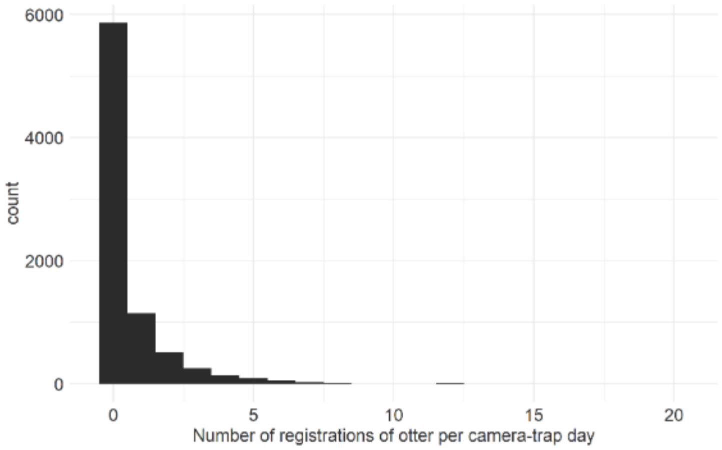


Figure 4-4 The distribution of the number of observations of otter per camera-trap day

Zeros in data can have different origins and are classed as structural or sampling zeros. An example of a zero-inflated model would be if the response variable was the count of otters sprainting per CT day. Zeros could arise from an absence of otter registrations (structural zeros – as observations of an otter sprainting would be impossible), or when otters are registered on a CT day but do not spraint (sampling zeros). A zero inflated model accounts for structural and sampling zeros in the data (i.e. when the count of an observation always has to be zero (structural zeros) and where the count can be either a zero or positive number (sampling zeros) (Hu et al. 2011)). Sampling zeros are therefore predicted by the model and included in the conditional part of the model (i.e. the count data) and the remainder of the zeros (structural zeros) are modelled with a binomial distribution. Hurdle models also account for excess zeros, but a hurdle model models all zeros with a binomial distribution. The non-zero count data is modelled with the distribution stated in the model which is truncated at 1 as it lacks any zeros.

A hurdle model structure was therefore considered most appropriate (Steel et al. 2013) as only one source of zeros was implicated which was the CT days when there were no recordings of otter. Furthermore, a hurdle model was beneficial as the model has a single AIC value, but the output is in two parts, the zero count data and the non-zero count data. This facilities interpretation of “presence/absence” of otter at structures in addition to the intensity of presence (i.e. the number of registrations of otter per day when they were present).

Instances of the CT triggering due to vegetation, or non-target species had been discarded, as had any days when the close CT had was not functioning, therefore any zeros generated were due to the CT not recording otter and were all considered to be structural (i.e. a genuine lack of otter registrations on that day).

A candidate list of models was created (Table 4-5) using combinations of variables in Table 4-4. To find the best fitting error distribution, the global model was fitted with

These were fitted as generalised linear mixed hurdle models with a truncated negative binomial error distribution using the R package glmmTMB (Brooks et al. 2017). Modelling was carried out in R version 3.6.2 (RCore Team 2015) within R Studio (RStudioTeam 2015). Plots of best fitting models were created using the R package sjPlot (Lüdecke 2019).

Table 4-5 Candidate model list where the response variable Y is the number of otter registrations per camera-trap day, and explanatory variables are defined in Table 4-4. Mixed models were fitted using site as a random factor, and with a hurdle model structure with a truncated negative binomial distribution for the count data.

Model
Y ~ NULL MODEL
Y ~ RS
Y ~ SEASON
Y ~MONTH
Y ~ln(MEAN.WIDTH)
Y ~ OPEN.CLOSED
Y ~ RS+SEASON
Y ~ RS*SEASON
Y ~ RS+MONTH
Y ~ RS*MONTH
Y ~ OPEN.CLOSED+SEASON
Y ~ OPEN.CLOSED*SEASON
Y ~ OPEN.CLOSED+MONTH
Y ~ OPEN.CLOSED*MONTH
Y ~ SEASON+ln(MEAN.WIDTH)
Y ~ SEASON*ln(MEAN.WIDTH)
Y ~ MONTH+ln(MEAN.WIDTH)
Y ~ MONTH*ln(MEAN.WIDTH)

4.4.2 Simulations to determine minimum camera-trap sampling duration to record a rest

The following analysis aims to use simulations based on the empirical distribution of resting events at each of the six resting sites (identified from paired events) in order to estimate the minimum number of CT days required to detect a rest with a reasonable level of certainty , with the aim of feeding into surveying guidelines.

Most of the resting days (95%) occurred in winter (December, January, February) and spring (March, April, May) (see Section 0) so summer and autumn were excluded. To calculate a sampling protocol which would have a 95% probability of determining a rest, and therefore determine whether a site is a resting site, separate simulations were run in consecutive winter and spring seasons at each of the six sites where rests were recorded from paired observations (Crailing, Frogden1, Frogden2, Gordon, Learmouth & Torquhan). No paired rests were recorded at any other sites. There are six months in winter and spring combined, sampling for one period could potentially require more survey effort than two sampling periods. However, as the results could potentially contribute to camera-trapping guidelines of resting site, simplicity of sampling is also advantageous. Therefore, a comparison was made between one sampling period and two equal sampling periods, one in winter and one in the following spring. This quantified the difference in sampling effort between the two sampling approaches to determine whether any reduction in sampling with two periods is justified against the simplicity of a single sampling period.

Simulations were run on eight winter-spring periods from the six sites (Table 4-6) to determine the duration of camera-trap days required have a 95% chance of detecting a rest. Simulations were first run to find the number of camera-trap days of a single sampling period, then simulations were run to find the number of camera trap days if there were two sampling periods of equal duration, one in the winter and the other in spring. The maximum duration of days for each scenario (i.e. a single sampling period, and a double sampling period), could then be compared. The maximum duration would have detected a rest on all eight winter-spring periods and could be used as a guide for survey effort to have a good (95%) chance of detecting a rest.

Eight winter-spring periods were used from the six sites (Table 4-6) which were treated separately.

Table 4-6 Summary of data used to simulate the duration of one, or two camera trapping periods which would have a 95% probability of a rest.

	WINTER		SPRING		
SITE (year)	No of rest days	No of days CTs operating	No of rest days	No of days CTs operating	% of days CTs operating in winter-spring period
CRAILING (17-18)	10	77	6	79	87
FROGDEN1 (17)	22	45	12	52	54
FROGDEN2 (18)	3	38	0	87	73
FROGDEN2 (18-19)	11	90	0	85	97
GORDON (16-17)	20	90	11	55	81
LEARMOUTH (17-18)	0	84	3	63	82
LEARMOUTH (18-19)	3	89	6	75	91
TORQUHAN (17-18)	6	56	10	90	81

4.4.2.1 Single period of camera-trap days

This analysis aimed to find the duration of a single period of camera-trapping that would have a 95% chance of detecting a rest. Simulations were run in R Studio (RStudioTeam 2015), code and data are available at https://github.com/melanieCTfindlay/Otter-CT-research.git . To run the simulations, each date was first allocated a number starting at 1 on the first day of winter (1st December), 2 for the second day (2nd December) etc. to the end of spring which could be used as an index within a loop function. If the winter-spring period was shorter than the full 181 days (182 in leap years), the first date of recording was allocated as 1. The probability of determining a rest was first calculated for a sampling duration of a single day. Starting at day 1, if a rest was recorded, a 1 would be entered into a prepared, empty vector and 0 if a rest was not recorded. This was repeated for day 2, day 3 and so on until all 1-day periods had been recorded. This was repeated for every possible consecutive 2-day sampling period, again starting on day 1 and recording a 1 if a rest was recorded or 0 if no rest was recorded in the two day sampling window, then moving onto day 2 and progressing through all possible 2-day periods. This was then repeated for a sampling period of 3 days and so on. For each sampling period (1 day, 2 days etc), the 1's were summed and divided by the total number of simulations to give the proportion of simulations when a rest was detected. If *t* was the sampling period in days and *s* was the number of days in winter and spring combined, then the number of possible simulations for a given *t* would be *s-(t-1)*. Because only resting sites were subsampled, there would be a 100% chance of detecting a rest where *t*=*s* and a 0% chance where *t*=0. As examples of the potential number of simulations, for a three-day sampling period, the number of simulations would be 179 (i.e. 181-(3-1)), and a twenty-day sampling period would be 162 (i.e. 181-(20-1)).

However, there were short periods where a camera had malfunctioned or where sampling ceased due to anticipated river spates. A variable was therefore included for each day to denote if the camera-traps were working (1) or not (0). Individual sampling periods could then be excluded if they did not reach a predetermined threshold of sampling days. This threshold was set so that simulations were only included if the close CT (i.e. the CT closest to the structure entrance), was functioning 6 out of every 7 days. However, simulations were retained if a rest was detected even if the CTs functioned less than 6 out of 7 days because a greater number of functioning CT days in that simulation would not have changed the outcome. This would also be applicable to consultants, that if a rest was detected before CTs malfunctioned, then that would be evidence of a rest, however if a rest was not detected and CTs malfunctioned this would not be sufficient to conclude there were no rests and further sampling would be needed.

The proportion of lost simulations was calculated per sampling window.

The probability of detecting a rest for a given sampling duration was plotted against each duration (between 1 and *s*) and the point at which this reached ≥ 0.95 was then taken as the minimum recommended sampling duration if a single camera-trapping period in winter-spring were to be adopted.

4.4.2.2 Two equal periods of camera-trap days: one in winter and one in spring

The analysis was repeated to simulate two periods of camera-trapping of equal length, one in winter and one in the subsequent spring. Instead of using the single index of days for winter-spring that was used in the single camera-trapping period analysis, a separate index was created for each season. The first day of monitoring in each season being recorded as 1, the second day as 2 and so on. Starting with a camera-trapping window of 1 day in winter, the simulation recorded whether there was a rest or not on the first day of winter or on the first day of spring. It then sampled the first day of winter and the second day of spring, then the first day of winter and the third day of spring etc., until all the days in spring have been sampled together with the first day of winter. This was repeated with the second day of winter, starting on the first day of spring and moving forward to sample all days of spring against the second day of winter. When all combinations of winter and spring had been realised, the process repeated using a 2-day camera-trapping window, then a 3 day window, and so on. Each simulation was coded as 0 (no rest detected) or 1 (rest detected in either winter, spring or both). If t was the sampling period in days, s_W was the winter length and s_S was the spring length (all in days), then the number of possible simulations for a given t would be $[s_W-(t-1)][s_S-(t-1)]$. As examples of the potential number of simulations, for a three-day sampling period, the number of simulations would be 7430 (i.e. [89-(3-1)][92-(3-1)]) and a 20d sampling period would be 6480 (i.e. [89-(20-3)][92-(3-1)]).

This was repeated, recording whether the close CT was working or not, so that in the final calculations each simulated CT window was only used if the threshold of 6/7 days was reached or if a rest was detected. These two criteria could be applied by a consultant ecologist if, for example their batteries ran out leaving a lower proportion of functional CT days than 86% (i.e. 6 out of 7), then additional camera-trapping would only be needed if they did not detect a rest. The probability of detecting a rest for a given sampling duration of two periods was plotted against that each duration (between 1 and s) and the point at which this reached ≥ 0.95 was then taken as the minimum recommended sampling duration if two camera-trapping periods of equal duration, one in winter and one in spring were to be adopted.

For each of the eight winter-spring periods, the site with the largest number of CT days to have a 95% probability of detecting a rest for a single sampling period can be compared to whichever of the eight winter-spring periods had the largest number of CT days to have a 95% probability of detecting a rest in the double sampling period to see which would be more efficient.

4.4.3 Does season affect event type (paired, single-entry, single-exit)

If season affects detection probability, the distribution of event types (paired, single-entry, single-exit) is likely to differ between seasons, since single entry or exit events are indicative of lower detection probability. A contingency table was first constructed containing the observed count of each of the three event types in both seasons, and this was used to calculate the frequencies which would be expected if the null hypothesis was true (i.e. that there was no relationship between season and event type). I used a chi-squared test to test whether the observed distribution differed from the expected distribution which would be due to random chance. The calculated expected frequencies were calculated from the observed frequencies (i.e. sum of column x sum of rows / total); the expected frequencies and the X^2 test were calculated in Rstudio (RStudioTeam 2015).

4.5 Results

4.5.1 Summary of camera-trap days per site

In CT studies, survey effort is usually defined by the number of CT days (Allan et al. 2011). The CT days in Table 4-7 represent days when there was at least one CT working in sites where there is a dual set up. As detectability of the close CT was likely to be higher than any CT further away (see Sections 2.4.1 & 3.4.2), the percentage of CT days where the only functioning CT is the “distant” CT is also given. These days have higher detection uncertainty; this only applies to sites where the dual set-up includes a close and a distant CTs. The bracketed percentage is the proportion of days that only the distant CT was operable in dual deployments. At Gordon, there were two entrances to the structure. One entrance was at ground level and was monitored by a close CT (cam 1), the other entrance was approximately 1m up a tree and was monitored by two CTs at different heights (cams 2 & 3). At Gordon, the bracketed percentage is the number of days where one of the entrances was not monitored (i.e. either cam 1 failed meaning the ground level entrance was unmonitored, or where both cam 2 & cam 3 failed meaning that the upper entrance was unmonitored). The proportion of incomplete observations are also quantified in Table 4-7, these are instances of “single events” where the complete movement of the otter in relation to the structure is not accounted for, e.g. where an otter is observed entering the structure but there is no observation of it leaving the structure.

Table 4-7 Summary for each site of the monitoring period, potential camera-trap days and actual camera-trap days when at least one of the camera-traps were operating. The figures in brackets indicate the percentage of days when only the distant camera-trap was working in dual camera-trap deployments, indicating reduced detection. Losses of days were due to battery depletion (‘Defunct’) and periods when the CTs were intentionally not deployed (‘Not set’) due river level rises. The number of otter registrations are shown in the last column for each site and the percentage of those registrations were “single events” where the observation was incomplete e.g. otter entered structure but there was no corresponding exit. The site was visited to replenish batteries and memory and record field-signs, termed “maintenance visit”.

	Monitoring Period		Summary of status of CTs (days)				Median days betw. maint-enance visits	Type of set-up	No. of otter registrations (% single events)
Site	Start	Finish	Potential	Defunct	Not set	Working			
Berwick 1	09/11/16	05/11/17	361	10	0	351 (11)	29	DUAL	32 (77)
Berwick 2	25/10/17	12/06/18	230	0	7	223 (40)	22	DUAL	31(0)
Crailing	23/04/17	27/05/18	399	25	17	357	18	DUAL	463(22)
Eden 1	11/02/16	24/02/17	379	3	3	373 (0)	22	DUAL	1206 (4)
Eden 2	29/05/18	21/05/19	357	0	0	357	25	DUAL	394(0)
Floors 1	25/04/16	24/04/17	364	0	3	361	32	DUAL	41(0)
Floors 2	21/01/18	08/02/19	383	4	22	357 (17)	25	DUAL	119(0)
Foggo	14/06/15	11/11/15	150	20	0	130	20	DUAL	9 (0)
Frogden 1	23/02/15	18/04/16	420	29	25	366	15	SINGLE	320 (7)
Frogden 1	15/01/17	20/04/17	95	0	0	95	15	SINGLE	105 (3)
Frogden 1	15/09/17	25/05/18	252	0	107	145	21	SINGLE	35 (27)
Frogden 2	14/01/18	25/05/18	131	8	0	123	27	SINGLE	12 (0)
Frogden 2	08/11/18	18/11/19	375	91	0	284	26	SINGLE	22 (0)
Galashiels	01/10/15	30/11/16	426	36	58	332 (<1)	22	DUAL	139
Gordon	26/02/16	25/04/17	424	19	0	405 (28)	26	TRIO	309 (81)
Hawick	27/09/16	20/08/17	327	0	109	218	15	DUAL*	208 (0)
Hownam	08/06/15	12/06/16	370	22	8	340 (6)	16	DUAL	173 (7)
Learmouth	03/12/17	19/05/19	532	15	49	468 (10)	23	DUAL	555 (5)
Lochside	15/07/15	18/11/15	126	0	0	126	19	DUAL	10 (0)
Marlefield	09/11/16	22/11/17	378	33	96	249 (5)	22	DUAL	230 (1)
Maxton	19/05/17	06/07/18	413	0	18	395 (22)	21	DUAL	28 (4)
Mill1	24/11/16	22/11/17	363	13	90	260 (25)	19	DUAL	58 (0)
Mill2	22/01/18	03/03/19	405	19	74	312 (4)	21	DUAL	53 (6)
Nenthorn	19/01/18	19/12/18	334	46	34	254	23	DUAL	48 (33)
Newhall	16/06/15	31/03/16	289	0	129	160	16	DUAL	98 (0)
Rutherford	01/04/16	24/04/17	388	0	0	388 (5)	29	DUAL	25 (0)
Slitrig	23/07/16	29/08/17	402	0	129	273	20	DUAL	41 (0)
Torqhan	31/12/16	27/05/18	512	5	49	458	21	DUAL	164 (5)
Yetholm loch	02/05/16	30/06/17	424	0	52	372 (1)	24	DUAL	173 (1)

*Hawick started with a dual set-up of two close CTs but the lower emplacement was removed as it was prone to submersion. Comparison of registrations on both CTs had almost perfect parity between the two CTs indicating that detection of the retained CT was not compromised.

4.5.2 Does season affect event type (paired, single-entry, single-exit)

The distribution of event types (paired, single-in, single-out), differed significantly between season (summer, winter) ($\chi 2 = 43.9$, df=2, $p<0.001$). Observed and expected (under the null hypothesis) frequencies are shown in Table 4-8.

Table 4-8 Contingency table of event types in summer and winter

		Season		
Event type		Summer	Winter	Total
Paired	Observed count	250	522	772
	Expected count	212.9	559.1	772.0
In	Observed count	14	120	134
	Expected count	36.9	97.1	134.0
Out	Observed count	4	62	66
	Expected count	18.2	47.8	66.0
Total	Observed count	268	704	972
	Expected count	268.0	704.0	972.0

The frequency of observed paired events was greater than that of the expected in summer, whilst the frequency of single entries and exits were lower than expected in summer (Table 4-8). In contrast, the frequency of observed winter paired events was lower than expected, with higher observed single entries and exits than expected.

4.5.3 Defining resting activity from presence

The distribution of time spent within the structures using all paired registrations shows a large peak where the otter has spent only a short time in the structure (Figure 4-5a). This peak is confined to less than 10 min (Figure 4-5b) and very few durations between 10 and 30min (Table 4-9). A threshold of 15 min inside the structure captures this peak of activity which is too short to be considered resting behaviour. Events where the duration within the structure is less than 15 min is therefore defined as a “visit”. When the first 15 min are excluded, the duration of rests across all sites has a peak in frequency for shorter rests (0 – 3 h) and very few very long rests of over 16 h (Figure 4-5c).

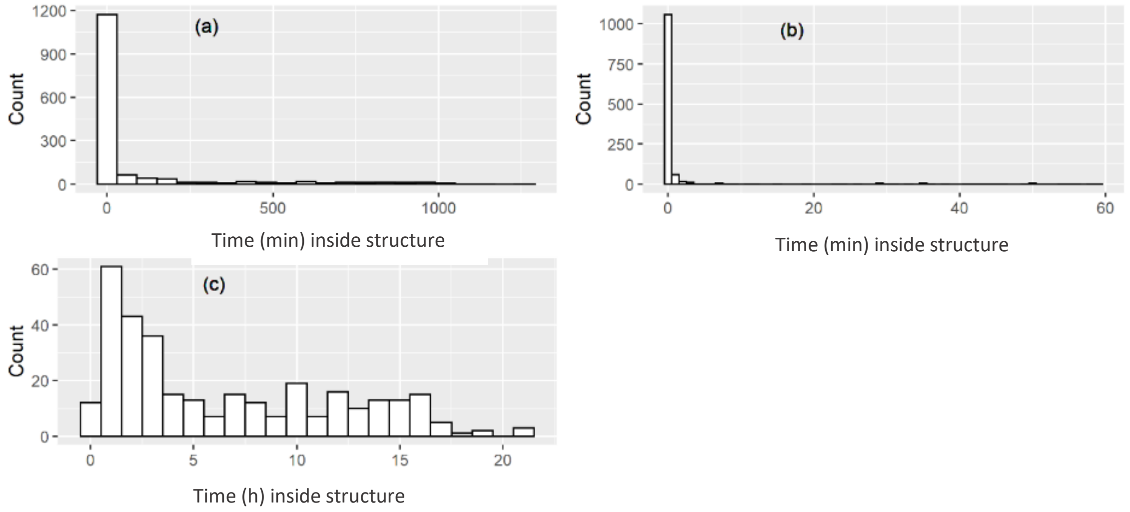


Figure 4-5 Distribution of time that otters spent in the structures on the Tweed catchment, using paired registrations (a) all paired registrations, (b) distribution through the first hour, (c) distribution of all rests in hours, excluding the first 15 minutes. Note variation in scales and units on x-axes.

Table 4-9 Distribution of duration where an otter is within the structure less than an hour

Duration (min) of time in the structure	Count
<10	1149
10-19	4
20-29	9
30-39	10
40-49	13
50-59	12

This 15 min threshold of an otter being within the structure to define a rest is the same duration that defined a rest in the long-term study site (Section 3.3.5). Using this criteria, six of the 26 sites in the River Tweed catchment included at least one rest and are therefore defined as resting sites: Crailing, Frogden1, Frogden2, Gordon, Learmouth and Torquhan.

4.5.4 Summary of otter activity

Presence per day is presented as a measure of whether at least one otter was registered at the structure for each day the site was actively being monitored by one or more CTs. As detectability of the close CT was likely to be higher than any CT further away (see Section 3.4.2), the % of CT days where the close CT failed, and the distant CT did not record an otter are stated in Table 4-10. These days have a higher level of detection uncertainty; this only applies to sites where the dual set-up includes a close and a distant CTs. Presence of otter was therefore calculated by using all instances where an otter was registered by any CT at that site on that day.

At least one otter was recorded at all study sites, see Table 4-10. The highest percentage of CT days that otters were present was 92% at Eden 1, whilst the lowest were at Rutherford and Lochside where otter was only present on 5% of CT days. Using paired events to define a rest of ≥ 15min, the highest percentage of CT days where a rest was recorded was at Frogden1 where a rest was detected on 10% of CT days. Of the sites where resting was detected from paired events, the lowest percent of CT days where a rest was recorded was at Learmouth, where a rest was recorded on 3% of CT days. However, two additional sites (Marlefield and Mill2) were thought to be resting sites based upon behavioural indicators (see discussion in Section 4.6.4). The % of CT days where a rest was recorded are indicative for these two sites.

Table 4-10 Percentage of CT days that otter was recorded as present, and that a rest was recorded, ranked on decreasing percentage of presence. Resting sites as defined by paired events are in bold, red text, resting sites indicated by behaviour are in bold, black text.

Site	CT days with a minimum of 1 CT (% of CT days when otter not registered, but only distant CT running)	Structure Description	Structure type	% Presence	% Rest
Eden 1	373 (0)	Burrow	Enclosed	92	0
Learmouth	**468 (5)**	**Hollow tree**	Enclosed	**63**	**3**
Hawick	218	Burrow	Enclosed	57	0
Newhall	160	Burrow	Enclosed	47	0
Marlefield	**249 (5)**	**Epicormic growth**	**Enclosed**	**47**	**<1**
Eden 2	357	Erosion feature	Open	46	0
Hownam	340 (4)	Hollow tree	Enclosed	38	0
Gordon	**405 (28)**	**Hollow tree**	Enclosed	**34**	**9**
Crailing	**357**	**Roots**	Enclosed	**32**	**6**
Galashiels	332 (< 1)	Burrow	Enclosed	30	0
Yetholm loch	372 (1)	Burrow	Enclosed	29	0
Frogden 1	**609**	**Hollow tree**	Enclosed	**28**	**10**
Floors 2	357 (15)	Erosion feature	Open	22	0
Torquhan	**458**	**Hollow tree**	Enclosed	**19**	**4**
Nenthorn	254	Hollow tree	Enclosed	15	0
Slitrig	273	Erosion feature	Enclosed	14	0
Mill1	260 (24)	Derelict building	Enclosed	13	0
Mill2	**312 (4)**	**Burrow**	**Enclosed**	**11**	**<1**
Berwick 2	223 (36)	Burrow	Enclosed	11	0
Floors 1	361	Burrow	Enclosed	10	0
Berwick 1	351 (11)	Ledge	Open	8	0
Frogden 2	**421**	**Hollow tree**	**Enclosed**	**8**	**5**
Fogo	130	Erosion feature	Open	7	0
Maxton	395 (17)	Rocks	Enclosed	6	0
Rutherford	388 (5)	Burrow	Enclosed	5	0
Lochside	126	Hollow tree	Open	5	0

4.5.5 Are there differences in the patterns of otter registrations at resting and non-resting sites?

For the hurdle model of count of otter observations per CT day, the best supported model related to whether the site was a resting site or not interacting with month (Table 4-9). There were no other models with a ΔAIC ≤ 2.

Table 4-11 Model selection table for presence of otter per camera trap day with the best supported model indicated in bold. Table includes the total number of parameters (K) (i.e. for both the zero-inflated and conditional parts of the models), Akaike Information Criterion (AIC), delta AIC (Δ_{AIC}) and AIC model weight W_i.

Model	K	AIC	Δ_{AIC}	W_i
RS*MONTH	**48**	**13061.4**	**0.0**	**1.00**
MONTH*ln(MEAN.WIDTH)	48	13101.6	40.2	0.00
OPEN.CLOSED*MONTH	48	13149.7	88.4	0.00
RS*SEASON	16	13178.4	117.0	0.00
SEASON*ln(MEAN.WIDTH)	16	13215.8	154.4	0.00
MONTH+ln(MEAN.WIDTH)	26	13247.4	186.0	0.00
RS+MONTH11	26	13251.8	190.4	0.00
MONTH	24	13255.1	193.7	0.00
OPEN.CLOSED+MONTH	26	13258.9	197.5	0.00
OPEN.CLOSED*SEASON	16	13281.8	220.4	0.00
SEASON+ln(MEAN.WIDTH)	10	13337.2	275.8	0.00
RS+SEASON	16	13341.2	279.8	0.00
SEASON	8	13344.1	282.7	0.00
OPEN.CLOSED+SEASON	10	13347.9	286.5	0.00
ln(MEAN.WIDTH)	4	13436.2	374.8	0.00
RS	4	13439.9	378.5	0.00
NULL MODEL	2	13442.6	381.2	0.00
OPEN.CLOSED	4	13446.2	384.9	0.00

The model plot for the best supported model is presented in context of the two components being modelled, the zeros as a proportion of all observations (Figure 4-6b & d) and the non-zero count of registrations per CT day (Figure 4-6a & c).

The zero-inflated model enables an interpretation of presence/absence per CT day by looking at the distribution of zeros (i.e. days when otters were not recorded), at resting and non-resting sites (Figure 4-6b & d). At non-resting sites, there are fewer zeros (i.e. greater number of CT days when otter was recorded) in November and December, and increased zeros in January but otherwise there are no other notable differences. At resting sites however, there is a strong seasonal pattern, with activity increasing to a peak in January, February and March (i.e. fewer zeros) and activity decreasing to a peak in late summer (i.e. peak of zeros occurring in August). This demonstrates that season has a stronger effect on activity at resting sites than non-resting sites.

The conditional model (Figure 4-6a & c) represents the non-zero counts of otter registrations per CT day. At non-resting sites, there are no clear trends, although the counts of registrations in January appear to be lower than in other months. The counts of otter registrations per CT day at resting sites are lower than non-resting sites with the highest in January and March with February and December also having higher counts per CT day than the rest of the months.

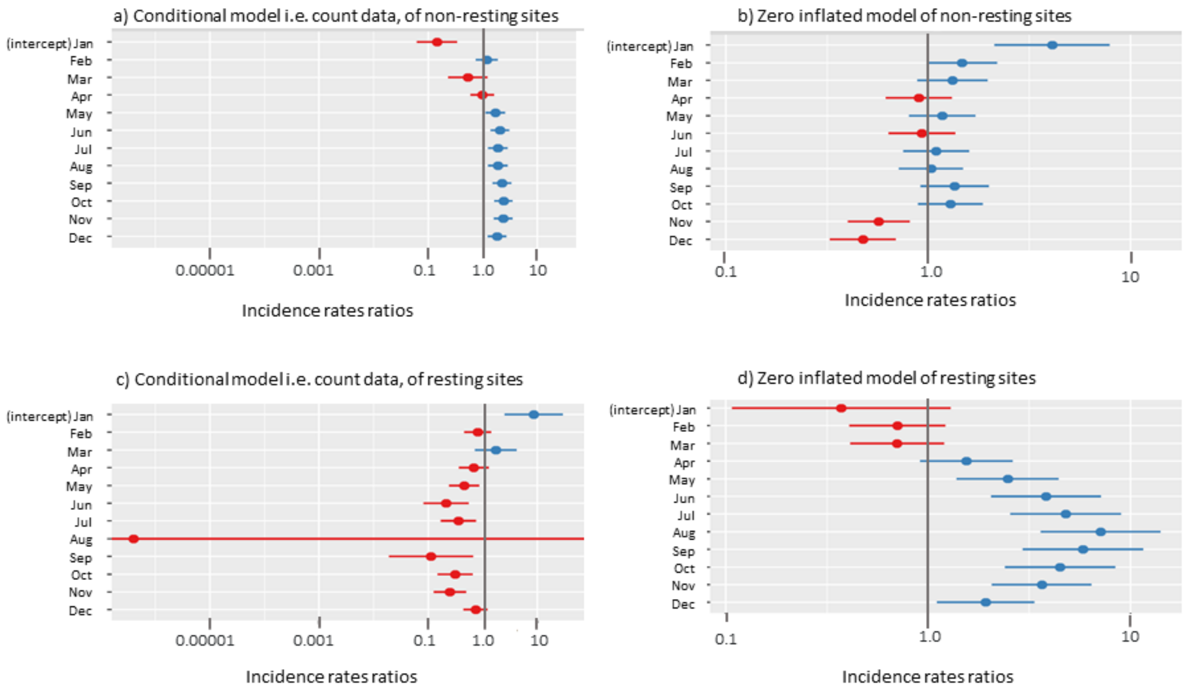
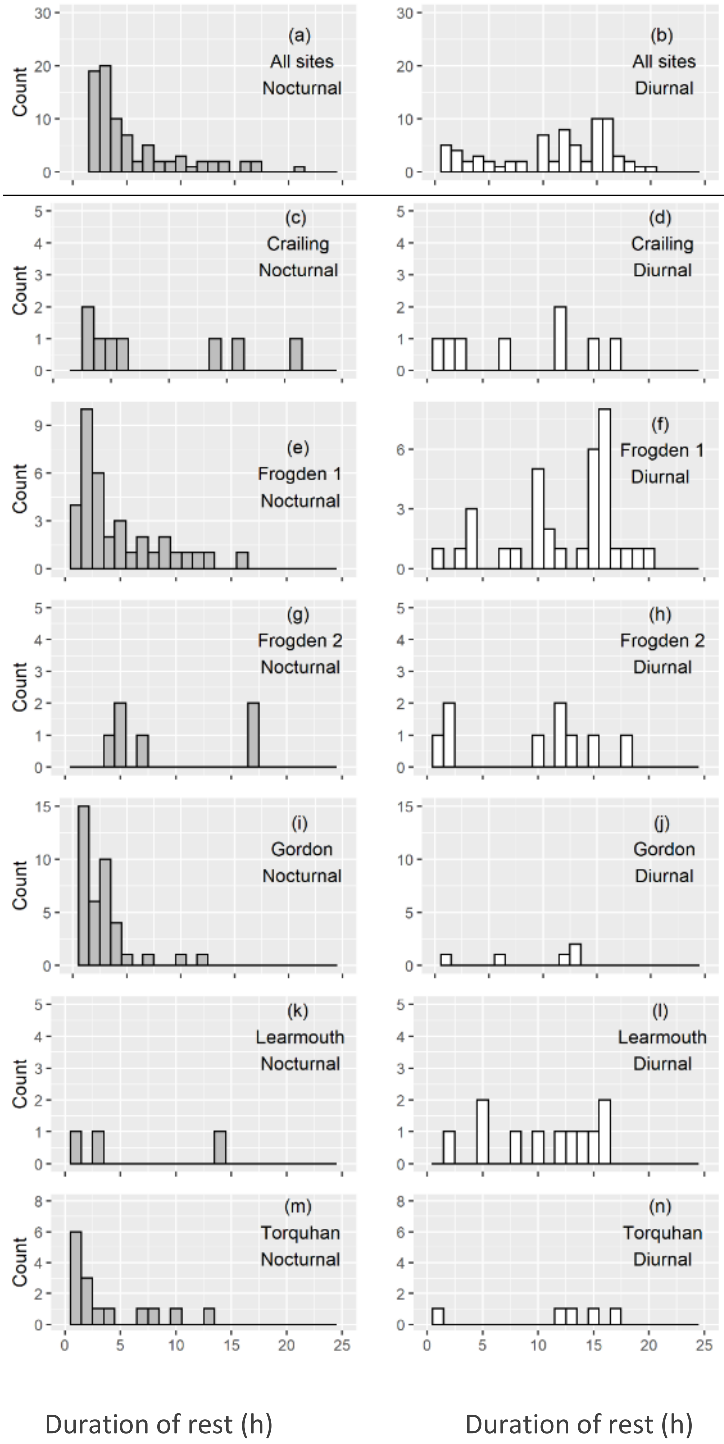


Figure 4-6 Plots from the hurdle model “count of otter observations per camera trap day related to whether the site was a resting site or not interacting with month”. The incidence rate ratio of 1 is indicated by a vertical line to aid interpretation, values greater than 1 are noted in blue, and less than 1 in red. For (a) and (c) an incident ratio of >1 indicates higher than average counts (i.e. observations of otter per camera-trap day), and vice versa. For (b) and (d) an incidence-rate ratio 1 indicates a higher than average probability of zero otter registrations per camera-trap day, and vice versa.

4.5.6 Patterns of otter rests

4.5.6.1 Is there a difference between the duration of nocturnal rests and diurnal rests?

Aggregating the six resting sites, there is a significant difference between rest duration of nocturnal and diurnal rests with diurnal rests being significantly longer than nocturnal rests (Figure 4-7a & b). When considered separately, one site showed a significant difference in the duration of nocturnal and diurnal rests, where nocturnal rests were significantly shorter than diurnal rests (Frogden1 (Figure 4-7e & f) when using a Bonferroni adjusted   value of 0.007 (0.05 divided by seven tests). No sites were used exclusively for diurnal or nocturnal rests, however rests at Learmouth are almost exclusively diurnal, while there are more nocturnal than diurnal rests at Gordon and Torquhan.



W = 6760 * P < 0.001 n = 187

Noct (h)		Diur (h)	
Med	IQR	Med	IQR
2.7	3.9	12.3	8.0

W = 82 p = 0.17 n = 23

Noct (h)		Diur (h)	
Med	IQR	Med	IQR
9.7	9.95	2.8	4.92

W = 1064 *p <0.001 n = 70

Noct (h)		Diur (h)	
Med	IQR	Med	IQR
3.1	5.4	14.9	5.9

W = 26 p = 0.95 n = 15

Noct (h)		Diur (h)	
Med	IQR	Med	IQR
6.0	9.4	12.1	10.5

W = 155 p = 0.04 n = 44

Noct (h)		Diur (h)	
Med	IQR	Med	IQR
2.3	2.1	11.7	6.8

W = 24 p = 0.29 n = 14

Noct (h)		Diur (h)	
Med	IQR	Med	IQR
2.8	7.0	11.9	7.7

W = 59 p = 0.07 n = 20

Noct (h)		Diur (h)	
Med	IQR	Med	IQR
2.4	4.9	12.8	2.4

Figure 4-7 distribution of nocturnal and diurnal rest durations for each site using unique rests (i.e. where a rest by a family group counts as a single observation), with associated Mann-Whitney-Wilcoxon values. The Bonferroni adjustment alpha level for these tests was 0.05/7 = 0.007, thus significant P-values are indicated by "*"

The combined distribution of nocturnal and diurnal resting duration across all sites by single otters, and groups are presented in Figure 4-8. A Kolmogorov-Smirnov test was used to test whether the distribution of rest durations by single otters was significantly different from otter groups, firstly for nocturnal rests, then for diurnal rests. The distribution of nocturnal rests for single otter and otter groups not significantly different (D = 0.16, p = 0.459), similarly, there was no significant difference between diurnal rests for single otter and otter groups (D = 0.35, p = 0.137). Therefore, there was no significant difference in the distribution of rest durations between single otters and groups of otter.

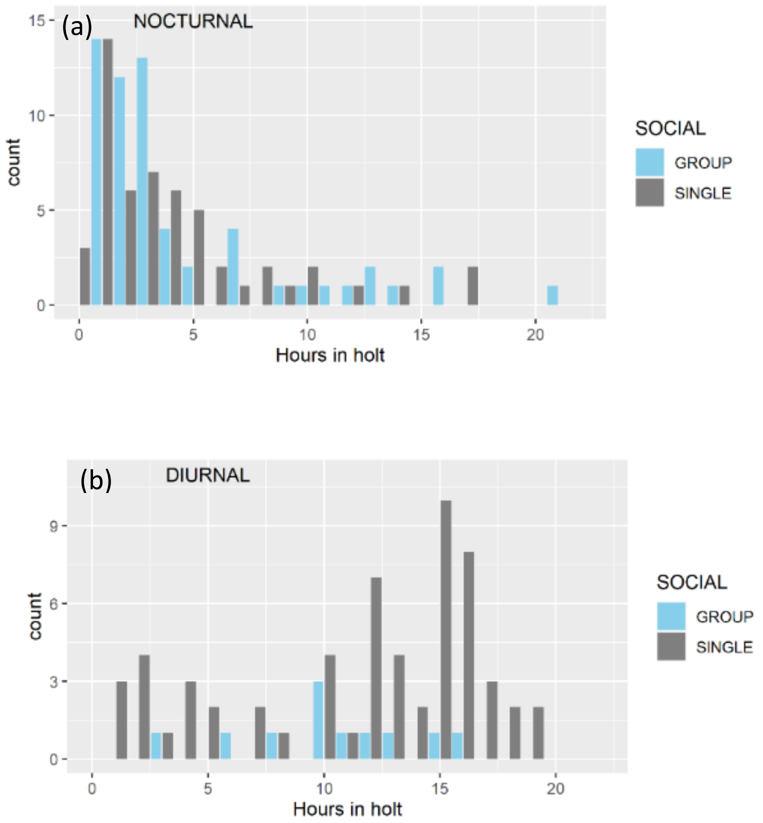


Figure 4-8 Frequency distribution of the rest duration of single otters and groups for (a) nocturnal rests (n=group 62, single 33) and, (b) diurnal rests (n= group 13, single 72)

When a structure was used by a female with cubs, often resting was not synchronous between all otters. The female could leave the cubs at the holt and undertake foraging trips on her own. When the cubs remained at the holt, they were not exclusively contained within the holt and could be active in the holt locality. The resulting footage was difficult to interpret as discriminating the adult from cubs is not always possible leading to inabilities to pair entries and exits to the holt. Pairing observations was not always possible.

4.5.6.2 Variation in frequency of resting site use through the year

There was a strong seasonal pattern for all resting sites, with most rests occurring in winter and spring (Figure 4-9). A single rest in summer was recorded at three sites, Crailing, Learmouth and Marlefield. Gordon was the only site where rests occurred in autumn: these were observed on seven CT days, with four of these relating to a group of otter (minimum of two otters).

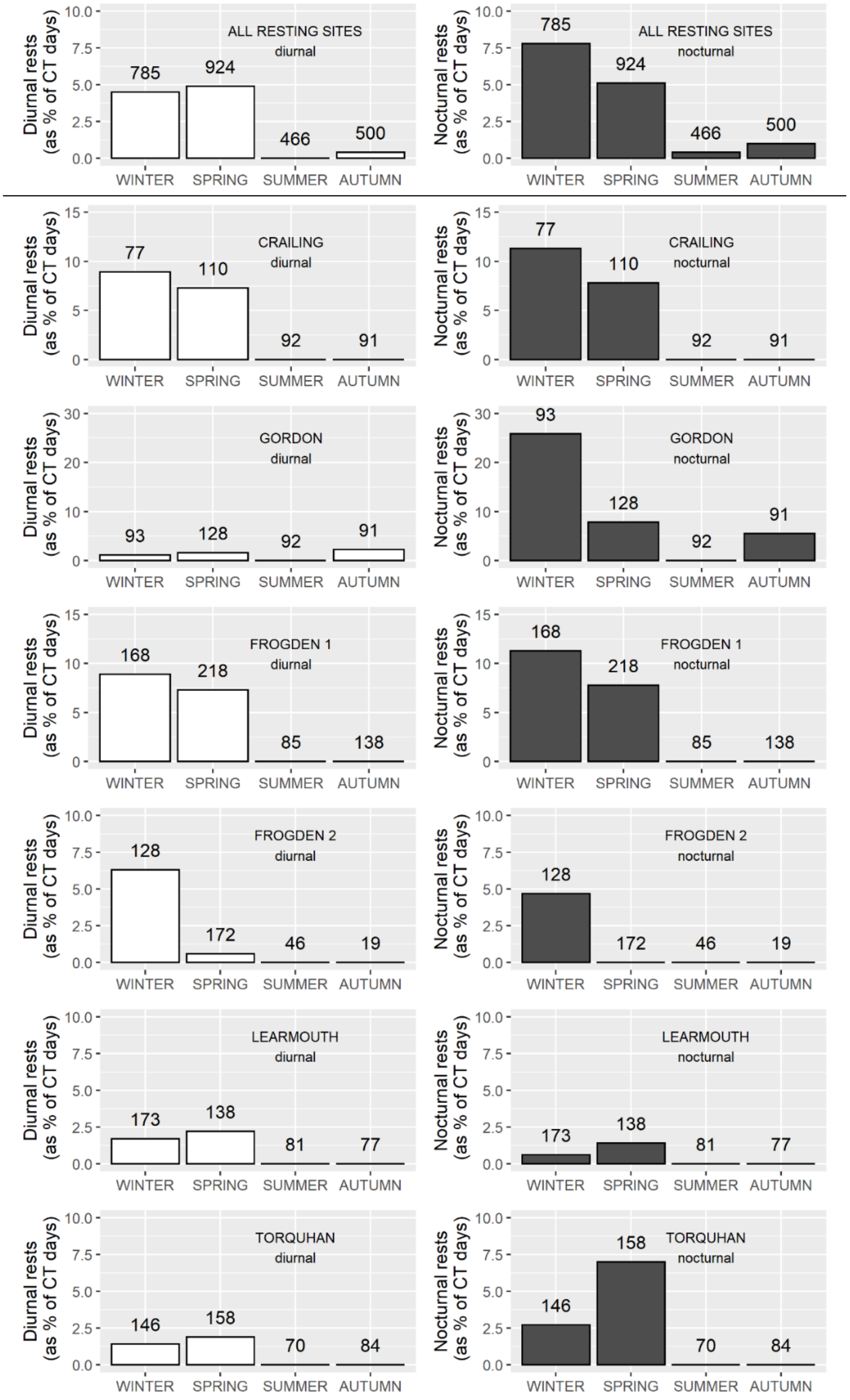


Figure 4-9 The percentage of camera-trap days where a rest was recorded for each season (winter: December 1st to February 28th; spring: March 1st to May 31st; summer: June 1st to August 30th; autumn: September 1st to November 30th) for diurnal rests aggregated from all six resting sites, nocturnal rests aggregated from all six resting sites and for each individual site. Numbers above bars are the number of camera-trap days.

1

4.5.6.3 Site re-use in successive winter-spring seasons

There were multiple rests at each of the six sites where resting was confirmed by paired events (Crailing, Frogden1, Frogden 2, Gordon, Learmouth and Torquhan). All these sites were re-used in the winter and/or spring of the following, or subsequent years (Figure 4-10).

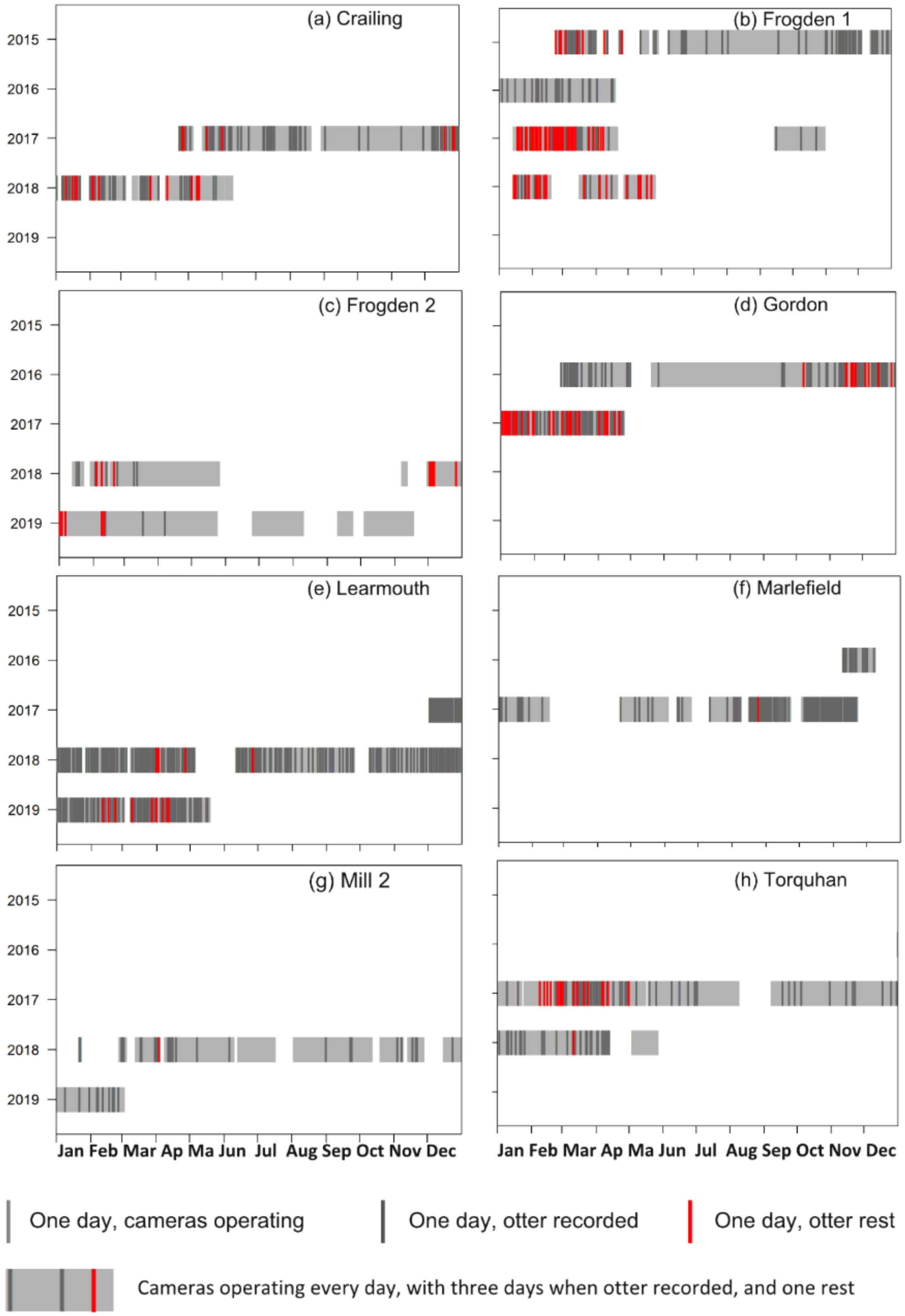
A build-up of woody debris downstream of Frogden1 coupled with heavy rainfall caused localised flooding in the winter/spring of 2015/2016. The CT at Frogden1 was above the water level and recorded the structure being flooded on at least four occasions (3rd & 4th, 26th & 27th December 2015; 6th, 27th January 2016). Otter rests are notably absent during this period.

Flooding was not thought to be an issue at the other structures. High water levels curtailed camera trap deployment at Crailing, Marlefield and Mill2, but it was not clear if the sleeping chambers became flooded.

A single rest was detected at Marlefield in summer when a fully dry otter left the structure.

Figure 4-10 Daily activity type (otter recorded or otter rest detected) in context with monitoring periods at each site used for resting (winter: December 1st to February 28th; spring: March 1st to May 31st; summer: June 1st to August 30th; autumn: September 1st to November 30th). Gaps in recording (e.g. due to malfunctions or flooding) are left as blank space.

1



4.5.7 Behavioural observations as indicators of resting behaviour

4.5.7.1 Bedding collection

Bedding collection was noted at five of the six habitually used resting sites, no bedding collection by otter was observed at Frogden 2. Bedding collection was not observed at any of the non-resting sites. Vegetation was invariably pulled up and carried into the structure in the otter's mouth, with the otter usually moving at a faster pace than typical. 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. For example, at Gordon, one of two otters resting in the structure exits the holt and returned within a few seconds with a mouthful of bedding tinyurl.com/rhj75a9, and similarly at Torquhan, an otter collected bedding locally to the holt tinyurl.com/tlge662.

Badgers were also observed taking bedding into Frogden 1 (five nights) and Frogden 2 (six nights) and mink were observed collecting bedding at Frogden 1 (two nights) and Crailing (one night). Of the 20 sites not identified as rest sites, there was one incidence of an otter taking a twig into the structure (Nenthorn), but the otter subsequently left, and no resting was observed at the structure. This was not considered bedding collection in the same manner as seen at the other sites. Also, a badger was observed taking bedding into the Hownam structure (also not identified as a resting site) on at least ten nights.

Bedding collection by otter is summarised in Table 4-12. It was observed in both sexes, and when a group of otter were resting at Gordon, two otters were observed simultaneously collecting bedding. See Appendix II, Table A4, for a more detailed account of bedding collection observations.

Table 4-12 Summary of bedding collection by otter at five of the six detected resting sites. No bedding collection by otter(s) was observed at one other confirmed resting site, nor in any of the 20 sites where resting was not detected.

Site	No of CT days observed (Total CT days)	% of CT days Single or group	Sex	Associated with paired rest event	Nocturnal or Diurnal activity
Crailing	2	100% Single	Male and an otter of unknown sex	50%	Diurnal
Frogden 1	12	75% single 25% group	Male Female	75%	Nocturnal and diurnal
Gordon	12	17% single 83% group	Male Female	25%	Nocturnal and diurnal
Learmouth	2	100% single	Unknown	100%	Nocturnal and diurnal
Torquhan	8	63% single 37% group	Male Female	75%	Nocturnal

4.5.7.2 Sedentary behaviour at structure entrance

Sedentary behaviour encompassed several types of behaviour. Initially these were recorded separately but as more video footage was watched, the number of behaviours increased and often several behaviours could occur in one event. There was no benefit in quantifying these separately in context of the research aims, so these were grouped as a single generic category of sedentary behaviours, and are described in Table 4-13.

Table 4-13 Descriptions of behaviours grouped into a single sedentary behaviour category

Behaviour	Description
Loafing	Otter lying down, stretched out on back or on stomach and with little to no movement. In a relaxed state, occasionally shutting eyes (Example: tinyurl.com/wnv723s at Learmouth)
Grooming	Otter licking fur and/or extended periods of scratching (Example: tinyurl.com/wnm7nsn at Frogden1)
Rolling	Otter lies down and rolls on back, often on loose substrate such as fragmented bark, fur often wet at start of behaviour and notably less wet when rolling ceases (Example: tinyurl.com/sgfqchc at Frogden1)

Sedentary behaviours (described in Table 4-13) were observed at some study sites (Table 4-14). This was more frequently observed at resting sites than non-resting sites, and the mean time of each observation was longer at resting sites than non-resting sites.

Table 4-14 Comparison of the frequency and duration of behavioural observations at resting sites and non-resting sites

	Total events where otter recorded	% of otter events when sedentary behaviour observed	Duration of sedentary behaviour events (min)		
			Mean	Min	Max
Non resting site	3116	1.57%	1.1 ±0.3	<1	2
Resting site	1672	10.65%	2.8 ±4.3	<1	32

4.5.7.3 Use of latrines

Otters were observed using a latrine associated with the structure, either just within the entrance of the structure or outside. Latrine behaviour was characterised by the otter visiting the latrine area and defecating with or without urinating. The droppings produced at latrines were noticeably larger than the deposits produced at spraint sites (example of latrine behaviour at Gordon tinyurl.com/vq9kydq and example of sprainting behaviour as a comparison at Hawick tinyurl.com/ul2ach2 ; the behaviours are described in more detail in the video descriptions). Otters would use latrines prior to, during, or after a rest. Often the fur of the otter would be dry as it had previously been resting in the holt. Only one active latrine was observed at each site. Latrine activity is summarised in Table 4-15. The latrine could be used once, or more (maximum of six times), during a resting event.

Latrine behaviour was observed at five of the six resting sites; Torquhan lacked observations of latrine behaviour. Latrine behaviour also occurred on three days at Mill2, the fur was not dry indicating an underwater holt entrance. This site was not included as a resting site as there were no paired events confirming time spent in the structure was over 15min but other observations suggested it may have been a resting site (the site is discussed in more detail, below).

There were no observations of latrine behaviour at any of the non-resting sites.

Table 4-15 Summary of latrine behaviour in relation to resting events based upon paired registrations. Note that the relatively large number of latrine observations per site is due to groups of otter resting and using the latrine on a day, also repeated use of the latrine per rest.

Site	No CT days (see Table 4-7)	No of days latrine behaviour observed	No of days latrine behaviour associated with a paired event	% of paired events where latrine behaviour observed, and a rest occurred	Total number of latrine behaviour observations
Crailing	357	19	11	91	40
Frogden 1	609	31	27	100	44
Frogden 2	421	5	5	100	5
Gordon	405	52	34	94	154
Learmouth	465	5	5	100	5
Mill2	312	3	0	NA*	11

*Mill2 could not be defined as a resting site based upon paired events

4.5.8 Data simulations to determine optimum camera-trap sampling duration to detect a rest

There was considerable variation between sites in the number of days required for a 95% probability of detecting a rest, both when a single or two equal periods of camera trapping were simulated (Table 4-16). In general, the total number of days required to have a 95% probability of detecting a rest was smaller when two equal periods were used (Table 4-16 D). The single period was more efficient in three of the eight site-periods, but in each only by ≤ 6d. The mean difference between a single period and a double period of camera-trapping is +23d, this suggests that using a double period is 35% more efficient (i.e. 23/65 (the mean of a single period)), or would require about three weeks less sampling effort overall to have the same confidence of detecting a rest.

For the six known resting sites, the longest required CT period to have a 95% chance of detecting a rest if using a single CT period would be 108d, compared with a total of 76d for a double period of CT sampling (Table 4-16)

Table 4-16 The number of camera-trap days required to have a 95% probability of detecting a rest if using a single camera-trapping window, or two equal periods. All values are in days. Negative values in D indicate the single winter-spring period was more efficient than the separate winter and spring periods, and positive numbers vice versa.

SITE (YEAR)	A **Single period** Winter-spring combined	B **Two periods** Per period	C **Two periods** Total of both periods (2*B)	D Difference between single period and total of two periods (A minus C)
CRAILING (17-18)	22	14	28	-6
FROGDEN1 (17)	12	4	8	4
FROGDEN2 (18)	94	11	22	72
FROGDEN2 (18-19)	107	30	60	47
GORDON (16-17)	13	7	14	-1
LEARMOUTH (17-18)	108	30	60	48
LEARMOUTH (18-19)	69	35	70	-1
TORQUHAN (17-18)	98	38	76	22
Mean	65	21	42	23
Maximum	108	38	76	72
Minimum	12	4	8	-6

The high degree of variation in the relationship between sampling duration and probability of detecting a rest for site-seasons are shown in Figure 4-11. The plots illustrate that the two period sampling strategy was generally more efficient, reaching 95% probability of detecting a rest more quickly.

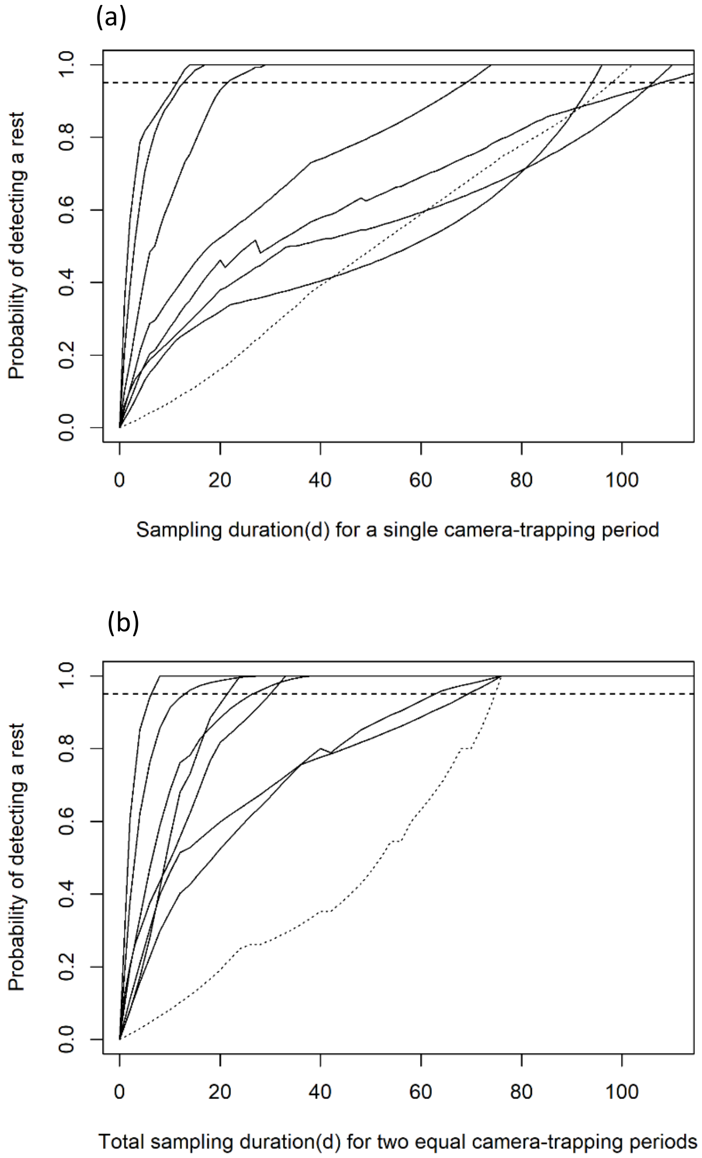


Figure 4-11 The probability of rest during 8 winter-spring periods at 6 resting sites based on simulated camera-trap surveys over different surveying durations (in days) for (a) a single period of camera-trapping, and (b) for two equal periods of camera-trapping, one in winter and one in spring. Torquhan is shown as dotted line due to poorer data, see Section 4.5.4.1 below. The 95th percentile is indicated by the horizontal dashed line

4.5.8.1 The effect of discarded simulations

The numbers of simulations discarded because the CTs were not operational (e.g. due to malfunctions or flooding) in ≥6 of every 7 days were generally greatest at lower sampling periods for both the single period and two equal period sampling strategies. Generally, the longer the CT sampling duration, the fewer simulations had to be discarded as they exceeded this threshold. Torquhan had a much higher rate of discarded simulations, which also continued for a longer sampling duration (shown with dotted line in Figure 4-11 & Figure 4-12). Unfortunately, the only hard copy of a 20-day period at Torquhan was irretrievably lost when the SD card was mailed from the research volunteer. Therefore, there was a gap in the data of this duration which resulted in a large number of simulations being discarded. This is evident in the longer duration of days required to detect a rest in the two equal sampling periods for this site (Figure 4-11b), and by the large proportion of lost data (Figure 4-12b).

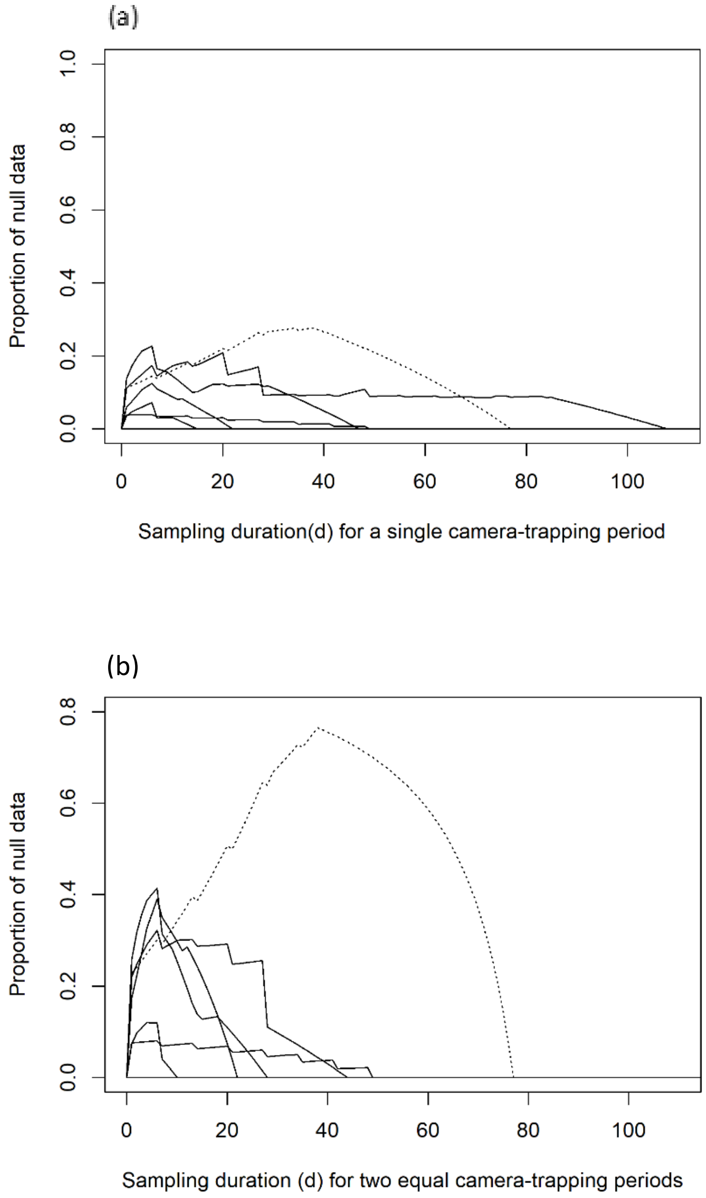


Figure 4-12 The proportion of null data rejected from calculations to determine the number of days required to have a 95% probability of a rest, (a) for a single sampling period, and (b) for two equal sampling periods. Torquhan is shown as dotted line due to poorer data

4.6 Discussion

4.6.1 Defining a resting site- the need for standardisation

The distribution of time spent in the structures on the River Tweed catchment enabled a resting site to be defined as a structure where otters stay within the structure for at least 15min. Using 15min to divide a visit from a rest relied upon having a time of entry and exit from the structures so that the time spent within the structure could be calculated. There was a clear peak in the frequency distribution of time spent in the structure in both the in the River Tweed data (see Figure 4-5) at 1—2min and at the long-term study site data (see Figure 3-3) at 1—10min, these were obviously visits. There are few (48) instances of otters being at the structure between 15min and an hour and so this “trough” in the data was used to demarcate a visit from a rest. Table 4-17 shows how the count of instances that would be classed as a rest would change using different thresholds to define a rest. A 20min threshold would have minimum impact on the number of rests, however if an hour were used, this would reduce the number of rests by 15%.

Table 4-17 The number of events that would have been defined as a rest across the whole study had the threshold time used to define a rest (≥15 min) had been extended (to up to >60 min). The threshold I used is shown in bold

Time in holt (min)	**>15**	>20	>30	>40	>50	>60
Count	**326**	323	314	304	289	278

The rationale behind the 15min window to define a rest was therefore based primarily on the data coupled with a necessary subjective assessment on how long an otter could be active within a structure without it being considered resting behaviour. The threshold provided meaningful separation which could be consistently applied on the Tweed study and was also consistent with the long-term study (section 3.3.5). Furthermore, paired registrations enabled the mid-point of the rest to be calculated, and the rest could be classed as a diurnal or nocturnal rest. Once a rest event was defined, sites could be categorised as a resting site or a non-resting site based upon whether a rest event had occurred at the structure or not. Without the use of CTs, identification of otter resting sites has previously been based upon expert opinion, which is an assessment of field-signs at a structure and its context. CTs are now widely used in research (Rovero et al. 2013) and are increasingly being used by consultants for monitoring structures suggested as resting sites. Therefore, a more precise definition that can be applied by consultants using CTs at a resting site is needed. The definition I use in this research could readily be applied, it is easily interpreted and is evidence based.

4.6.2 Nocturnal and diurnal resting

Rest events from paired events were detected at six of the 26 sites. It was hypothesised that the duration of nocturnal rests would be shorter than diurnal rests. The data strongly supports this hypothesis as nocturnal rest duration (median = 2.7h) was significantly shorter than diurnal (median = 12.3h). This is in agreement with radiotracking studies where these primarily nocturnal animals have been recorded taking short rests after bouts of foraging during the night, but rest continuously during the day (Green et al. 1984). However, the data did not support the hypothesis that there would be a difference in rest duration between groups of otter and single otters. Groups of otter recorded were mainly females with young, having greater energy demands (Ruiz-Olmo et al. 2011) and an assumed increased requirement for shelter than a single otter. This suggests that families may take longer rests to conserve energy, and/or shorter rests due to longer bouts of foraging. No overall difference was found in the distribution of rest durations between groups and single otters.

4.6.3 Seasonal trends

The distribution of event types (paired, single-in, single-out) differed significantly between season (summer, winter). While I could not measure detection probability directly, this result does infer that detection probability varies with season, since a paired event implies better detection that single events (where either the entry or the exit is missed). The greater than expected frequency of paired events in summer (and less than expected in winter) thus indicates better detection of otter in summer. This could be due to the temperature of river water being significantly lower than the temperature range on land (See Figure 2-3). It is possible that the detection of rests in winter could thus be under-represented, however, if this is the case, the observed seasonal bias of resting towards winter in this study may be even stronger. Ninety-five percent of rests were recorded in winter and spring and 4% of rests were in autumn but were only recorded at one site (Gordon). Summer resting was rare and only occurred once at each of three sites (Crailing, Marlefield and Learmouth) which was <1% of all rests.

The highest number of CT days when otter was registered at resting sites was January to March which sits within the winter-spring period when resting sites are used the most, and the lowest activity is in late summer. This indicates that otter activity and interest in resting sites is generally limited to the time when they are being used. When they are not used for resting the otters do not appear to invest energy in visiting the resting sites in order to check or scent mark them to claim ownership. Interestingly, the peak in the number of CT days an otter was recorded in January, February, March at resting sites corresponds to lower presence at non-resting sites. As all the resting sites were on small rivers, with a mean width of between 2 and 9m (see), this may indicate a seasonal shift in the core area of activity of otter populations in winter-spring to smaller rivers. There could be one, or several reasons for such a seasonal habitat change. It may be due to a preference for winter-spring breeding (Green et al. 1984; Mason and Macdonald 1987a) together with a preference for breeding on smaller watercourses (Green et al. 1984). It may be associated with the avoidance of spates on the large rivers which make foraging difficult and which may also flood any rest sites there. There may also be better seasonal availability of prey in winter and spring, such as frogs (Weber 1990; Brzeziński et al. 2006). If seasonal breeding on small water-courses drives this seasonal change in the centre of otter activity, it would follow that the peaks of otter at non-resting sites in November and December may be due to individuals prospecting for structures to give birth in or rear cubs, or olfactory signalling between females and males. The low point of activity seen at non-resting sites in January may be due to the females moving to smaller watercourses to breed. These potential patterns in the spatial use of home-range cannot be tested directly with my data but could be tested with a future radiotracking study.

During the summer, occurrence at non-resting sites is higher, further supporting the hypothesis of a seasonal shift of activity between larger and small rivers.

4.6.4 Behavioural indicators of resting

The data show that some behaviours are indicative of resting. Once resting and non-resting sites were identified, variations in behaviour could be compared between these categories. Sedentary behaviours, such as loafing and grooming, were observed at a greater frequency and with longer duration at resting sites although they were not exclusively observed at resting sites. Bedding collection was observed at five of the six resting sites, excluding Frogden2. The latter site contained bedding material but this had been collected by badgers. Bedding collection was observed by both males and females; therefore, it cannot alone be used to define if a structure is used for breeding or not. The absence of bedding collection behaviour at any of the sites where resting was not observed indicates that observations of this behaviour would be good evidence to identify a resting site. As many structures are too difficult to inspect completely, bedding may not always be visible increasing the value of observations of bedding collection by CT.

As with bedding, latrine behaviour was observed at five out of the six resting sites and was not recorded at any non-resting sites, therefore it could also potentially be used diagnostically to identify resting sites. The usefulness of behavioural indicators of resting is illustrated by Mill2, where latrine behaviour was recorded in the absence of any paired registrations of ≥ 15min in the structure (thus indicative of a rest). Mill2 had an entrance above ground on the bank but also a concealed entrance accessed from a ledge on the riverbank behind roots. Both entrances were monitored, but there were no paired registrations to signal resting behaviour. At the end of the monitoring period, the river level dropped exposing a previously unobserved entrance which would normally have been underwater; uncountable otter prints were present on the muddy margins. It is very likely that Mill2 was a resting site, evidenced by the latrine behaviour, but one entrance could not be monitored leading to incomplete data. This scenario is unlikely to be unique when monitoring otter structures, although holts with underwater entrances were described as “not common” in a radiotracking survey in Sweden (Erlinge 1967). Descriptions of holts with underwater entrances would naturally be rare as the underwater entrances would be difficult to observe, so it is not known how common this feature is. However, as the sleeping chamber would need to be above the water-level, these are more likely to be associated with deeper rivers. In such cases where an entrance is below water, additional criteria to the paired events would be critical to identify the structure as a resting site.

Few studies of Eurasian otter make a distinction between a “latrine” and a “spraint site”. Both terms have been used to describe the same feature (i.e. a small number of spraints deposited together). “Spraint site” is the preferred term used in some studies (Green 2000; Remonti et al. 2011; Parry et al. 2013; Yoxon and Yoxon 2014). Other studies use the term “latrine” when referring to a collection of very few spraints, for example 1—3 spraints (Ruiz-olmo et al. 2001), and some studies offer a definition of a latrine as a location containing three or more spraints (e.g. Depue and Ben-David 2010; Almeida et al. 2012). Occasionally the terms are used interchangeably (e.g. Georgiev 2008). In these studies, the function of the latrines and spraint sites are described within the context of scent marking. The observations on the River Tweed indicate a functional distinction between sprainting behaviour characteristic of scent-marking (i.e. small token amounts) and latrine behaviour which is digestive elimination, although the latter could also function as an olfactory signal. There are similarities between the latrines identified in this study with other studies that describe the same type of feature. One study of Eurasian otter refers to latrines being found underground within holts (Moorehouse 1988), whilst another study of spraint distribution refers to “big latrines” of 79—282 spraints, which were all associated with dens and caves (Ruiz-olmo and Gosalbez 1997). There is a parallel between the latrines in these two studies and the latrines found in this study; the large number of droppings, and also that they are within resting sites (Moorehouse 1988) or an implied resting site (Ruiz-olmo and Gosalbez 1997). This distinction between latrines and other types of scent marking is present in other Mustelid species, for instance pine marten (Kleef and Tydeman 2009), badger (Böhm et al. 2018) and honey badger *Mellivora capensis* (Begg et al. 2003). This distinction between latrines and spraint sites in other mustelids indicates the plausibility of such a distinction in Eurasian otter. Recognition of this distinction by ecologists would further surveying methodology for otter.

4.6.5 Use of resting sites by family groups

Sexing of otter using primary characteristics (i.e. presence of scrotum, presence of nipples, source and direction of urine stream) was possible on 21% (n = 1,565) of observations of adult otter at resting sites.

Five of the six resting sites were used by both adult male(s) and females with cubs although shared use of individual structures were not synchrous. The sixth resting site (Learmouth) was also shared; a male used the structure, as did a dyad of unknown sexes. These were considered siblings as their behaviour was similar. From my observations, a dyad comprising a female with a fully-grown cub is usually identifiable; she is less energetic and more wary, often looking out of and away from the holt, whereas the cub often initiates interactions with the female and is less attentive to the surroundings. The River Tweed data contrast with a recent radiotracking survey of nine otters in Austria, where only 0.03% (n = 285) sites were used by both males and females (Weinberger et al. 2019). This may, however, be due the inherent difference between radio tracking and CT monitoring. The former samples the spatial positions and movements of a subsample of individual otters, thus potentially missing individuals, while CTs continuously monitoring small areas of interest, such as rest sites, and potentially records all occurrences of all otters within the small area being monitored.

4.6.6 Re-use of resting sites between years

The re-use of resting sites needs to be considered within the context of a specified timescale. Generally, resting sites were repeatedly re-used within and between years. However, one site (Marlefield) was only used once for resting during approximately a year of monitoring (see). Finding such infrequently used sites using CTs would require monitoring for such long periods as to make the aim of finding such sites impractical. The aim, and perhaps more importantly, the expectation of consultants should be to locate and confirm resting sites that are re-used, especially in context with the legislation which protects resting sites where there is an expectation of re-use (see Section 1.1.4.1). The data shows that resting site use was clustered in the winter-spring period with each of the resting sites being used repeatedly. Of the four resting sites where monitoring was extended to cover two or more winter/spring seasons, repeated resting between years was observed. Repeated use in the same season, and implied re-use between years indicates that the structure and locale make a significant contribution to that home-range.

4.6.7 Methodological considerations

4.6.7.1 Sampling duration

Camera-trapping a site for a year is not usually feasible for consultancy applications. Understanding any patterns of use could facilitate identification of resting sites with a shorter sampling duration. The seasonal trend of resting at structures indicates that camera-trapping would be more efficient in the winter—spring seasons, but six months is still a large sampling duration. The simulation approach therefore aimed to see if rests could be detected with a reasonable degree of confidence with a shorter sampling duration. The comparison between a single period of camera-trapping over the winter—spring period, and two equal periods with one in winter and one the following spring shows that for the six resting sites it would have been significantly more efficient to adopt the latter sampling strategy. The simulations also allow for a proportion (approximately 15%) (i.e. one day in seven) of camera-trap days to be lost due to malfunctioning camera-traps. Ideally, a consultant would have no data loss but the inclusion of an allowance for a small proportion of non-functioning CT days would reflect real world situations where CTs can malfunction. It would also draw attention of practitioners and statutory authorities that this is an important methodological point to be included in CT survey reports as it contributes to an assessment of quality.

The small loss of data was greater in shorter camera-trap durations, and as such, did not have an effect on the duration of days required to have a 95% probability of a rest; the sampling durations required were usually long enough that the proportion of lost simulations had substantially fallen to a negligible value. However, one site (Torqhuan) was missing 20 consecutive days and this led to a high proportion of excluded simulations. Excluding Torquhan due to the imperfect data, two periods of 35d (based upon Learmouth (18-19)) was the sampling effort required to have a 95% probability of detecting a rest (i.e. two periods of 5 weeks, one in winter, one in spring). This compares to a single sampling duration of 108 days (15.4 weeks) (based upon Learmouth (17-18)). Guidance states that protection is afforded to resting sites where there is a "*reasonable probability that the species will return*" (EU 2007). The detection of a single rest is likely to be sufficient to afford protection under the "precautionary principle". The precautionary principle in commercial ecology recognises that "*lack of scientific evidence should not be used as a reason for avoiding steps that might prevent environmental damage*" (Snell and Cowell 2006). Therefore, if only one rest was detected after two CT periods of 35d, it could be considered that subsequent rests may be likely given that the structure has been proved to be suitable for resting otter.

Using eight simulations from six resting sites may be considered too small to base any concrete recommendations on, but the method described here, provides a framework that could be repeated at more resting sites over a larger geographical range to enable refinements to any sampling protocol. In the absence of any other data, these analyses demonstrate the level of survey effort required. Consequently, surveys with low sampling effort such as two weeks that do not detect a rest, can readily be assessed as not being fit for purpose. If two sampling periods of 35d over a period of six months were introduced, given that there is currently no camera-trapping protocol for assessing the use of structures as otter resting sites, this may be perceived as a high level of monitoring. However, the cost of running the CTs is relatively cheap; the person-hours would be minimal. Each duration of monitoring would require a site visit to deploy the CTs, one maintenance visit after two to three weeks and a third visit to retrieve the CTs. The maintenance visit would be optional as high quality non-rechargeable batteries are likely to run for 35d. However, if a CT fails, or is stolen or flooded, this would be a significant loss of data, whereas a check mid-monitoring period could rectify any issues and the monitoring period extended until recommended number of CT days is reached. More frequent checking would not be advisable due to potential disturbance, and maintenance at approximately two week intervals did not cause any measurable differences in activity and scent-marking behaviour in the long-term study site (see Section 3.4.1). Two sampling periods of 35d would only be required if no rests were detected, if a rest were detected at any point, then monitoring could cease.

Derogation license applications require a statement on whether the structure is a breeding structure; in Scotland there is a presumption against granting a license for damage to, or disturbance of a structure currently used by breeding otter (Scottish Natural Heritage n.d) so determining that a site is a resting site may not be enough on its own for a license application especially if there is a method to determine breeding status.

The cost of analysis time of the videos or images would vary, but even if two full monitoring periods of 35d each were undertaken, the costs should not be prohibitive even with a dual CT arrangement. The main issue would be that there would be firmer seasonal guidance on when camera-trapping should be implemented, also that a 70d monitoring (if the two surveys are undertaken back-to-back) would be required to demonstrate that enough effort had been invested to determine a lack of evidence of resting.

4.6.7.2 Logistical constraints

For the evidence from the River Tweed sites to be used to generate generalisable guidelines for identifying resting sites, it is important that the sites sampled are representative of those that would be initially identified as potential resting sites by ecologists. The River Tweed sites were found by the same surveyor and had to have a low risk of inundation which precluded some potential sites. There were health and safety considerations surveying the larger rivers such as the rivers Tweed and Teviot, and safe access to CTs when the rivers were rising also had to be considered. This precluded some habitats that were potentially ideal, such as islands by old mill caulds (weirs that raise water levels to increase flow into mill lades) which were a common feature in the lower Tweed catchment, and also sections of river bank which were backed by steep wooded embankments. Additionally, features close to the water were excluded due to vulnerability of equipment coupled with the small distance between the water and entrance likely leading to missed detections due to soaking wet animals failing to trigger the CT (see Section 2.5.5). The logistical constraints of finding suitable sites will be the same as those encountered in other CT studies of otter resting sites, and the same as those encountered by consultants. The findings are therefore in context with the study mode.

Detection heterogeneity (i.e. differences in detection between sites due to topographical, vegetation and other differences), was an accepted constraint from inception of the study. In accordance with the findings from Chapters 2 and 3, CT deployment was designed to minimise false-negatives; two or more CTs were used at most sites with at least one CT at each site close (within 1.5m) to the structure entrance. Additionally, the otters were not expected to run though the field of view (and slower animals tend to have higher detection probability – see Chapter 2). Signs such as spraints indicated that otter had some interest in the sites included and were not simply passing through. It was anticipated that behaviour such as scent-marking and sniffing would result in loitering in the detection zone and field of view which increases the probability of capture (see 2.4.2). Only 8% (n = 13,847) of observations were defined as 'incomplete' (i.e. unpaired), for instance if an otter was observed exiting a structure with no prior entry recorded, indicating that detection success was at an acceptable level. This figure also includes occasions where there was a lack of certainty that an otter leaving the structure was the same individual as that observed entering, especially if there were groups of otter and/or repeated visits at the structure by single otters. These were recorded as single events (i.e. incomplete observations). However, they were related to the inability to distinguish individual otters and so were not entirely related to detection. The remaining observations were considered complete, in that the activity of the otter in relation to the structure was fully accounted. There are also likely to be false-negatives, where an otter was present, or rested, but this was not recorded at all. Although these cannot be quantified, they were minimised by careful deployment. Failure of the CT to trigger or register a pass, and activity during the re-arm time of the CT (i.e. the time between each successive videos of the same CT) are likely to be the primary causes of false-negatives. Both were minimised by using one or more close CTs which would have different detection areas and trigger at different times. Staggered trigger and re-arming times would make missed detections less likely.

The necessity for bespoke CT deployment at each site cannot completely avoid detection heterogeneity, although it was minimised as far as possible by informed deployment. These are unavoidable logistical constraints which were managed to minimise false-negatives, however their impact on the applied findings is not of major concern as they are issues that a practitioner will also be faced with.

4.6.8 Conclusions

Of 26 sites studied, six were confirmed as resting sites by camera-trapping observations with two more resting sites implied from behavioural indicators. Rests at thr ee study sites occurred almost exclusively in winter and spring and were also generally more active in terms of number of CT days otters were observed, and the number of observations of otter per CT day during these seasons. Latrine behaviour and bedding collection were exclusively observed at the resting sites and can be used as a strong indicator of resting when observed on CT footage. All resting sites were used by at least one otter, and there was repeated use of structures within, and between years. These structures would qualify as resting sites under the Habitat Regulations where guidance states that resting places are "*areas essential to sustain an animal or group of animals when they are not active*" and that there is "*reasonable probability that the species will return*" to use the site/place (EU 2007). Furthermore, the use of CTs enables nocturnal resting sites to be confirmed and studied, which is out with the usual remit of radio-tracking studies.

The observations on the River Tweed provide a basic understanding of what activity can be expected at resting sites and non-resting sites. The study contributes a strong evidence-base towards methodological considerations such as seasonal constraints and minimum sampling effort to determine if a structure is used for resting (see Chapter 6 for further discussion).

Chapter 5 Can field-signs alone be used to identify an otter resting site

5.1 Abstract

Otter resting sites are protected by UK and European legislation. Ecological consultants must identify otter resting sites so they can be fully considered during development projects. Field-signs are usually used to identify resting sites, but the relationship of field-signs to resting sites is assumed. This study aims to test whether quantity or patterns of field-signs can be used to identify resting sites, and whether some types of field-sign are more reliable than others. Intensively camera-trapping 26 structures across the River Tweed catchment (Chapter 4) provided a data set of resting and non-resting sites to compare field-signs between and within. Field-signs were recorded at each site at approximately three-week intervals for approximately a year. Each site was monitored with camera-traps to determine which sites were resting sites. Otter latrines (i.e. significant accumulations of droppings where a count of deposits is not possible, see Glossary, P11) were the only reliable field-sign indicator of a resting site. Presence of bedding could be used, however potential confusion with bedding dropped by badgers and windblown vegetation make this less reliable. Other field-signs (spraint counts, presence of a path, presence of spraint piles) were not related to whether a site was a resting site or not. Spraint counts in the vicinity of the structure were higher at resting sites if the site had recently been used for resting, but this trend was not strong and could not be applied to any field survey protocol. This study found that it is unlikely that most field-signs could be used to reliably identify resting sites, except for the presence of an active latrine. Previous literature is ambiguous in the distinction between spraint sites and latrines, but these should be treated as different types of field-signs as they have different morphology and different functions are inferred. A spraint is a small faecal deposit used to scent mark while a latrine is a large mass of faeces comprising uncountable droppings. This study concludes that camera-traps are required to complement field-sign surveys to increase the accuracy of resting site identification.

5.2 Introduction

Guidance notes by statutory authorities (Scottish Natural Heritage; Northern Ireland Environment Agency 2017; Natural England and Department for Environment Food & Rural Affairs 2019) state that an otter surveyor must identify otter resting sites as holts (underground structures) or couches (above ground resting sites) but offer no further advice on methods to do so. The has led to a practice where consultants can only state in report methodologies that otter resting sites will be found and classified as a couch or a holt as there is no industry guidance (pers. obs.). In addition to identifying whether a structure is a resting site or not, there is also a need to determine if the site is used for breeding and if it is currently active. Breeding sites are more significant in Ecological Impact Assessments, and impacts from construction can be avoided or reduced by avoiding times when the resting or breeding site is active (CIEEM 2019).

Therefore, there is a need to establish whether field-signs can be used to (a) identify resting and breeding sites and also (b) determine current occupation (i.e. whether one or more animals are in the structure or have been recently). Using field-signs is likely to be the most time-efficient, cost-effective and accessible method, but a reliable approach is needed. Comparing interpretation from field-sign surveys with another method, that is more time-consuming but which can reliably identify resting sites and recent usage, such as a CT survey could validate the use of field-signs and enable a more prescriptive method of identifying resting and breeding sites from field-signs. However, if this relationship cannot be validated, there would be a need for an alternative approach such as CT surveys, but this too would need a robust survey protocol.

Previously underlying assumptions have been made that spraint at a structure indicates a resting site, and that the amount of spraint relates to the frequency of resting (e.g. Waldemarin and Colares 2000). Other field-signs (or field evidence) such as bedding, presence of an otter path (often termed an “otter slide”), finding otter hairs and otter footprints have all been all perceived as indicators of resting when found at a structure which is assessed as offering potential shelter (O’Sullivan 1993). Using spraint and other field-signs to indicate resting sites would be robust if such field-signs were always, and only ever, present at resting sites, or if there was a clear difference in the magnitude, pattern or type of field-signs left at resting sites and non-resting sites. Otters have numerous spraint sites, using features such as prominent rocks, the shores of small islands, under bridges and at river confluences (Ruiz-olmo et al. 2001; Prigioni et al. 2006). They can also use vegetation to accentuate spraint sites, scratching up vegetation to produce a mound before sprainting on it, often referred to as a "sign heap" (Erlinge 1967; Mason and Macdonald 1987b), which can sometimes give the appearance of abandoned bedding (pers. obs.). As spraint has been used as a key indication of a resting site when it is found at a feature that may offer shelter, it would be critical to be able to distinguish sprainting activity associated with a resting site from "regular" spraint sites, if such a distinction exists. Many factors are thought to affect sprainting behaviour such as season, breeding status and habitat, (see Section 1.1.3 for discussion of sprainting). Any differences in variation of the number or spatial arrangement of spraints at resting sites and non-resting sites would need to be consistent if it is to be used as a diagnostic feature to identify resting sites. The correct identification of field-signs is also important, and whilst some field-signs are well described such as footprints, rolling places, slides runs, spraint sites and sign heaps (Erlinge 1967), those such as bedding and latrines at resting sites are not explicitly described.

To my knowledge, published studies that link field-signs to the use of resting sites are limited to the coastline of the Shetland Isles (Kruuk et al. 1989; Kruuk 1992); a group of islands between Scotland and Norway. There are fundamental differences between the Shetland population of otters and mainland riparian otters. Otter home-ranges are generally smaller on Shetland and otters are active during the day (Kruuk and Moorhouse 1991a); their coastline habitat comprises treeless peatlands and so holts are usually burrow structures readily found in the open habitat (Moorehouse 1988). Shetland holts are typically burrows in peat with polished (smooth) entrances that are wider than their height, with accumulations of spraint, prints and soiled vegetation outside, and importantly, they can be confirmed by watching otter activity at holts (Moorehouse 1988). Using field-signs to identify holts is a standard approach for other species of otter. For example, the survey protocol for the giant otter *Pteronura brasiliensis* states that holts are one of the main features that confirm presence of the species (Groenendjik et al. 2005). The protocol identifies giant otter holts as large, riverside burrows, with a flattened area outside which has a surface layer of dispersed hard parts of fish, and tracks in or leading to the entrance. It is therefore understandable why identifying Eurasian otter holts using field-signs is not questioned, especially given the legislative imperative to protect such sites during development.

Many studies have been undertaken to find drivers of sprainting behaviour by looking at spraint distribution (see Section 1.1.3), but few have looked at spraint in relation to resting sites. Visual observations of otters at holts on Shetland recorded otters sprainting at holts before entering (10 occasions), sprainting outside a holt without entering (11 occasions) and entering a holt without sprainting (14 occasions). Visits to holts with no sprainting were also observed (2 occasions) (Moorehouse 1988). This indicates inconsistent sprainting behaviour at holts, but analysis was not taken any further. At spraint sites, a correlation has been found between spraint counts and visitation rates of both the Eurasian otter (Guter et al. 2008) and the northern river otter (Day et al. 2016) by pairing visits recorded by video recording and daily spraint counts. Spraint counts were less successful in quantifying the number of otter registrations, but there was a positive, but weak, relationship between otters registered by cameras and spraint counts in both studies. Therefore, one could hypothesise that a high number of spraints at a resting site equates to a higher number of times an otter has been present. However, camera-trapping on the River Tweed has demonstrated that sites can have very high levels of otter visits without being rested in (see Table 4-10, p117), challenging the assumed link between high otter presence at a structure and it’s use as a resting site.

5.2.1 Aims

The three aims of this chapter are: (i) to provide descriptions of field-signs found at 26 structures known to have been visited by otters across the River Tweed catchment (described in Chapter 4); (ii) given that these structures contained known resting and non-resting sites, to test the assumption that field-signs can be used to identify resting sites, and (iii) within the six known resting sites, to test whether there was a relationship between field-signs and recent resting behaviour (i.e. current occupancy).

5.3 Methods

This study uses the CT data collected at the 26 study sites on the Tweed in combination with field-signs which were collected at each site when the CTs were maintained (i.e. when the CT unit was exchanged with a different one with fresh batteries and empty SD card). The selection, location and CT monitoring methods were described in Section 4.3, with details of field-signs collection described here.

Each time sites were visited for change-over of cameras (see Section 4.3.3), an inspection of the structure was also undertaken where possible, and field-signs were recorded (Table 5-1). However, on 19% (n = 396) of maintenance visits, it was not possible to collect field-signs as the water levels were too high to safely climb down the bank sufficiently to view the structure, or the area outside the structure was submerged. To minimise disturbance, field-sign data were collected only on maintenance visits during daylight hours and not between maintenance visits.

Table 5-1 Summary of field evidence recorded at each site on each camera-trap maintenance visit

Field evidence	**Units**	**Descriptions**
Recorded within each distance band from structure (at entrance, to 1m and 1—5m)		
SPRAINT	Count	The number of individual spraints, including an estimate of spraints within spraint piles
SPRAINT PILES	Count	Count of piles with ≥ 4 spraints
Recorded within chamber, tunnel and entrance to 1m		
BEDDING	Present/absent	Clumps of loose vegetation that are out of context with surroundings e.g. clump of loose moss on bare ground outside structure
Recorded as present/absent across all distance bands combined		
LATRINE	Present/absent	Characterised by large collection of droppings creating a distinct area with lateral spread over ground/substrate.
PATH	Present/absent	Presence of a path linking structure to water
SUBSTRATE FOR FOOTPRINTS	Present/absent	Substrate within 5m of structure which would potentially register footprints such as deposited silt or mud.
FOOTPRINTS	Present/absent	Otter footprints, sub-categorised as adult or young.

When recording the field-signs, the aim was to record what was present but not to distinguish what was new since the last visit as there was no intention to compare the field-signs from one survey to the next. Therefore, the data represented what a field surveyor would find with no prior knowledge of the structure. Field evidence was also recorded with no prior review of the CT footage.

To keep disturbance to a minimum, the inspection was non-invasive (i.e. did not include an endoscope or use of a torch inside the structure). This would emulate the level of inspection available to a non-licensed ecologist. Although I did hold a license for invasive surveys at sites in both Scotland and England, most ecologists do not hold a license to disturb otters when surveying (pers.obs.); using a torch inside a structure suspected to be a resting site would constitute disturbance. According to the type of structure, field signs were identified (see Brown et al. 2004) and recorded within five discrete spatial areas: (i) “chamber” - the assumed sleeping area characterised by a flat, dry area of a minimum of 50cm with/without bedding; (ii) “tunnel” - any area of tunnel/burrow visible from the entrance to the structure; (iii) “entrance” - the threshold where the cover from the structure becomes open; (iv) “1m zone” - from the entrance to 1m, excluding any spraint at the entrance threshold; and, (v) “5m zone” - the area within 1—5m of the entrance. The ability to record signs in the (i) chamber and (ii) tunnel was often not possible for some sites, but they were recorded in all cases where they were visible without an invasive search.

Signs were not recorded beyond 5m as the topography made accessing some of the steep riverbanks difficult; extending the search further than 5m would result in inequality of survey between sites. The distance of 5m was considered an achievable standard for most sites. Additionally, it was assumed that signs beyond 5m would be less likely to be associated with a structure by a field surveyor.

Most categories of field evidence were recorded as being present or absent, for example bedding and otter footprints (see Table 5-1). Spraints, however, were counted. Spraints are rarely deposited as neat parcels, they are usually amorphous or semi-amorphous. Scattered spraints could be counted with reasonable accuracy, but several deposits in the same area, such as on the same tree root, had to be estimated by looking at the amount and differences in weathering of the deposits as well as identifying individual deposits where possible from their form. 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. Spraint piles were also counted, defined as four or more spraints being deposited directly on top of each other. The spraint counts included an estimate of the deposits within any spraint piles, e.g. a pile of eight spraints and two single spraints would be recorded as a count of 10 spraints and one spraint pile. It was accepted that the spraint counts would not be fully accurate, but application of a consistent approach would enable valid comparisons between sites, and these limitations would also be faced by practitioners. During the fieldwork, substantial accumulations of spraints/droppings were found at some structures. The individual deposits in these accumulations could not be counted, they formed an uninterrupted mass of droppings at least 15cm across and several cm deep. These were recorded separately from the spraint counts as “latrines” (examples shown in Figure 5-1a, b & c). In some instances the latrines contained a mix of amorphous deposits (Figure 5-1a) whilst the droppings in other latrines were drier with a three-dimensional form (Figure 5.1b & c).

The presence of a path linking a structure to the water is purported to be evidence of a breeding or natal site (Liles 2003). Therefore, the presence of a path was recorded, this could be a path though the vegetation, or a pathway of trampled or compacted earth when on bare ground (Figure 5.1d & e).

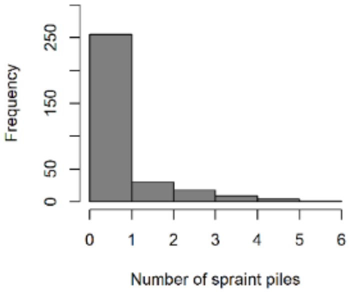
Figure 5-1 Examples of field-signs identified at study sites: (a) a latrine on open ground at Gordon; (b) a latrine sheltered by the structure at Learmouth; (c) a latrine at Frogden1 (note cylindrical pellet droppings); (d) a well-defined otter path with a smooth, compacted substrate and no vegetation at Eden1 between the structure and the water (e) a well-defined otter path through vegetation at Learmouth linking the structure to two watercourses.

5.4 Analyses

5.4.1 Simplification of variables

The sample size and number of levels in ordinal and categorical variables had to be rationalised to reduce the number of parameter estimates in models. The rationale for simplification of variables is described in Table 5-2.

Table 5-2 Simplification of field data to reduce complexity of models, .BIN has been used to denote binary variables

Variable	**Simplified variable**	**Description of simplified variable**	**Rationale**
Footprints	Not used	Not used	Of 67 observations where suitable substrate was present, footprints were only found at 15. Footprints were excluded from further analyses
Bedding	BED.BIN	Presence or absence	Bedding can be moved by wind and animals
Spraint piles	SPILES.BIN	Presence or absence	There were zero counts for 68% of 319 observations and a limited count range 1—6 when present. 
Spraint counts	SPRAINT1M	Spraints count at the entrance and to 1m	Spraint could not be seen in the chamber and tunnel of most of the closed structures, so these categories were not included. Categories included can be applied to all structures
	SPRAINT1.5M	Spraint count 1—5m from entrance	
	ALLSPRAINT	Sum of SPRAINT1M and SPRAINT1.5M	

5.4.2 Can field evidence be used to distinguish resting sites from non-resting sites?

Models were constructed to determine if field-signs were related to whether a site was a resting site or not. Resting site was used as a binary response variable (1 = site used for resting over whole study duration, 0 = site not used for resting) and site was used as a random factor within a generalised linear mixed model structure with a binomial error distribution. A hypothesis-driven list of candidate models (Table 5-3) was created using explanatory variables from Table 5-2.

Models were fitted to the data in R studio (RStudioTeam 2015), using package lme4 (Bates et al. 2015) and MuMin (Barton 2016) to generate model comparison tables. Models were compared using AIC, and models with a Δ_{AIC} of ≤ 2 were considered as having good support (Burnham and Anderson 2004).

Mill2 was omitted from the analysis as it was unclear whether this was a regularly used resting site (see Section 4.5.1). Additionally, it was the most difficult site to access and conditions were rarely conducive to count spraint to a 5m radius. Marlefield was also excluded as only one rest was recorded there (see Section 4.5.1). Crailing, Frogden1, Frogden2, Gordon, Learmouth and Torquhan were coded as resting sites as each had multiple recorded rests (see), and the remaining 24 sites were considered non-resting sites during their monitoring.

The models were initially fitted to the dataset containing all seasons (n = 297 CT maintenance visits where field-signs were surveyed). They were then fitted to a subset of field data including winter and spring which are the seasons when 95% of rests occurred (n = 141) (see Section 4.6.3).

Table 5-3 Candidate model set of generalised linear mixed models, using site as a random factor and Y as a binary response variable of whether the site is a resting site (1) or not (0).

Model set	Key to Explanatory variables
Y ~ NULL MODEL Y ~ BED.BIN Y ~ PATH Y ~ SPRAINT1M Y ~ ALLSPRAINT Y ~ SPRAINT1.5M Y ~ SPILES.BIN Y ~ BED.BIN+SPILES.BIN Y ~ PATH+SPILES.BIN Y ~ SPRAINT1.5M+PATH Y ~ SPRAINT1.5+BED.BIN	ALLSPRAINT: count of spraints from and including entrance to 5m BED.BIN: presence/absence of bedding to 1m PATH: presence/absence of path within 5m SPRAINT1M: count of spraints from and including entrance to 1m SPRAINT1.5M: count of spraints from 1—5m SPILES.BIN: presence/absence of spraint piles to 5m

5.4.3 Can field evidence be used to evaluate recent use of a resting site?

The previous analysis (Section 5.4.2) examined whether field evidence can be used to distinguish a resting site from a non-resting site. Once a resting site has been confirmed using CT data, it is often necessary to know at a later date if it is in current use, for example to decide if potentially disturbing construction activities can go ahead. The following analysis is therefore restricted only to sites I identified as resting sites and aims to determine whether field evidence can be used to assess if a structure has recently been used for resting.

This analysis used a subset of data only containing the six habitually used resting sites (i.e. Crailing, Frogden1, Frogden2, Gordon, Learmouth and Torquhan). Continuous CT data immediately prior to the field-signs being recorded was required, so that the field-signs could be analysed in context with any rests recorded on the CTs. There were 129 maintenance visits to the six resting sites, and, of these, field-signs were recorded on 106. For this analysis, the CTs needed to have been operational prior to the collection of field-sign data, but camera-malfunctions would reduce the sample size. To avoid excessive reduction of sample size, the analyses included observations of field evidence where a minimum of the close CT (the CT within 1—1.5m of the structure entrance) was running for the previous 10 days, thus reducing the sample size to 97.

Two variables relating to otter rests were derived from the camera-trapping data. For the five-day periods prior to each of the dates when field evidence was collected, a binary variable was created to denote if resting had been recorded at the structure or not (DAY5PRIOR, 1 = at least one rest recorded, 0 = no rest recorded). A second variable was similarly created for the previous 10 days prior to collection of field evidence (DAY10PRIOR).

A hypothesis-driven list of candidate models was constructed (Table 5-4). These were fitted to the data, first using DAY5PRIOR as the response variable, then using DAY10PRIOR. Models had a generalised linear mixed model structure with a binomial error distribution. Models were compared using AIC, and models with a Δ_{AIC} of ≤2 were considered as having good support (Burnham and Anderson 2004).

Table 5-4 Candidate model set fitted to the data when Y is a binary variable of presence or absence of a rest in the previous five days before field evidence was collected. The models were refitted when Y is a binary variable of presence or absence of a rest in the previous five days before field evidence was collected.

Model	Key to explanatory variables
Y ~ NULL MODEL Y ~ BED.BIN Y ~ PATH.BIN Y ~ SPRAINT1.5M Y ~ ALLSPRAINT Y ~ SPRAINT1.5M Y ~ BED.BIN+SITE Y ~ SPILES.BIN Y ~ BED.BIN+SPILES.BIN Y ~ PATH.BIN+SPILES.BIN Y ~ SPRAINT1M+SITE Y ~ SP.ALL+SITE Y~ SPILES Y~SPRAINT1.5M+PATH.BIN Y~SPRAINT1.5M+BED.BIN	ALLSPRAINT: count of spraints from and including entrance to 5m BED.BIN: presence/absence of bedding to 5m PATH.BIN: presence/absence of path within 5m SPRAINT1M: count of spraints from and including entrance to 1m SPRAINT1.5M: count of spraints from 1—5m SPILES.BIN: presence/absence of spraint piles to 5m

5.5 Results

5.5.1 *Summary of field evidence*

The individual types of field-signs observed are initially described and summarised, followed by the results of the analyses relating field-signs to otter activity.

5.5.1.1 Latrines

All confirmed resting sites had latrines (single latrines at Crailing, Frogden2, Learmouth and Torquhan; two latrines at each of Frogden1 and Gordon). Of these, the latrines at Frogden2, and one of the latrines at Frogden1 were within the structure and finding them required an invasive search which was undertaken after monitoring had ceased. Invasive searches of these sites were carried out as latrine behaviour had been observed on the CT footage which was not watched until monitoring had ceased in order to avoid bias. The latrine at Torquhan was observed after the structure, a hollow ash *Fraxinus excelsior* tree, was blown over by high winds after monitoring ceased. This latrine had been fully concealed and was not in the field of view of the CTs and could not be seen during CT monitoring or normal field-sign data collection.

Mill2 had a disused latrine at commencement of monitoring (Figure 5-2) which was washed away after five weeks by a spate. Mill2 was latterly thought to have been an active resting site during the monitoring period although this had not been observed using CT data (see Section 4.4.1).

Figure 5-2 Latrine at Mill2, with head torch for scale and approximate area of latrine indicated by dashed line. One of the entrances is within 0.5m of the latrine.

A latrine was also present at Maxton when the site was initially found during walked surveys to locate potential structures for this study (see Section 4.3.3). However, this latrine was never refreshed, and resting behaviour was not recorded during CT monitoring. This latrine was in a semi-covered tunnel above the level of the most extreme spates experienced during the monitoring period. It was found on 4/6/17 and was considered absent by 19/2/18, thus lasting for up to 36 weeks without being refreshed but was never submerged by the river and was only likely to be rained on in extreme rain/wind.

Table 5-5 Location of latrines associated with resting sites. “Initial” and “second” refer to the order they were observed. Sites where latrines were not observed during the data collection phase, but only after invasive search at the end of data collection are in italics.

Within structure	Within 1m of entrance	Within 5m of entrance
Crailing	Gordon, second latrine	Frogden1, initial latrine
Frogden1, second latrine	Maxton	
Frogden2	Mill2	
Gordon, initial latrine		
Learmouth		
Torquhan		

The Learmouth latrine was made by the otters during the monitoring period and was visible as part of the non-invasive surveys for field-signs. The latrine was first recorded on 27/3/19 following six rests documented on CTs between 12/2/19 and 27/3/19. The last resting activity prior to 12/2/19 had been in June 2018.

5.5.1.2 Bedding

Vegetation within the chamber of the structures was seen at three resting sites, Gordon, Frogden2 and Torquhan. At Gordon, this was clearly a “made” nest (Figure 5-3) comprising a large amount of collected vegetation with a central depression where an animal has lain. Similarly, at Frogden2, there was a large quantity of bedding, often partially blocking the entrance, although bedding collection was only observed on CTs by badgers. Small amounts of fresh green bedding were observed in the hollow tree at Torquhan but these didn’t form a nest structure.

Loose vegetation within 1m of the structure, interpreted as dropped bedding material, was found at four of the non-resting sites, although at one of these (Hownam) bedding collection was observed by badgers (Table 5-6). On 26 occasions, bedding was noted in the field with no bedding collection behaviour detected on the CTs. However, at Frogden2 and Gordon, the nests were present throughout monitoring, so 23 of these observations referred to the presence of a nest with no active bedding collection recorded on CTs.

At the non-resting sites, ‘bedding’ was recorded but with no corroborating CT footage of bedding collection by any species on 14 occasions, these field observations were likely to have been incorrect interpretations of the origin of the vegetation, e.g. it may have been windblown debris.

There were also seven instances where bedding collection by otter was recorded by the CTs but not recorded at the subsequent inspection for field-signs, presumably as none had been dropped, or any dropped vegetation had blown away. The collected bedding was out of sight within the structure. These observations indicate that field-signs are not an accurate reflection of activity. There is potential for false-negatives (no bedding observed in the field yet CTs showed bedding being collected) and also false-positives (apparent bedding observed in the field yet CTs do not show any bedding collection) in terms of recording of bedding.

Figure 5-3 Nest of collected bedding at the resting site at Gordon, a partially open hollow alder *Alnus glutinosa* tree

Table 5-6 Frequencies of contingencies, at resting and non-resting sites, of observations of bedding material recorded in the field at a maintenance visit (a) and whether bedding collection was recorded on the camera-traps on footage since the last maintenance visit by (b) otters, or (c) badgers. Y = yes, N = no. The figures are based on periods when field evidence was recorded, and data was available from camera-traps (noted in brackets).

Contingency			Frequency of contingency at resting sites and non-resting sites	
(a) Bedding recorded in field	(b) Bedding collection by otter observed on CT	(c) Bedding collection by badger observed on CT	Resting site (n = 87)	Non-resting site (n = 181)
Y	Y	N	7 (8%)	0 (0%)
Y	N	Y	4 (5%)	4 (2%)
Y	N	N	26 (30%)	14 (8%)
N	Y	N	7 (8%)	0 (0%)
N	N	Y	1 (1%)	1 (0.5%)
N	N	N	42 (48%)	162 (88%)

5.5.1.3 Paths

The presence or absence of an otter path at each site showed little change over time and between sites. At ten sites, a path was never present, two of which were resting sites, Torquhan and Frogden2; there was soft grassy vegetation in front of Torquhan which would have registered a path. A climb of about 1m up a large willow tree was necessary to access the entrance of Frogden2, which would need considerable traffic of either otter or badger to register wear or staining on the bark. Gordon also had an entrance approximately 1m up a tree, and a near vertical stained run was clearly visible on the outside of the trunk (see tinyurl.com/thsy9jn).

A path was present at every visit at three confirmed resting sites (Crailing, Gordon and Learmouth), and Mill2 which was probably a resting site (Section 4.4.1). A path was present at every visit at the non-resting sites Nenthorn, Hownam and Eden1.

5.5.1.4 Spraint counts and spraint piles

The number of spraints at resting sites and non-resting sites are summarised in Table 5-7. These suggest there is a greater difference in spraint numbers in the general vicinity of the structure (i.e. in the distance zone of 1—5m compared to near the immediate structure entrance).

Table 5-7 Summary of spraint counts at resting sites and non-resting sites

	Count to 1m		Count from 1 to 5m	
	Resting	Non-resting	Resting	Non-resting
Number of observations (n)	106	213	106	213
% of observations with presence of spraint	66%	65%	3%	38%
Median	2	1	0	0
1st Quartile	0	0	0	0
3rd Quartile	4	6	5	2
Max	18	20	54	15

In the winter and spring, the median spraint counts at resting sites were generally higher close to the holt (i.e. the entrance and to 1m), with less spraint between 1m and 5m (Table 5-7). The median count between 1m and 5m is notably higher in the summer whilst the autumn count is negligible at both non-resting sites and resting sites.

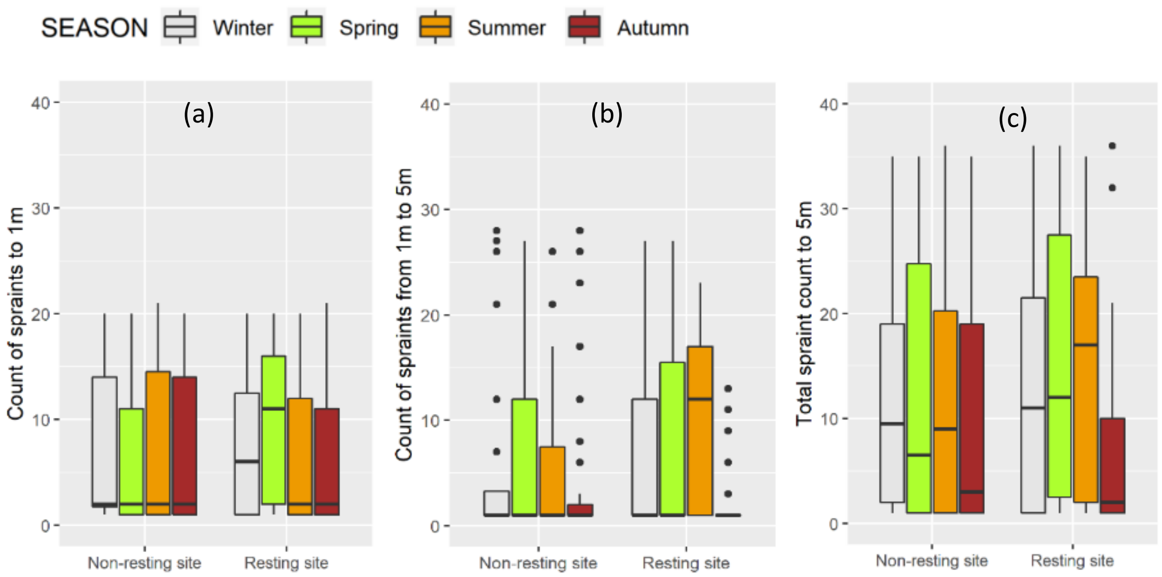


Figure 5-4 Distributions of spraint counts to different distances from entrance by season and resting site vs non-resting site (a) includes spraint at the entrance and to 1m, (b) from 1m to 5m, and (c) total spraint count from entrance to 5m

The number of spraint piles at resting sites and non-resting sites are summarised in Table 5-8.

Table 5-8 Summary of the counts of spraint piles at resting and non-resting sites

	Resting site	Non-resting
Number of observations (n)	106	213
% of observations with presence of spraint pile	37%	30%
Median	0	0
1st Quartile	0	0
3rd Quartile	1	1
Max	6	5

5.5.1.5 Footprints

Observations of conditions that were suitable to register footprints were infrequent (19% of all observations) with nine sites never having suitable substrate within 5m of the structure. Footprints were therefore very rare, adult footprints were registered within 5m of the structure in only 5% of all observations (24% of all observations where suitable substrate was present). They were observed once at four non-resting sites, and once at Mill2 which is thought to have been a resting site. At resting sites, they were recorded at Frogden1 on five occasions and Learmouth on two occasions. Prints within 1m of the structure were rarer still, with three non-resting sites having a single observation of adult prints per site. Cub footprints were recorded once, within 5m of a non-resting site (Yetholm Loch).

5.5.2 Can field evidence be used to distinguish resting sites from non-resting sites?

Models in Table 5-3 were fitted to data including all four seasons to determine whether field-signs were related to whether a site was a resting site or not. Seven models have $\Delta_{AIC} \leq 2$, however the null model has the most support (Table 5-9). Even though the support for the null model is poor, with a model weight of 0.26, the remaining models are not considered further because the null hypothesis could not be excluded.

The fitting of the same models in Table 5-3 were repeated using a subset of data from winter and spring, the period when 95% of rests were recorded. Again, seven models have a $\Delta_{AIC} \leq 2$ with the null model having the most support, so the models with less support are not considered further (Table 5-10).

Table 5-9 Model selection table, using data from all seasons, when the binary response variable is whether the site was a resting site or non-resting site. Explanatory variables are explained in Table 5-2. A + indicates inclusion of a categorical variable. Models with $\Delta_{AIC} \leq 2$ are in bold and represent the models with most support and the null model is in italics. df = model degrees of freedom, logLik = log likelihood of the model, AIC = Akaike information criterion, Δ_{AIC} = difference in AIC between that model and the model with the lowest AIC, and W_i = Akaike's weight.

MODEL	(Int)	SP.ALL	BED -DING	SPRAINT 1M	PATH .BIN	SPRAINT 1.5M	SPILES .BIN	df	logLik	AIC	Δ_{AIC}	W_i
NULL MODEL	***-15.31***							***2***	***-10.05***	***24.10***	***0.00***	***0.26***
BED.BIN	**-15.58**		**+**					**3**	**-9.99**	**25.99**	**1.89**	**0.10**
PATH.BIN	**-15.67**				**+**			**3**	**-10.04**	**26.08**	**1.98**	**0.10**
SPRAINT1.5M	**-15.44**					**0.02**		**3**	**-10.05**	**26.09**	**1.99**	**0.10**
SPILES.BIN	**-15.42**						**+**	**3**	**-10.05**	**26.09**	**2.00**	**0.10**
SPRAINTALL	**-15.45**	**0.01**						**3**	**-10.05**	**26.09**	**2.00**	**0.10**
SPRAINT1M	**-15.42**			**0.02**				**3**	**-10.05**	**26.10**	**2.00**	**0.10**
BED.BIN+SPRAINT1.5M	-15.67		+			0.02		4	-9.99	27.98	3.88	0.04
BED.BIN+SPILES.BIN	-15.63		+				+	4	-9.99	27.98	3.89	0.04
PATH.BIN+SPRAINT1.5M	-15.76				+	0.02		4	-10.04	28.07	3.97	0.04
PATH.BIN+SPILES.BIN	-15.75				+		+	4	-10.04	28.07	3.97	0.04

Table 5-10 Model selection table, using subset of data including winter and spring when the binary response variable is whether the site was a resting site or non-resting site. Explanatory variables are explained in Table 5-2. A + indicates inclusion of a categorical variable. Models with $\Delta_{AIC} \leq 2$ are in bold and represent the models with most support and the null model is in italics. df = model degrees of freedom, logLik = log likelihood of the model, AIC = Akaike information criterion, Δ_{AIC} = difference in AIC between that model and the model with the lowest AIC, and W_i = Akaike's weight.

MODEL	(Int)	SP.ALL	BED -DING	SPRAINT 1M	PATH .BIN	SPRAINT 1.5M	SPILES .BIN	df	logLik	AIC	Δ_{AIC}	W_i
NULL MODEL	***-13.98***							***2***	***-9.83***	***23.66***	***0.00***	***0.26***
BED.BIN	**-13.92**		**+**					**3**	**-9.69**	**25.38**	**1.72**	**0.11**
PATH.BIN	**-14.30**				**+**			**3**	**-9.82**	**25.65**	**1.98**	**0.10**
SPRAINT1M	**-14.23**			**0.04**				**3**	**-9.82**	**25.65**	**1.99**	**0.10**
SPRAINT1.5M	**-14.12**					**0.02**		**3**	**-9.83**	**25.65**	**1.99**	**0.10**
SPRAINTALL	**-14.16**	**0.01**						**3**	**-9.83**	**25.66**	**1.99**	**0.10**
SPILES.BIN	**-14.06**						**+**	**3**	**-9.83**	**25.66**	**2.00**	**0.10**
BED.BIN+SPILES.BIN	-13.98		+					4	-9.69	27.38	3.71	0.04
BED.BIN+SPRAINT1.5M	-14.32		+			0.02		4	-9.71	27.42	3.76	0.04
PATH.BIN+SPRAINT1.5M	-14.43				+	0.02		4	-9.82	27.64	3.98	0.04
PATH.BIN+SPILES.BIN	-14.36				+		+	4	-9.82	27.64	3.98	0.04

5.5.3 Can field evidence be used to predict recent resting behaviour?

While field evidence could not predict whether a site was a resting site or not, there was good support for a relationship between a rest having been detected in both the previous five days and the count of spraints between 1 and 5m (Table 5-11 and Figure 5-5a). In the preferred models with $\Delta_{AIC} \leq 2$, all the models showed a positive relationship between the explanatory variables and the response variables. The presence of bedding and spraint count between 1 and 5m was related to a slightly higher probability of resting behaviour having occurred in the previous 5 days (Figure 5-5b) and the presence of a path was also related to a slightly higher probability of resting behaviour having occurred (Figure 5-5c) although these effects were small.

The trends seen in the models using rests detected in the previous 10 days mirrored those seen in the models using the five-day response variable, but the trends were generally weaker. Again, there was most support for a relationship between resting behaviour having occurred in both the previous 10 days and the count of spraints between 1 and 5m (Table 5-12 and Figure 5-6a). The presence of bedding had a higher probability of resting behaviour having occurred than no bedding with the spraint count to 1—5m (Figure 5-6b). The remaining models with $\Delta_{AIC} \leq 2$ supported a positive relationship of spraint count at 1m (Figure 5-6c), a spraint count to 5m (Figure 5-6d) and the spraint count 1—5m with the presence of a path (Figure 5-6e).

None of the trends in Figure 5-5 and Figure 5-6 were definitive, with the maximum probability of a rest having occurred in the 5 days and 10 days prior being approximately 60% at the highest recorded numbers of spraints, so there was still a reasonable chance of having high numbers of spraints without a recent rest having occurred.

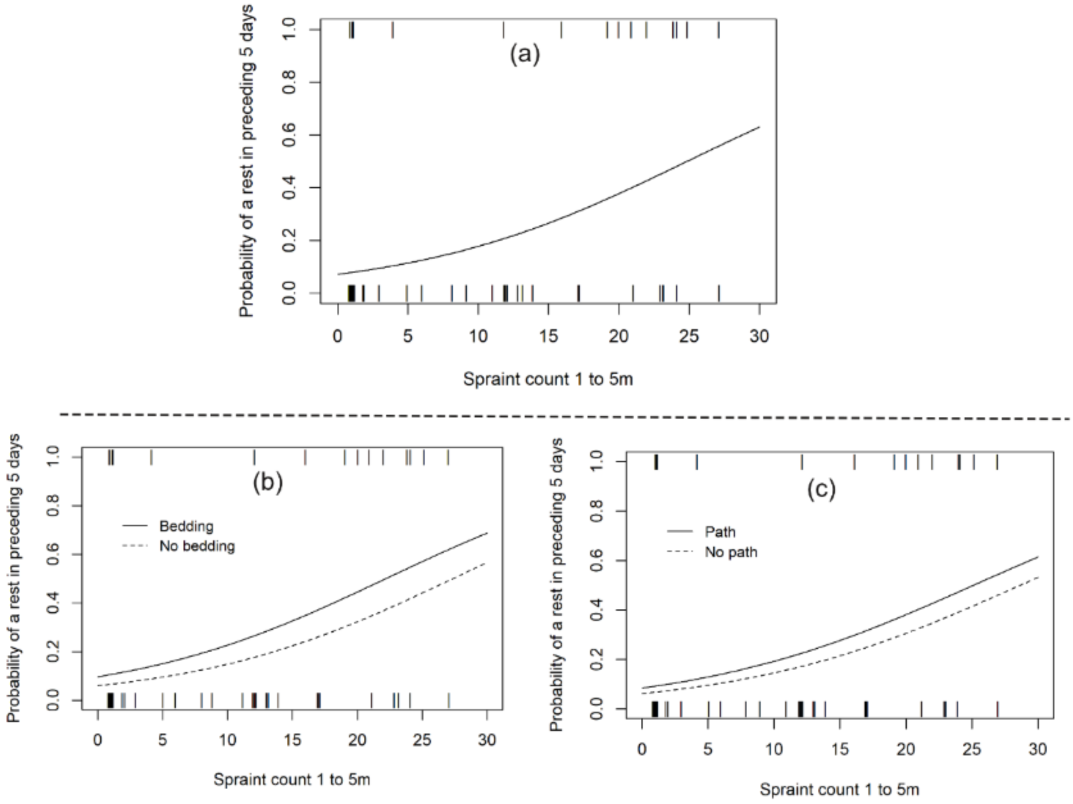


Figure 5-5 Plots of models with most support ($\Delta_{AIC} \leq 2$) in Table 5-11, (a) best supported model, spraint count 1—5m; (b) spraint count 1—5m and presence of bedding, and (c) spraint count 1— 5m and presence of a path. Distribution of binary data when Y = 0 and Y = 1 indicated by '|' symbol.

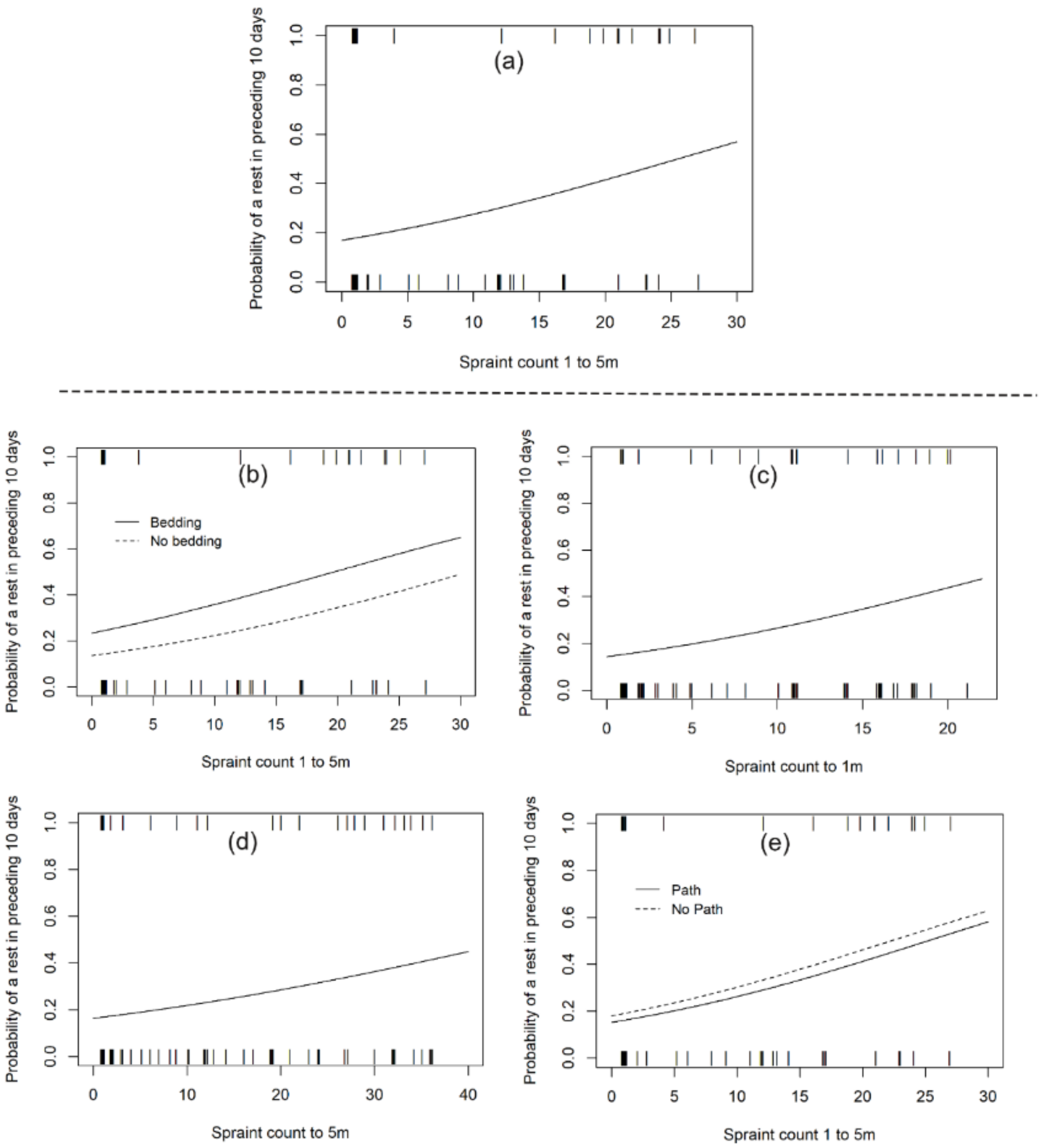


Figure 5-6 Plots of models with most support ($\Delta_{AIC} \leq 2$) in Table 5-12, (a) best supported model, spraint count 1—5m; (b) spraint count 1—5m and presence of bedding; (c) spraint count to 1m; (d) spraint count to 5m, and (e) spraint count to 5m and presence of a path. Distribution of binary data when Y = 0 and Y = 1 indicated by ‘|’ symbol.

Table 5-11 Model selection tables where Y=where rest detected in previous five days. Explanatory variables are explained in Table 5-2. A + indicates inclusion of a categorical variable. Models with $\Delta_{AIC} \leq 2$ are in bold and represent the models with most support and the null model is in italics. df = model degrees of freedom, logLik = log likelihood of the model, AIC = Akaike information criterion, Δ_{AIC} = difference in AIC between that model and the model with the lowest AIC, and Wi = Akaike's weight.

	(Intercept)	BED .BIN	PATH .BIN	SPRAINT 1M	SPRAINT ALL	SPRAINT 1.5	SITE	SPILES .BIN	df	logLik	AIC	Δ_{AIC}	Wi
SPRAINT1.5M	**-2.57**					**0.10**			**2**	**-37.57**	**79.14**	**0.00**	**0.48**
BED.BIN+ SPRAINT1.5M	**-2.76**	**+**				**0.10**			**3**	**-37.20**	**80.39**	**1.25**	**0.26**
SPRAINT1.5M+PATH.BIN	**-2.72**		**+**			**0.09**			**3**	**-37.48**	**80.97**	**1.83**	**0.19**
SPRAINT.ALL	-2.33				0.05				2	-41.24	86.48	7.34	0.01
SPRAINT1M	-2.38			0.08					2	-41.24	86.49	7.35	0.01
PATH.BIN	-2.51		+						2	-41.26	86.52	7.38	0.01
SPRAINT1.5M+SITE	-2.47					0.10	+		7	-36.45	86.89	7.75	0.01
PATH.BIN+SPILES.BIN	-2.55		+					+	3	-41.13	88.25	9.11	0.01
NULL MODEL	*-1.62*								*1*	*-43.44*	*88.87*	*9.73*	*0.00*
SPILES.BIN	-1.93							+	2	-42.53	89.06	9.92	0.00
BED.BIN	-1.89	+							2	-42.77	89.54	10.40	0.00
BED.BIN+SPILES.BIN	-2.20	+						+	3	-41.88	89.76	10.62	0.00
SPRAINT1M	-1.86			0.06			+		7	-37.90	89.81	10.66	0.00
SPRAINT.ALL+SITE	-1.41				0.02		+		7	-38.36	90.72	11.58	0.00
BED.BIN+SITE	-1.11	+					+		7	-38.52	91.04	11.90	0.00

Table 5-12 Model selection tables where Y=where rest detected in previous ten days. Explanatory variables are explained in Table 5-2. A + indicates inclusion of a categorical variable. Models with $\Delta_{AIC} \leq 2$ are in bold and represent the models with most support and the null model is in italics. df = model degrees of freedom, logLik = log likelihood of the model, AIC = Akaike information criterion, Δ_{AIC} = difference in AIC between that model and the model with the lowest AIC, and Wi = Akaike's weight.

	(Intercept)	BED .BIN	PATH .BIN	SPRAINT 1M	SPRAINT ALL	SPRAINT 1.5	SITE	SPILES .BIN	df	logLik	AIC	Δ_{AIC}	Wi
SPRAINT1.5M	**-1.59**		**+**			**0.06**			**2**	**-51.53**	**107.07**	**0.00**	0.23
BED.BIN+ SPRAINT1.5M	**-1.85**	**+**				**0.06**			**3**	**-50.64**	**107.28**	**0.22**	0.21
SPRAINT1M	**-1.78**			**0.08**					**2**	**-51.73**	**107.47**	**0.40**	0.19
SPRAINT.ALL	**-1.63**				**0.04**				**2**	**-52.45**	**108.91**	**1.84**	0.09
SPRAINT1.5M+PATH.BIN	**-1.52**		**+**			**0.07**			**3**	**-51.48**	**108.96**	**1.89**	0.09
BED.BIN	-1.41	+							2	-53.16	110.32	3.25	0.05
NULL MODEL	*-1.11*								*1*	*-54.27*	*110.54*	*3.48*	*0.04*
PATH.BIN	-1.39		+						2	-53.85	111.70	4.64	0.02
BED.BIN+SPILES.BIN	-1.55	+						+	3	-52.87	111.74	4.68	0.02
SPILES.BIN	-1.25							+	2	-53.97	111.94	4.87	0.02
PATH.BIN+SPILES.BIN	-1.41		+					+	3	-53.76	113.53	6.46	0.01
SPRAINT1M+SITE	-1.60			0.07			+		7	-50.06	114.12	7.05	0.01
SPRAINT1.5M+SITE	-1.50					0.06	+		7	-50.27	114.54	7.47	0.01
BED.BIN+SITE	-0.81	+					+		7	-50.46	114.92	7.86	0.00
SPRAINT.ALL+SITE	-1.14				0.03		+		7	-50.80	115.60	8.54	0.00

5.6 Discussion

5.6.1 Field evidence as indicators of a resting site

5.6.1.1 Latrines

Active latrines were only found at resting sites. This is of significance as current literature makes no distinction between spraint sites and latrine sites and uses the terms indiscriminately (see Section 4.6.4). The exclusive relationship between active latrines with active resting sites strongly indicate that spraint sites and latrines should be recognised as different entities, fulfilling different functions. Spraints are characteristic of scent markings whereas latrine activity is digestive elimination but may also have an olfactory function. Latrine behaviour was also observed during the fieldwork with captive otters in Devon which informed Chapter 3; large latrines were present outside the wooden holts and the keeper confirmed that the animals did not defecate in the sleeping chamber itself. Latrines are readily distinguished from spraint sites as they comprise a large accumulation of faeces (see Figure 5-1) and often individual faeces have a cylindrical or pellet form (Figure 5-1c), which is unusual in otter spraints (pers.obs) which are described as "*shapeless*" and/or "*tarry*" and "*sometimes very liquid*" (Kruuk 2006a). They could therefore be used as a diagnostic field-sign for resting sites, especially as they have good longevity when not exposed to weather. However, latrines can be difficult to find. Four of the ten latrines found in this study could not have been found without an invasive search. In Europe and the UK, a requirement for a license to disturb otters when undertaking routine surveys is therefore implicated as there would be a need for an invasive survey of structures to locate latrines. In the UK, licenses are issued by the statutory nature conservation bodies, Scottish Natural Heritage, Natural England, Natural Resources Wales and Northern Ireland Environment Agency. The alternative would be to have a tiered approach to otter surveys, with non-licensed surveyors identifying structures that suggest suitability as resting sites, and a second, invasive survey undertaken of these structures by a licensed surveyor. An additional issue is that not all structures can be examined thoroughly enough, even with a torch and/or endoscope, to be confident that a latrine is absent. Therefore, examination of a structure could have three outcomes (1) a latrine is present and the site is reported as a resting site; (2) that spraint is erroneously identified as a latrine and the site is mis-identified as a resting site; (3) a thorough examination does not find a latrine and the site is reported as unlikely to be a resting site, and (4) a full inspection is not possible, in which case no conclusion can be drawn and further evidence would be required to identify whether the structure is a resting site or not.

5.6.1.2 Bedding

Bedding was recorded at nine sites, although it was only observed being collected by otters at five of the six resting sites on CT footage. Therefore, whilst bedding at a structure is a good indicator of a resting site, there is potential for confusion with bedding dropped by badgers, or even vegetation deposited by the wind or high-water levels. This was likely to be the source of loose vegetation recorded as bedding when no bedding collection had actually been observed on the CTs. The bedding collection method employed by badgers differs from that of otters. Badgers move larger quantities by dragging it backwards and can lose some on the way. In contrast, the CT observations all showed otters carrying in bedding a mouthful at a time, usually forwards, suggesting less chance of dropping any. This was also observed at the long-term study site (Chapter 3). This was the commonest method of bedding collection observed on Shetland, although one individual otter was seen dragging bedding in backwards in the same way that badgers collect bedding (Moorehouse 1988). Clumps of bedding outside the structure may therefore be more likely to be of badger origin than otter. Nests of bedding within a structure can be made by otter (e.g. at Gordon, see Figure 5-3) but at Frogden2, bedding was taken in by badger and not otter, but both species rested in the structure at different times. A nest of bedding seen within a structure, where the structure facilitates such a view, as opposed to loose vegetation at its entrance, should be taken as a strong indication of an otter rest site provided that the structure is large enough and dry. Observations of otter nests are rare in published studies but there are examples of constructed nests in reedbeds (Norfolk and Norwich Naturalists Society 1874; Taylor and Kruuk 1990) and bedding used within structures (Moorehouse 1988; Durbin 1996a) but as a comprehensive inspection of some sites may not be possible, the inability to fully investigate the site means that the presence of bedding may not be a viable field-sign at all sites.

5.6.2 Field evidence at resting sites

A strong relationship between field evidence types (spraint counts, presence of spraint piles, presence of a run and presence of vegetation suggesting bedding) and whether a site is a resting site or not could potentially be used to identify resting sites. The resting sites identified on the River Tweed were used seasonally, with 95% of rests in the winter-spring period. For a relationship between field-signs and resting sites to be used by surveyors at any time of the year, implies that field-signs generated by resting behaviour must have good longevity, or that otters generate field-signs throughout the year at resting sites, even when they are not using them for resting. For instance, if the resting sites are always accompanied by large spraint counts as the otters scent-mark them as a resource. However, no relationship was found between field evidence and resting sites when analysing data from all seasons, or when restricting the data to the winter-spring period.

5.6.3 Field-evidence as an indicator of recent resting activity: determining current use

The models testing whether field evidence was related to a rest within preceding days found a positive relationship between spraint counts 1—5m from the resting site entrance and resting in the previous five days. The presence of bedding in conjunction with the spraint count at 1—5m marginally improved the likelihood of a rest in the previous 5 days, as did the presence of a path in conjunction with the 1—5m spraint count. However, these effects were very weak in the context of using them diagnostically. The summary of spraint counts from 1—5m also suggested a difference between resting and non-resting sites (see 5.5.1.4). The best supported model predicted 60% probability of a rest in the previous five days at the maximum observed number of spraints (27) within 1—5m. When rests were included in the previous ten days, the results were similar in terms of the positive relationship of spraints within 1—5m.

Therefore, otters appear to spraint more around the vicinity of their resting sites during the periods when they are actually resting at those sites than when they are not, but this trend is relatively weak. As otters have large home-ranges of many kilometres in riparian habitats (see Section 4.3.2), using scent marks to maintain ownership of all their resting sites all of the time is unlikely to be energetically feasible which is why spraint numbers at resting sites may vary according to use. As these trends are relatively weak, spraint numbers and distribution at a structure are not suitable for using as criteria for classing a structure as a resting site or not as it risks false-positives and false-negatives.

5.6.4 Success rate of identifying resting sites using field evidence

There was a low proportion of resting sites with eight resting sites out of the 26 sites monitored (31%) (i.e. six resting sites confirmed by CT observations of rests and two likely resting sites based upon field-signs and behavioural observations) included in the study which is a testament to the difficulties of identifying otter resting sites from field-signs. All sites were included in the study based upon a subjective assessment of their suitability as resting sites and accompanying field evidence of otter, and otters were recorded at all of these sites during the study. Of the 18 sites that were not used for resting during this study, several could be described as "typical holts" due to their structure and associated field-signs, (i.e. burrows in a river bank with strong runs to the water and marked locally by spraints in and around the entrance ()). As examples, Hownam and Eden1 were chosen for inclusion as study sites due to the presence of clean runs down the riverbank, often termed "otter slides" and were marked with spraint at the structure entrance, on the run and at the water's edge. Yet otter rests were not recorded at either site during the study period. Eden1 had the highest proportion of CT days when otter was recorded (see Table 4-10), with as many as eight registrations in one CT day, but no rests were recorded. Often the floor of the outer burrow was wet from passes of otter the previous night. These would almost certainly be recorded as otter resting sites by most ecological consultants. Derogation license applications, mitigation measures, species protection plans and monitoring plans would follow if any impacts were implicated. These false-positives identifications which are based upon field-signs incur time and fees. However, although these sites are not resting sites, otter activity can be very high and otters are entering the structure for some unknown reason. This indicates that sites with such frequent visits as Eden1 have some other importance to the otters, possibly as a grooming site, a spraint site or other type of scent marking site.

Figure 5-7 Hownam: a hole leading into a dry chamber, marked with spraints and a clear run to the water would be considered a resting site based upon its structure and associated field-signs, but no resting was recorded

5.6.5 Constraints and further research

The field study sites were found by a single surveyor and this may be a source of bias relating to the level of experience and skill of the surveyor. A valuable extension to this study would be to test any variation in structure classifications as resting or non-resting sites between different ecological consultants. Initially, I considered using a group of consultants who had no prior knowledge of any of the sites, to assess each of the study sites on the River Tweed structures as resting sites or not. This would have required the involvement of consultants though out the four years of fieldwork to include resting sites when they were active and inactive, and also non resting sites. This was not logistically feasible. Another source of bias is that the structures which were included had to have a reasonably low risk of inundation or theft of CTs. This too, was an unavoidable constraint, but these criteria would have to be applied to any CT monitoring. Monitoring sites with a lower risk of flooding may increase the likelihood of monitoring sites that are used habitually, as sites prone to inundation may only be used when conditions are favourable. Sites prone to inundation would also be habitually washed of spraint and latrines, as seen at Mill2. Identifying resting sites with entrances close to, or below the water remains a challenge to methods other than radio-tracking.

Using CT observations to provide a comparative record of otter activity enables relationships between field-sign and otter activity to be investigated. Detection of otter by the CTs is unlikely to have been perfect, and unlikely to have been the same across all sites. However, the analysis of data from the long-term study site (Chapter 3) and the research on the components of detection by CTs (Chapter 2) guided CT deployment and settings on the River Tweed study sites. This resulted in a low proportion of incomplete observations 8% (n = 13,847) (i.e. where the full interaction of the otter and the study site was not accounted for, such as an otter recorded entering a structure with no corresponding exit). Whilst there may be some additional non-detections, the overall data quality offers a good control to provide context for field-sign data.

5.6.6 Conclusions

This study has found that the most types of field-signs are unlikely to be reliable as indicators that a site is a resting site or not, or that a resting site has recently been utilised. Therefore, assessments of sites that may be used as otter resting sites that are based upon field-signs alone have limited capacity to fulfil the legal imperative to protect otter resting sites. Use of field-signs alone, an approach which has been used by consultant ecologists, could lead to an unacceptable proportion of mis-identifications of resting or non-resting sites, both in the form of false-positives (a non-resting site is misidentified as a resting site) or false-negatives (a resting site is misidentified as a non-resting site). The only field-sign that could be used with a reasonable degree of confidence to identify a resting site is the presence of an active latrine. However, the ecologist must be able to inspect the structure thoroughly in order to confirm that a latrine is present or absent; this may not be possible in some structures and an invasive survey would necessitate a license to disturb otters. Bedding, especially a made nest in the structure is also another good positive indicator of a resting site but would have to be in context with the position of the structure and its accessibility to badgers. Although badger and otter are protected by UK legislation, the legislation for each species is different (badgers are protected under the Protection of Badgers Act 1992). The licenses are therefore species-specific so that species-appropriate mitigation can be implemented. Caution would therefore be needed to avoid misidentification of resting sites between the two species. Using the number of spraints to confidently identify a resting site appears not to be possible based on results on the River Tweed.

Although no relationship was found between spraint numbers and identification of resting sites *per se*, at the subset of resting sites there was a positive relationship between spraint count and the probability of a rest in the previous few days. Therefore, a high number of spraints in the vicinity of the structure could be used as a “rule of thumb” to indicate an active resting site. Advocating such an approach would require prior knowledge that the site was a resting site, which could have come through recent CT surveying or identification of an active latrine. The highest observed spraint count of 27 only predicted a 60% probability of a rest in the previous five days, whilst some rests were associated with a low spraint count. The latter could lead to a false-negative assessment of the structure. It is questionable whether the relationship between spraint numbers and previous resting is strong enough to be used as a predictor across all active resting sites.

This study is the first to explore the relationship of resting sites and field-sign using CTs to validate any relationships. The analyses strongly indicate that camera-trapping should routinely be used by consultants as a second-tier method to confirm resting sites after field-sign surveys have located potential resting sites.

Chapter 6 Discussion

6.1 Research overview

The research in this thesis covers three related studies over four chapters which contribute to the evidence base for methods used to identify otter resting and breeding sites.

Chapter 2 examines methodological considerations in CT studies of otter (as well as considering badger and fox for comparison) using CTs in parallel with CCTV which is used as a control. It presents detection by CTs as a sequential framework of four processes: (1) encounter probability; (2) trigger probability; (3) registration probability; and, (4) capture quality probability. Using CCTV as a control to document animal passes, and the novel framework that recognises the four main processes, it was possible to understand how key variables (the distance of the animal from the CT, the animal's gait and whether it paused or loitered) affected processes 3 and 4. This enabled false-negatives to be quantified in relation to both processes. Understanding how variables including distance of animal from the CT and speed of the passing animal can affect detection in front of the CT enables an informed deployment to minimise false-negatives.

Methodological considerations are also the theme of Chapter 3 which presents empirical analyses of data from a unique long-term CT study of a holt to examine how CT settings and set-up can be optimised in terms of data quality and analysis time. A method to organise data for analyses of resting behaviour was developed called an "events list", which used the arrival and departure dates and times of an otter to define an event, with specified behaviours such as sprainting or bedding collection recorded within each event. The frequency distribution of the duration of time each otter spent in the holt was used to provide a data-driven delineation between 'rests' (≥ 15min within structure) and 'visits' (< 15min in the structure). This was a fundamental step towards identifying a site as a resting site, as required by EU and UK legislation. The patterns of these two activities were then investigated for any changes in response to the researcher visits every two weeks as an assessment of disturbance. Once it was established that the researcher's visits did not affect activity patterns, the data were analysed to determine how long a CT would have needed to be deployed to have a 95% chance of detecting a rest. A comparison was made between data gained from a single CT and a dual CT set-up and how distance can affect the type of data recorded, e.g. ability to sex an otter and registration of behaviour.

Chapters 2 and 3 provide guiding principles for CT methodology at a given structure which were applied to the catchment-wide study of sites identified as having potential as otter resting sites on the River Tweed in Chapters 4 and 5. To minimise false-negatives, dual CT systems were used wherever possible, with 20s video setting and with at least one CT deployed within 1.5m of the structure entrance. These two chapters describe the patterns of activity, selected behaviours and field-signs at 26 study sites, representing approximately 26 CT-years of surveillance in all seasons. Chapter 4 examines resting patterns from analyses of the CT data which show seasonal trends in resting at the structures and behaviours that are linked to resting. This confirms that CTs have the potential to be a highly effective tool to identify resting sites, as required by legislation, provided a robust set-up is used. The analysis in Chapter 4 also provided a unique data set of known resting and non-resting sites against which other approaches to identification of resting sites, such as use of field-signs, could be compared.

Chapter 5 analyses field-signs in context with the known activity types from the CT study, which tests the validity of the traditional approach to identify resting sites using field-signs. This is the first study to investigate any relationships between field-signs and resting sites in the context of CT data which is effectively used as a control.

6.2 Key findings

6.2.1 Camera-trap deployment: minimising false-negatives

Camera-trap studies do not always account for, or even discuss imperfect detection even though it is an important consideration in all CT studies (Burton et al. 2015). The increased use of CT methods to estimate abundance or density through capture-recapture studies of animals with individual pelage markings or by the developing random encounter model (REM) have highlighted the importance of detection. Investigation of factors influencing detection probability is now a common focus of CT studies (e.g. Anile and Devillard 2016; Hofmeester et al. 2017; Apps and McNutt 2018a).

The use of continuous recording using CCTV, acting as a control, enabled exploration of how false-negatives occurred when an animal passed the CT. Increased distance between the CT and the animal had a strong negative effect on trigger probability, and a mild positive effect on registration probability. Distance has been shown to have a negative effect on trigger and registration combined (Hofmeester et al. 2017) (i.e. capture probability), with the mass of the animal, density of intervening vegetation and time of day (see Hofmeester et al. 2019). Uniquely, the use of CCTV facilitated trigger and registration probabilities to be examined separately. This exposed the magnitude of imperfect triggering of the PIR which caused false-negatives at all distances. The mild positive effect of increasing distance on registration probability can be countered by using a CT with a fast trigger speed, as demonstrated by the improved registration probability using still image capture which has a faster trigger speed (see Figure 2-8). Once this effect has been negated, the main source of false-negatives would be due to the strong negative effect of distance on trigger probability. This is due to IR losing intensity according to the inverse square rule, compounded by other factors such as vegetation density. It is the failure of the PIR to trigger on wet otters after exiting water that causes the excess of false-negatives noted by Lerone *et al.*(2015), although in my study, thermal imaging of otters after exiting water indicated that this effect is limited in duration. In the Tweed data, a significant difference was found in the distribution of event types (paired, single-entry, single-exit) (see section 4.5.1) in winter and summer, with apparent better detection (i.e. greater than expected paired events) in summer. Otters going into a structure are likely to have previously been immersed in water. This difference may be due to wet otters in the summer having a colder thermal footprint than the terrestrial habitats due to cold river water being held in their fur. Further studies would be needed to confirm this, for example taking thermal images of otter across a range of different water and air temperatures.

Often holts, including those with entrances near water level, have platforms or ledges at the entrance where spraints and/or footprints can be found (pers.obs.). Sniffing and scent-marking would be expected at these areas which increases the time spent in front of the CT and which will improve both trigger and registration probability (see Chapter 2). However, CT data from holts which lack such a platform may have a high proportion of false-negatives when wet otters enter the structure caused by poor trigger success. Otters exiting a structure are likely to trigger the CTs more successfully as they will be drier and warmer in comparison to the background. Expecting paired registrations in order to identify the site as a resting site would be unrealistic. Physical triggers, such as a pressure plate could be considered, and have been used with some success (Lerone et al. 2015) but this is not an off-the-shelf solution. Structures that are unsuitable for monitoring with CTs are likely to be rare, but the limitations of CTs need to be understood.

Deployment of two CTs at a study site results in more reliable capture rates, especially of single otters (see Section 3.4.2). Setting the CTs to target the same area but with differing detection zones and fields-of-view, such as at different angles or different distances potentially yields a wider range of data as well as better interpretation (e.g. the ability to determine sex and observations of sprainting behaviour). Other studies that deployed two CTs that targeted the same spatial area also found increased detection with two CTs (Glen et al. 2013; Newey et al. 2015b). It has been shown that the magnitude of increased gain in capture rates by having two CTs varies for different species (Negrões et al. 2012). It has been suggested from a study using labrador-sized dogs in mown grassland, that camera-traps set at just below the shoulder height of the focus species and parallel with the ground will yield the best detection probability (Apps and McNutt 2018a). Increased height and dip (downwards angle) reduced detection as it reduces the size of the detection area. Translating this to wild scenarios may require some compromise. Dense vegetation potentially prevents some or all, of an animal's emitted IR from reaching the CT, thus compromising trigger probability. "Gardening" (i.e. cutting back vegetation to ground level) is recommended to obviate this problem (Apps and McNutt 2018b) but this may not be advisable at a resting site as it could elicit changes in activity or make the site more vulnerable to predation or human interference. The topography in front of resting sites is rarely flat and density of vegetation will vary with the season so the decision on what height to set CTs should balance these considerations and rarely will a standard set-up be achievable across sites.

In the context of using CTs at potential otter resting sites, a minimum of two CTs is recommended to improve the capture rate of animal passes and facilitate better interpretation.

6.2.2 Camera-traps as a non-intrusive observation method

CTs can emit ultrasonic noise when batteries are near depletion and the wavelength of frequencies of IR LEDs can be detected by some species (Meek et al. 2014b). A behavioural study found that predatory mammals reacted to CTs in the field indicating that CTs are detected by some mammal species (Meek et al. 2016).

Analyses of resting events, presence and sprainting patterns at the long-term study site showed no changes due to the maintenance visits by the researcher every two weeks to change batteries at the long-term study site. Habituation to the scent of the researcher may have been a factor. Based upon this analysis, a three-week period between researcher visits on the River Tweed was considered to have minimal potential to cause disturbance. Reactions to the CT by the otter, such as sniffing it, although not recorded as part of the methodology, were rarely observed (per.obs.). More reactions to the CTs were observed by passing badgers. Behaviours such as rolling, grooming and even sleeping were recorded close to the CTs indicating that otters were not sensitive to the CTs.

6.2.3 Camera-trap deployment at otter resting sites: optimisation of settings

Behavioural studies with CTs often use video setting (Rovero and Zimmermann 2016) as it potentially offers more information than still images. When camera-trapping a potential resting site, there would be a need to distinguish latrine behaviour from sprainting as it is only the former that appears to be a diagnostic behaviour for resting sites. There would also be the need to identify the sex of animals, as repeated rests by a single female otter may indicate small cubs within the structure, lending more importance to a breeding structure in an impact assessment. Observing the position of the source of a stream of urine, and the direction of a urine stream is often the most helpful characteristic in sexing an otter (see 3.3.5). This is unlikely to be distinguishable on still images given the poor image quality from night photography taken with IR flash. Identification of bedding collection would also be required as this is also linked to resting. Bedding collection can be identified if bedding is observed in the otter's mouth being carried into the structure. It is usually undertaken at a fast run and comprises of several swift passes with the otter often holding its head higher than usual when carrying the bedding and with rustling heard when the otter is not in the field of view (CTs that record sound would therefore be needed). These characteristics contribute to the identification of bedding collection. It is likely that still images are less able to detect bedding collection as images of a running otter are more likely to be blurred and other indications, such as the sounds of otters pulling up vegetation would not be recorded. This could be tested using a paired set up with one CT set to record video and one to record stills.

The main drawback of video data is that it is more time consuming and can be a major obstacle in research (Caravaggi et al. 2017). They also use more battery power and need more memory storage. Methods to automate analysis of still images are being developed (Yu et al. 2013; Norouzzadeh et al. 2017), and potentially offer considerable time-savings when fully developed and tested. These methods are for still images. CTs can be programmed to record up to a minute of video, but all the required information may be present in the first few seconds. Optimising the video length can reduce analysis time, as well as save battery power in deployed CTs. Analysis of the long-term study site found the optimum video length to be 20s to enable identification of sex, group size and behavioural observations (i.e. c. 95% of these observations could be achieved in 20s of video compared to 30s), and this approach was subsequently applied in the River Tweed study. Setting the duty time of the CTs (i.e. programming a daily period of dormancy would also present savings of battery power and analysis time). The long-term study site found that activity peaked prior to sunrise and after sunset. Setting duty time was considered for the River Tweed sites but was not used as it was anticipated that some sites may be nocturnal resting sites and setting a duty time could potentially miss rests. Additionally, duty times could not be programmed on the Bushnell Trophy CTs. Setting a duty time, however, could be a time-saving strategy with other species or scenarios provided the CTs have this facility, but a full assessment of the likely proportion of data loss would need to be made first.

6.2.4 Camera-trap deployment: sampling duration

Survey effort is a key consideration in CT survey protocols which is often overlooked (Hamel et al. 2013). Faunal inventories assess whether the sampling duration has been long enough by plotting a species accumulation curve (Tobler et al. 2008; Rovero et al. 2014; Si et al. 2014). Similarly, in capture-recapture studies, the number of new individuals are plotted against CT days (or sampling periods); the cumulative number of new individuals increases and eventually levels off indicating that further survey effort will not yield any/many more new individuals (Rovero and Zimmermann 2016).

There are many reasons why a mammal den may be surveyed with CTs, for example proof of use (Fahimi et al. 2011), counting litter size (Kluever et al. 2013) or observing inter-specific interactions (Brzeziński et al. 2014). There is no standard approach to determining survey effort for such studies and the number of CT days is rarely justified, especially if the study aim is realised. Camera-trapping at resting sites could also take this approach and cease monitoring when there is evidence that a structure is used for resting. However, not every site camera-trapped will be a resting site, and there needs to be an accepted minimum survey effort to demonstrate that a negative result is likely to be a true-negative.

From the six resting sites identified across the River Tweed catchment, simulations established that 35d of monitoring in winter and 35d in the subsequent spring (i.e. two periods of five weeks), would have had a 95% probability of detecting a rest at all resting sites considered (see Section 4.6.7.1) and that this would be more efficient than a single 70d period. The long-term study site found that resting frequency was significantly related to the holt’s current function (i.e. whether the holt was functioning as a natal, early, mid or late rearing or non-breeding structure) (see Section 3.4.3). The younger the cubs were, the more frequent rests were recorded. When the holt was not used for breeding, a minimum of 28d camera-trapping was needed to have a 95% probability of recording at least one rest. This difference between a single period of 28d and two periods of 35d is substantial but is a good illustration of the need to base any recommendations on multiple sites and not a single site. My recommendation for sampling duration and frequency would therefore have to be two periods of 35d. However, if the purpose of monitoring was only to identify whether a site was a resting site, then monitoring could potentially cease as soon as enough data was collected to confirm resting. Surveyors may wish to continue monitoring to ascertain if breeding occurs.

Ninety-five percent of CT days on which a rest was recorded on the River Tweed were in winter and spring, with only 4% in autumn. This concurs with the large seasonal bias found at the long-term study site in Fife, approximately 100km north of the Tweed catchment, where 88% of CT days with a recorded rest were in winter and spring, and 6% in autumn. This also broadly concurs with a recent radiotracking study in Austria which found more use of holts when the summer vegetation had died back (Weinberger et al. 2019).

The use of structures for resting is indicated more in months/seasons of poor weather, providing shelter to otters. However, any recommendation for a “seasonal window” within a CT protocol would have to be caveated to allow for geographic variation. For example, to advocate summer CT surveys for coastal populations on Shetland and the North coast of Scotland where breeding is in the summer (Kruuk and Moorhouse 1991b).

6.2.5 Using camera-trap data to define and monitor resting behaviour

Legislation refers to a resting site as an “*area essential to maintain an animal or a group of animals when they are not active*”, and in wide-ranging species this is “*a locality that can be clearly delimited*” (EU 2007). However, a more precise definition of what constituted a rest was first needed in order to define what a resting site was, and before patterns in resting behaviour and field-signs could be investigated. Otter observations were first organised into an events list for the long-term study site (see Section 3.3.5) and this was extended to the River Tweed study as it had worked so well.

The data facilitated an understanding of how much time otters spent at these structures. Very brief visits of otters to the structures of one to two minutes were the most frequent duration, otherwise otters tended to stay in the holt for at least an hour. A practical threshold of 15min or longer inside the structure was used to define a rest, and a resting site was defined as a site where one or more rests had been observed. Several methods have been used to study mammal den sites. Radio-tracking is frequently used (Dame 1993; for example see Brainerd et al. 1995; Lim and Ng 2008), snow-tracking has been used for wolverine (Magoun and Copeland 1998) and temperature loggers have also been used to monitor the activity of female pine marten at natal dens, an abrupt rise of temperature marking the arrival of a breeding female and a fall in temperature marking her departure (Kleef and Tydeman 2009). This latter study has parallels with the long-term study in Fife and the River Tweed study in that the duration of time spent in the den was analysed. The pine marten study gave a good account of den occupation periods but was limited to analyses of changes in temperature which contrasts with the diversity of data available from CTs. A study of pine-marten dens using local knowledge and questionnaires, defined dens as places used for a prolonged bout of sleeping or resting and made the distinction between natal dens used for birth and the initial rearing of young, and other dens (Birks et al. 2005). Sites that pine marten used for brief periods of rest or shelter (also known as lie-ups) were mentioned and excluded. Whilst differences in the types of rest (prolonged at a den site and a brief period at a lie-up site) were defined and these distinctions offer an insight into pine marten denning habits, they are not specific enough to be used across studies.

Using CTs facilitates a precise definition of a rest and a resting site, and these can be consistently applied to other sites that are camera-trapped for otter and would be a robust demonstration of a site’s status in context with its legal protection. The approach to defining resting sites by the same criteria (i.e. time spent within the structure) could be used as an approach for other species. The “events list” would be an accessible method for consultants to use as standard. It is readily interpreted, and activity can be summarised and presented to statutory authorities as evidence of resting (or non-resting).

6.2.5.1 Seasonal use of structures for resting

Rests in winter and spring accounted for over 95% of all rests in the River Tweed resting sites, and 88% of rests at the long-term study site. The eight resting sites on the River

Tweed, and the drift mine structure in the long-term study site in Fife (see Section 3.3.2) all offered a good level of shelter. Gordon was a semi-enclosed hollow tree and all the other sites were enclosed. Frogden1, Frogden2, Torquhan and Learmouth all comprised large hollow trees. Hollow trees have good insulative properties (Coombs et al. 2010) and are often chosen as den sites by other species (Brainerd et al. 1995; Fernández and Palomares 2000; Prigioni et al. 2006). Resting otters do not always use a structure to rest in, they often rest in dense vegetation, even in low temperatures (Kruuk et al. 1998). However, there is low re-use of these sites and usually no associated field-signs (Green et al. 1984; Isabel and Freire 2011). A radiotracking study in Austria found that holts were used more when vegetation cover was less (i.e. in the winter, and that this was a more important variable than temperature in the choice between holts and couches for diurnal rests). The study suggested that the cover provided by riparian vegetation outside the winter period provided sufficient refuge and protection from human disturbance (Weinberger et al. 2019). The River Tweed study reflects this increased use of holts in seasons of low vegetation cover, whether for protection from disturbance or from extreme temperatures. However, there was a peak in holt use on the River Tweed structures between January to March (see Section 4.6.3 &) and this is not fully explained by temperature/weather or by vegetation cover which are also low in the early winter.

6.2.6 Identification of behaviour recorded on camera-trap footage that are indicators of an otter resting site

If the CT set-up is robust enough to minimise false-negatives, then the time of entry into, and exit from a structure can be used as robust evidence of the duration of time within the structure and interpreted as a rest or not, and this approach has been used before, albeit using temperature loggers within a den (Kleef and Tydeman 2009). However, not all sites can be camera-trapped with complete confidence as there may be hidden entrances, such as at Mill2 (see Section 4.6.4). Identifying latrine behaviour (i.e. repeated use of a specific site for defecation (and urination)), also appears to be strong evidence for resting behaviour. Observations of bedding collection behaviour recorded on CTs were strongly associated with resting sites and were not observed at any non-resting sites.

Camera-trap observations of latrine behaviour and bedding collection could be used as behavioural indicators of resting, even in the absence of paired rests. Sedentary activities such as loafing and grooming were more frequent at resting sites, although they were observed at non resting sites too. Sedentary behaviours cannot therefore be used as a criterion on their own.

6.2.7 Testing the validity of field-sign surveys to identify otter resting sites

Finding and interpreting field-signs is the main approach currently taken by consultants to classify a structure as an otter resting site. Latrines can be identified as a different type of field-sign to spraints (see Section 5.6.1.1), but previously have not been identified as separate features, or as having different functions in the published literature. The distinction between latrine and sprainting behaviour, and the former's relationship to resting sites, represents a novel observation that contributes to existing knowledge of scent marking in Eurasian otter, as well as potentially being a significant contribution to otter survey methodology. This distinction also has implications for studies of otter diet from analysing the remains of fish (and other prey items) in their spraints. Dietary studies are a common research theme in relation to the importance of wild and commercial fisheries (Kemenes and Nechay 1990; Jacobsen 2005; Kloskowski 2005). These, and more general dietary studies (Brzeziński et al. 2006; Ruiz-Olmo and Jiménez 2009; Ottino and Giller 2012) rely on quantifying the undigested remains of prey in spraints. Spraints comprise less faecal matter than droppings in latrines, so excluding latrines from dietary studies may introduce significant bias. The River Tweed study found that active latrines were closely associated with active resting sites and were readily identified from spraint sites. A large latrine was also noted in the tunnel of the drift mine at the long-term study site in Fife, but the significance of this was not understood at the time.

Bedding collection was observed at all resting sites by the CTs. Loose vegetation was occasionally erroneously recorded as bedding, and there was also potential confusion with badger activity. Sharing of badger setts by multiple species has been documented with CTs in Italy (Mori et al. 2015). Badger and otter both used Frogden2 for resting, and both used the same latrine site within the structure; otter spraint was also noted in a badger latrine at Frogden1. Further investigation of holt sharing would inform what potential there is for misidentification of holt sites due to field-signs left by badger or other species. Camera-traps are ideally suited to such a study.

No relationship was found between spraint counts at a structure and the structure's status as a resting site. The other field-signs analysed (spraint numbers and distribution, presence of a path, spraint piles) also could not be used to distinguish a resting site from a non-resting site. While there was a positive relationship between spraint counts at a structure and the probability of a rest having occurred recently, the relationship was not strong enough to enable it to be used diagnostically.

The River Tweed research illustrates a hierarchy in the importance of field-signs as evidence of a resting site. Latrines are good evidence and bedding is also strong evidence provided it is correctly attributed to otter activity. Other signs such as spraint counts should not be used.

6.3 Contribution to a methodology to identify otter resting sites: first steps towards standardised guidelines

The research has provided an evidence-base to inform several important aspects of methodology which would be required to identify a resting site: detection in front of an individual CT, CT set-up at a site and settings, sampling effort, behavioural indicators of resting and field-sign indicators of resting. Combined with other information in the literature, these need to be incorporated into a standard methodological approach that is readily interpreted by consultants and statutory authorities. Here I provide some initial recommendations that might be incorporated into future guidelines.

6.3.1 Field-sign surveys

At the time of writing, the Mammal Society are currently reviewing and refreshing survey and mitigation guidelines for a range of UK mammals, including the otter. The research in this thesis can make a significant contribution to these guidelines.

The research has highlighted the importance of undertaking a thorough inspection of each potential structure and establishes the limitations of most field-signs in identifying resting sites; conversely the presence of a latrine has been proved to be a reliable indicator of a resting site.

A decision tree to identify a resting site from field-signs (Figure 6-1) has been formulated from my findings from the River Tweed study. This is designed to be in a format that is likely to be familiar to consultant ecologists. It presents a series of questions and outcomes which lead to one of three conclusions: (i) a resting site; (ii) not a resting site; or, (iii) a potential resting site, which should be monitored with CTs to identify its status.

If the decision tree is used in future guidance, supporting text and photographs would be needed to clarify the difference between a latrine and spraint sites, and bedding forming a nest. A license to disturb otter resting sites would also be required to facilitate an intrusive survey.

The main caveat in using this decision tree is the uncertainty of the seasonal recommendations if rolled out nationally and how this could bias results. For example, breeding in the coastal population on Shetland is in the summer (Kruuk and Moorhouse 1991b) and monitoring with CTs in the winter/spring would potentially miss breeding activity in such populations.

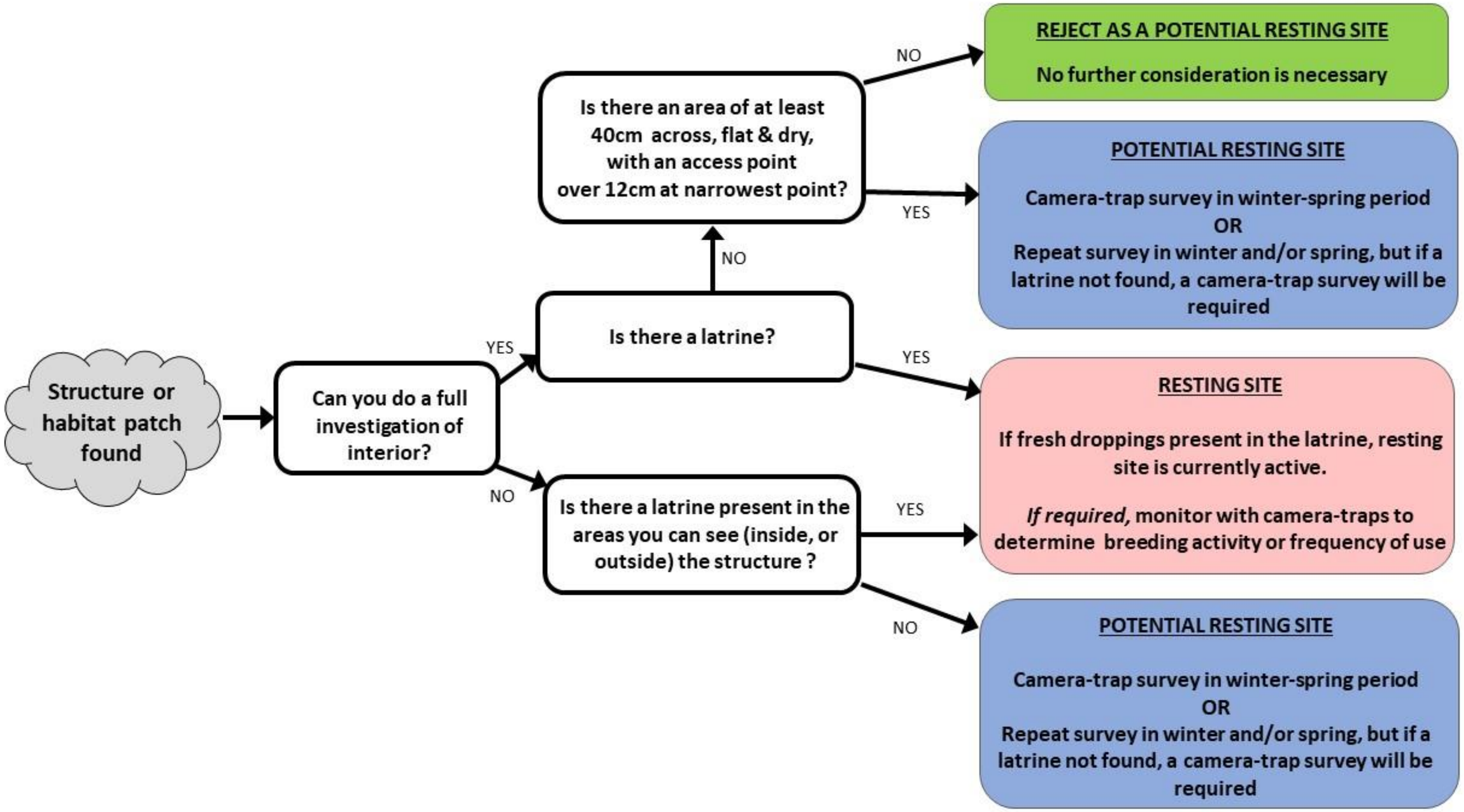


Figure 6-1 Decision tree to assess the resting status of a structure or habitat patch using field signs

6.3.2 Camera-trap methodology

The research provides a suite of recommendations to be included within a methodology to CT potential otter resting sites and many of the principles can be applied to other den surveys. Firstly, the evidence-based definition of a rest event as 15min or longer within a structure could be a standard definition in CT studies of otter resting sites. This would require data to be analysed as paired registrations so that resting duration can be calculated. The methodology would describe behavioural indicators of resting so that these can be recognised (i.e. latrine behaviour and bedding collection).

To implement the above, the deployment of the CTs and settings would need to be optimised, summarised here: CTs with fast trigger speeds (< 1s) on video setting should be used - video potentially records richer data, and the fast trigger speed minimises false-negatives arising from poor registration probabilities associated with slower trigger speeds; the use of two or more CTs per observation area to improve detection probability per site; there should being at least one close CT (1—1.5m) to improve detection probability; video length is recommended to be set to 20s for economy of batteries and analysis time; the survey effort should comprise two sampling periods, 35d in winter and 35d in spring (caveated to facilitate seasonal differences according to geographic areas).

Given the diversity of structures that can be used for resting, a prescriptive set-up which can be applied across the board to all sites is not possible. It is therefore most important that practitioners understand how data quality can be affected by CT deployment so that practitioners can fine-tune CT placements in response to each site. The area of interest at a resting structure is small, the focus being on the entrance area of a den structure such as a burrow or tree-hole. Aligning the CT so that the structure entrance and the area immediately outside the entrance with the centre of the field-of-view and detection area will increase detection probability as the animal cannot circumnavigate this area when using the den and is also likely to loiter to sniff or spraint, thus increasing registration probability (see section 2.4.2, Figure 2-7). The effect of the CT height and angle must be considered. A low CT height potentially captures morphological features (such as presence of scrotum) to allow sex to be identified but may incur the necessity for more trimming of vegetation which may not be appropriate at sensitive sites. A greater height may be necessary due to steep topography and lack of ground in front of the structure (e.g. if it is on a steep bank adjacent to water). The practitioner must be aware of the blind-spot below the CT and the reduced angle of detection, however as the target area is generally small, careful deployment can obviate these potential issues.

There are other broader considerations if camera-trapping of potential resting sites is to be carried out to a good standard. Consultants must provide a good account of their methodology during reporting. This has been recognised as an important issue in academic CT studies (Meek et al. 2014a) and it is equally important to have a standardisation of reporting the methodology in consultancy. The CT models, settings, deployment (number of CTs, height and distances from the structure, dates of surveys) should all be described clearly. Non-functioning CT days caused by battery depletion for example, should be reported and any other incidents that may affect the results. The proportion of single events (i.e. where the complete interaction of the otter and the structure were not captured, for example an otter observed entering a structure but not subsequently leaving) should be stated as this is an approximate gauge of any issues of detection. Paired events should be presented, and any observations of any behavioural indicators should be quantified in terms of frequency and duration.

The current standard of camera-trapping at resting sites is understandably varied (pers.obs.), as currently there are no guidelines. Examples of commercial camera-trapping reports are difficult to source because they are not routinely published, only two examples relating to camera-trapping potential resting sites were found online and are briefly summarised. Example 1: a structure was camera-trapped for one month between 16th April—16th May (30d) to inform impacts of a new bypass. The CT did not face the structure, and recorded videos at a duration of 1min. There were no registrations of otter (Thomson Ecology 2014). Example 2: a structure was camera-trapped 12th June—21st July and 4—25th October (39 and 21d) to inform impacts for a high voltage electricity cable between Norway and Scotland. One CT was used at 2m from the structure entrance on video setting with no stated clip duration. There were no registrations of otter (NorthConnect 2017). The only similarities between the examples is that they both used a single CT, they stated model of CT used, they both reported the sampling durations and both recorded video. The survey duration, seasons and position of CT in relation to the structure were different. The survey duration and season are likely to be in response to the projects timetable rather than any underlying ecological rationale. The introduction of a CT methodology for otter resting sites which requires monitoring over two seasons is significantly different from the current approach which is usually based upon a single visit at any time of year. However, many types of ecological surveys are seasonally limited or require sampling in specific seasonal windows (Brown and Shepherd 1993; Hancock et al. 1999; Collins 2016) so a methodology that requires two seasons data should not be perceived as exceptional by practitioners.

The recommendations set out here could be presented as a coherent methodology, but a consultant would require a certain level of competence and experience to implement it. Training in the methodology, extracting data from videos and reporting would be an essential prerequisite for a consultant prior to commercial CT contracts, but also for decision-making bodies such as local government ecologists and staff from the statutory nature conservation bodies.

6.3.3 Application of camera-trapping method to legislation

The Tweed study found that structures indicated to be "holts" (i.e. enclosed resting sites) from associated field signs were often not used for resting yet still had a high frequency of otter registrations (see Table 4-10). For example, Eden 1 was the busiest site with at least one registration of otter on 92% of CT days, but was not used for resting during the study. Such structures must have some function or importance, such as a grooming site or type of scent-marking site but are not explicitly protected under existing legislation. Resting sites are defined as "*areas essential to sustain an animal or group of animals when they are not active*" (EU 2007, p. 42). For some species this is broadened out further to include other functions when an animal is inactive other than resting, for instance, places used for thermoregulatory behaviour of the sand lizard *Lacerta agilis*. If structures such as Eden 1 fulfil an essential function, this would set them apart from other sites which are visited frequently but are not essential such as an individual scent-marking site. Extending the interpretation of Article 12 of the Habitats Directive to include sites which fulfil an essential function could be achieved by amending the existing guidance document (EU 2007) as the example of the sand lizards thermoregulation areas sets a precedent, but this may be tenuous as the otter is clearly active and not resting at such sites. A better approach would be to include such sites within any amended domestic legislation which may arise post-Brexit. However, the function of such sites as Eden 1 is currently unknown, and further research would be needed to determine why the frequency of otter presence is so high before these sites could be considered important.

6.4 Further research

A key logistical constraint of having CT emplacements by watercourses are the changes in water levels, thus precluding some sites from study and resulting in gaps in data collection for others. Submersible equipment would remove this as a constraint. While a single unit housing a camera, PIR and illumination LEDs is likely to be more robust, there were disadvantages as there must always be compromise between the most efficient distance for both trigger and registration probabilities (see Chapter 2). A system where these components are separate would be greatly beneficial, one or more PIRs could be placed close to the targeted monitoring area and the camera unit could be placed at a greater distance. The analyses in Chapter 2 indicate that this would greatly improve trigger and registration probabilities. Such a modular system would also allow a camera to be placed inside a structure, with the battery and memory unit being placed outside the structure so that maintenance of the battery and memory causes minimal disturbance. CTs, while used extensively by research and consultant ecologists, are still largely marketed towards hunting and shooting purposes. However, the continued rise in ecological CT studies and demand for adaptable designs for academic purposes may be at a critical mass that such modifications become commercially viable. Finally, the research on the River Tweed offers a methodology to monitor structures with CTs, to identify rests and resting sites, and analyse resting patterns. Extending the geographical coverage of this study by monitoring resting sites elsewhere would further increase understanding of the effects of seasons and geographical patterns which could be used to refine and modify CT studies of otter resting sites by consultants.

6.5 Closing summary

The overarching objective of this research was to increase the evidence base for methods used to identify otter breeding and resting sites so that they could be better identified and protected. There are currently no fit-for-purpose guidelines for otter survey, specifically the identification of protected resting sites, which are endorsed by competent authorities such as the statutory nature conservation bodies. This contrasts with very prescriptive survey guidelines for other species with the same legislative protection such as Chiroptera (bats). The absence of guidelines to identify otter resting sites mostly appears to be due to a lack of research in this area. My research provides a substantial contribution to developing robust otter survey techniques in context with the very sparse evidence-base. It provides reliable field-sign indicators of resting sites, and methodological guidance for camera-trapping at potential resting sites, as well as a framework for organisation and interpretation of CT data to determine resting sites from non-resting sites. As more experience and research accrues, and with improving technology, the methodologies can be updated to reflect these.

REFERENCES

Adamič MH, Smole J (2011) Phototraps as a non-invasive method of monitoring otters (*Lutra lutra*). What can we expect? IUCN Otter Spec Gr Bull 28(A):60–69

Allaire JJ (2014) manipulate: Interactive plots for RStudio. http://cran.r-project.org/package=manipulate

Allan F, O'Connel JD, Nichols K, Karanth U (2011) Camera traps in animal ecology. Springer Japan, Tokyo

Almeida D, Barrientos R, Merino-Aguirre R, Angeler DG (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. https://doi.org/10.1016/j.anbehav.2012.09.020

Ambarli H, Mengulluoglu D, Bilgin CC (2010) First camera trap pictures of Eurasian lynx from Turkey. CATnews 52 2–5

Anile S, Devillard S (2016) Study design and body mass influence RAIs from camera trap studies: Evidence from the Felidae. Anim Conserv 19:35–45. https://doi.org/10.1111/acv.12214

Apps P, McNutt JW (2018a) Are camera traps fit for purpose? A rigorous, reproducible and realistic test of camera trap performance. Afr J Ecol 56:710–720. https://doi.org/10.1111/aje.12573

Apps PJ, McNutt JW (2018b) How camera traps work and how to work them. Afr J Ecol 56:702–709. https://doi.org/10.1111/aje.12563

Arbon K (2019) Predation of porcupine *Hystrix africaeaustralis* in the den by honey badger Mellivora capensis. Biodivers Obs 10:1–3. https://doi.org/10.15641/bo.v10i0.597

Arrendal J, Vilà C, Björklund M (2007) Reliability of noninvasive genetic census of otters compared to field censuses. Conserv Genet 8:1097–1107. https://doi.org/10.1007/s10592-006-9266-y

Barton K (2016) MuMIn: Multi-Modal Inference. R package version 1.42.1. https://CRAN.R-project.org/package=MuMIn

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Begg CM, Begg KS, Du Toit JT, Mills MGL (2003) Scent-marking behaviour of the honey badger, *Mellivora capensis* (Mustelidae), in the southern Kalahari. Anim Behav 66:917–929. https://doi.org/10.1006/anbe.2003.2223

Birks JDS, Messenger JE, Halliwell EC (2005) Diversity of den sites used by pine martens. Mamm Rev 35:313–320

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

Bivand R, Rundel C (2016) rgeos: Interface to geometry engine - Open Source (GEOS).

Böhm M, Palphramand KL, Newton-cross G, et al (2018) The spatial distribution of badgers , setts and latrines : the risk for intra-specific and badger-livestock disease transmission. Published by : Wiley on behalf of Nordic Society Oikos URL : https://www.jstor.org/stable/30244606. 525–537. https://doi.org/10.1111/j.2008.0906-7590.05314.x

Bradshaw A, Beckmann M, Stevens R, Slater F (2011) Anal scent gland secretion of the European otter (Lutra Lutra). Chem Signals Vertebr 9 313–319. https://doi.org/10.1007/978-1-4615-0671-3_42

Brainerd SM, Helldin J-OO, Lindström ER, et al (1995) Pine marten (*Martes martes*) selection of resting and denning sites in Scandinavian managed forests. Ann Zool Fennici 32:151–157

Brinck C, Gerell R, Odham G (1978) Anal pouch secretion in mink Mustela vison . Chemical communication in Mustelidae. Oikos 30:68–75

Brooks ME, Kristensen K, van Benthen, K J, et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Brown AF, Shepherd KB (1993) A method for censusing upland breeding waders. Bird

Study. https://doi.org/10.1080/00063659309477182

Brown JR, Lawrence MJ, Pope J (2004) Animal tracks, trails and signs (Hamlyn Guide). Octopus Publishing Group

Brzeziński M, Rodak Ł, Zalewski A (2014) “Reversed” intraguild predation: Red fox cubs killed by pine marten. Acta Theriol (Warsz) 59:473–477. https://doi.org/10.1007/s13364-014-0179-8

Brzeziński M, Romanowski J, Kopczyński Ł, Kurowicka E (2006) Habitat and seasonal variations in diet of otters, *Lutra lutra* in eastern Poland. Folia Zool 55:337–348

Burnham KP, Anderson DR (2004) Multimodel inference: Understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304. https://doi.org/10.1177/0049124104268644

Burton AC, Neilson E, Moreira D, et al (2015) Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. J Appl Ecol 52:675–685. https://doi.org/10.1111/1365-2664.12432

Caravaggi A, Banks PB, Burton AC, et al (2017) A review of camera trapping for conservation behaviour research. Remote Sens Ecol Conserv 3:109–122. https://doi.org/10.1002/rse2.48

Chadwick EA, Sherrard-Smith E (2010) Pregnancy among otters (*Lutra lutra*) found dead in England and Wales: foetal development and lack of seasonality. IUCN Otter Spec Gr Bull 27:33–41

CIEEM (2019) Guidelines for Ecological Impact Assessment in the Uk and Ireland: Terrestrial, Freshwater, Coastal and Marine

Collins J (ed) (2016) Bat surveys for professional ecologists: Good practice guidelines (3rd edn)

Coombs AB, Bowman J, Garroway CJ (2010) Thermal properties of tree cavities during winter in a northern hardwood forest. J Wildl Manage 74:1875–1881. https://doi.org/10.2193/2009-560

Crawley M (2005) Statistics: an introduction using R, 1st edn. John Wiley & Sons

Dame N (1993) Influence of age , sex , season and availability on den selection by raccoons within the central basin of Tennessee. Am Midl Nat 129:116–131

Day CC, Westover MD, Hall LK, et al (2016) Comparing direct and indirect methods to estimate detection rates and site use of a cryptic semi-aquatic carnivore. Ecol Indic 66:230–234. https://doi.org/10.1016/j.ecolind.2016.01.039

Deiner K, Altermatt F (2014) Transport distance of invertebrate environmental DNA in a natural river. PLoS One 9:e88786. https://doi.org/10.1371/journal.pone.0088786

Depue JE, Ben-David M (2010) River otter latrine site selection in arid habitats of western Colorado, USA. J Wildl Manage 74:1763–1767. https://doi.org/10.2193/2008-065

Dunstone N (1998) Adaptations to the semi-aquatic habit and habitat. In: Behaviour and Ecology of Riparian Mammals. Cambridge University Press, pp 1–16

Durbin LS (1996a) Communications from the Mammal Society-No. 67. J Zool 240:761–764. https://doi.org/10.1111/j.1469-7998.1993.tb01944.x

Durbin LS (1996b) Individual differences in spatial utilization of a river-system by otters *Lutra lutra*. Acta Theriol (Warsz) 41:137–147

Erlinge S (1967) Home range of the otter *Lutra lutra* L. in southern Sweden. Oikos 18:186–209

Erlinge S (1968) Territoriality of the Otter *Lutra lutra* L. Oikos 19:81–98

EU (2007) Guidance document on the strict protection of animal species of Community interest under the Habitats Directive 92/43/EEC

European Commission The State of Nature in the EU. – Article 17 reporting. Accessed 10 Apr 2020

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

Fahimi H, Yusefi GH, Madjdzadeh SM, et al (2011) Camera traps reveal use of caves by Asiatic black bears (*Ursus thibetanus gedrosianus*) (Mammalia: Ursidae) in southeastern Iran. J Nat Hist 45:2363–2373.

https://doi.org/10.1080/00222933.2011.596632

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

Fernández N, Palomares F (2000) The selection of breeding dens by the endangered Iberian lynx (*Lynx pardinus*): Implications for its conservation. Biol Conserv 94:51–61. https://doi.org/10.1016/S0006-3207(99)00164-0

Findlay MA, Briers RA, Diamond N, White PJC (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. https://doi.org/10.1007/s10344-017-1143-0

Foster RJ, Harmsen BJ (2012) A critique of density estimation from camera-trap data. J Wildl Manage 76:224–236. https://doi.org/10.1002/jwmg.275

Galway County Council (2018) N6 Galway city ring road. Bat derogation licence application

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. Proc Anniv Sci Conf Ecol 236–240

Gese EM (2001) Monitoring of terrestrial carnivore populations. In: Gittleman J, Funk S, Macdonald D, Wayne R (eds) Carnivore Conservation. Cambridge University Press, Ithaca, New York, pp 372–396

Gibeau ML, McTavish C (2009) How to prevent camera traps from skewing animal behavior. Wildl Prof 3:35–37

Glen AS, Cockburn S, Nichols M, et al (2013) Optimising camera traps for monitoring small mammals. PLoS One 8:1–7. https://doi.org/10.1371/journal.pone.0067940

Goldberg CS, Strickler KM, Pilliod DS (2015) Moving environmental DNA methods from concept to practice for monitoring aquatic macroorganisms. Biol Conserv 183:1–3. https://doi.org/10.1016/j.biocon.2014.11.040

Gorman ML, Jenkins D, Harper RJ (1978) The anal scent sacs of the otter (*Lutra lutra*). J Zool 186:463–474. https://doi.org/10.1111/j.1469-7998.1978.tb03933.x

Green J, Green R, 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 Gr Bull 17:1–9

Groenendjik J, Hajek F, Duplaix N, et al (2005) Surveying and monitoring distribution and population trends of the Giant Otter (*Pteronura brasiliensis*). GN-Gruppe Naturschutz

Grolemund G, Hadley W (2011) Dates and times made easy with lubridate. J Stat Softw 40:1–25

Guter A, Dolev A, Saltz D, Kronfeld-Schor N (2008) Using videotaping to validate the use of spraints as an index of Eurasian otter (*Lutra lutra*) activity. Ecol Indic 8:462–465. https://doi.org/10.1016/j.ecolind.2007.04.009

Gužvica G, Bošnjafile I, Bielen A, et al (2014) Comparative analysis of three different methods for monitoring the use of green bridges by wildlife. PLoS One 9:1–12. https://doi.org/10.1371/journal.pone.0106194

Halliwell EC, Macdonald DW (1996) American mink *Mustela vison* in the upper thames catchment: Relationship with selected prey species and den availability. Biol Conserv 76:51–56. https://doi.org/10.1016/0006-3207(95)00072-0

Hamel S, Killengreen ST, Henden JA, et al (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. https://doi.org/10.1111/j.2041-210x.2012.00262.x

Hancock M, Baines D, Gibbons D, et al (1999) Status of male black grouse tetrao tetrix in britain in 1995-96. Bird Study. https://doi.org/10.1080/00063659909461110

Hofmeester TR, Cromsigt JPGM, Odden J, et al (2019) Framing pictures: A conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. Ecol Evol 9:2320–2336.

https://doi.org/10.1002/ece3.4878

Hofmeester TR, Rowcliffe MJ, Jansen PA (2017) A simple method for estimating the effective detection distance of camera traps. Remote Sens Ecol Conserv 3:81–89. https://doi.org/10.1002/rse2.25

Howe EJ, Buckland ST, Després-Einspenner M-L, Kühl HS (2017) Distance sampling with camera traps. Methods Ecol Evol 8:1558–1565. https://doi.org/10.1111/2041-210X.12790

Hu M-C, Pavlicova M, Nunes E V. (2011) Zero-inflated and hurdle models of count data with extra zeros: examples from an HIV-risk reduction intervention trial. Am J Drug Alcohol Abuse 37:367–375. https://doi.org/10.3109/00952990.2011.597280

Huang ZP, Qi XG, Garber PA, et al (2014) The use of camera traps to identify the set of scavengers preying on the carcass of a golden snub-nosed monkey (*Rhinopithecus roxellana*). PLoS One 9:1–6. https://doi.org/10.1371/journal.pone.0087318

Hutchings MR, White PCL (2000) Mustelid scent-marking in managed ecosystems: Implications for population management. Mamm Rev 30:157–169. https://doi.org/10.1046/j.1365-2907.2000.00065.x

Isabel S, Freire M (2011) Day resting site use and fidelity of Alpine otters (*Lutra lutra*) in southeast Austria

Jacobsen L (2005) Otter (*Lutra lutra*) predation on stocked brown trout (*Salmo trutta*) in two Danish lowland rivers. Ecol Freshw Fish 14:59–68. https://doi.org/10.1111/j.1600-0633.2004.00076.x

Jenkins D (1980) Ecology of otters in northern Scotland: I. Otter (*Lutra lutra*) breeding and dispersion in mid- Deeside, Aberdeenshire in 1974-79. J Anim Ecol 49:713–735. https://doi.org/10.2307/4223

Joint Nature Conservation Committee (2007) Second Report by the United Kingdom under Article 17 on the implementation of the Habitats Directive from January to December 2006.

Kanchanasaka B (2001) Tracks and other signs of the hairy-nosed otter (*Lutra sumatrana*). IUCN Otter Spec Gr Bull 18:2–7

Karanth KU (1995) Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. Biol Conserv 71:333–338. https://doi.org/10.1016/0006-3207(94)00057-W

Kean EF, Müller CT, Chadwick EA (2011) Otter scent signals age, sex, and reproductive status. Chem Senses 36:555–564. https://doi.org/10.1093/chemse/bjr025

Kemenes I, Nechay G (1990) The food of otters *Lutra lutra* in different habitats in Hungary. Acta Theriol (Warsz) 35:17–24. https://doi.org/10.4098/at.arch.90-3

Khanal C, Baniya S, Acharye M (2017) First confirmed record of striped hyaena (Hyaena hyaena) den in Nepal. J Biodivers Endanger Species 05:3–5. https://doi.org/10.4172/2332-2543.1000195

Kilshaw K, MacDonald DW (2011) The use of camera trapping as a method to survey for the Scottish wildcat. Scottish Natural Heritage Commissioned Report. 479:1–32

Kleef HL, Tydeman P (2009) Natal den activity patterns of female pine martens (*Martes martes*) in the Netherlands. Lutra 52:3–14

Kleiman DG (1966) Scent marking in the Canidae. Symp Zool Soc London 18:167–177

Kloskowski J (2005) Otter *Lutra lutra* damage at farmed fisheries in southeastern Poland, II: exploitation of common carp *Cyprinus carpio*. Wildlife Biol 11:257–261. https://doi.org/10.2981/0909-6396(2005)11[257:olldaf]2.0.co;2

Kluever BM, Gese EM, Dempsey SJ, Knight RN (2013) A comparison of methods for monitoring kit foxes at den sites. Wildl Soc Bull 37:439–443. https://doi.org/10.1002/wsb.261

Koepfli KP, Deere KA, Slater GJ, et al (2008) Multigene phylogeny of the Mustelidae: Resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biol 6:1–22. https://doi.org/10.1186/1741-7007-6-10

Kollias G V, Fernandez-Moran J (2010) Mustelidae. In: Janis CM, Scott KM, Jacobs LL (eds) Evolution of tertiary mammals of North America. Cambridge University Press, Cambridge, pp 152–173

Kruuk H (1996) Wild Otters: predation and populations. Oxford University Press

Kruuk H (2006a) Otters: ecology, behavior and conservation. Oxford University Press

Kruuk H (1992) Scent marking by otters (*Lutra lutra*): Signaling the use of resources. Behav Ecol 3:133–140. https://doi.org/10.1093/beheco/3.2.133

Kruuk H (2011) Ecological research and conservation management of otters

Kruuk H (2014) Otters and eels: Long-term observations on declines in Scotland. IUCN Otter Spec Gr Bull 31:3–11

Kruuk H (2006b) Otters: Ecology, behaviour and conservation. Oxford University Press

Kruuk H, Carss DN, Conroy JWH, Gaywood MJ (1998) Habitat use and conservation of otters (*Lutra lutra*) in Britain: a review. In: Behaviour and Ecology of Riparian Mammals. Cambridge University Press, pp 119–134

Kruuk H, Conroy JWH, Moorhouse A (1991) Mortality of Otters (*Lutra lutra*) in Shetland in relation to fish abundance. J Appl Ecol 28:95–101

Kruuk H, Moorhouse A (1991a) The spatial organization of otters (Lutra lutra) in Shetland. J Zool 224:41–57. https://doi.org/10.1111/j.1469-7998.1991.tb04787.x

Kruuk H, Moorhouse A (1991b) Recruitment to a population of otters (Lutra lutra) in Shetland, in relation to food abundance. J Appl Ecol 28:95–101

Kruuk H, Moorhouse A, Conroy JWH, et al (1989) An estimate of numbers and habitat preferences of otters Lutra lutra in Shetland, UK. Biol Conserv 49:241–254. https://doi.org/10.1016/0006-3207(89)90046-3

Kuhn R, Meyer W (2009) Infrared thermography of the body surface in the Eurasian otter *Lutra lutra* and the giant otter *Pteronura brasiliensis*. Aquat Biol 6:143–152. https://doi.org/10.3354/ab00176

Langton T, Beckett C, JP F (2001) Great crested newt: Conservation Handbook. Froglife, Halesworth

Larrucea ES, Brussard PF, Jaegar MM, Barrett RH (2007) Cameras, Coyotes, and the assumption of equal detectability. J Wildl Manage 71:1682–1689. https://doi.org/10.2193/2006-407

Lerone L, Carpaneto GM, Loy A (2015) Why camera traps fail to detect a semi-aquatic mammal: Activation devices as possible cause. Wildl Soc Bull 39:193–196. https://doi.org/10.1002/wsb.508

Liles G (2003) Otter Breeding Sites: Conservation and Managament. Conserving Natura 2000 Rivers Conservation Techniques Series No.5

Lim NTL, Ng PKL (2008) Home range, activity cycle and natal den usage of a female Sunda pangolin *Manis javanica* (Mammalia: Pholidota) in Singapore. Endanger Species Res 4:233–240. https://doi.org/10.3354/esr00032

Lucherini M, Reppucci JIJ, Walker RS, et al (2009) Activity patterns and segregation of Carnivores in the High Andes. J Mammal 90:1404–1409. https://doi.org/10.1644/09-MAMM-A-002R.1

Lüdecke D (2019) sjPlot: Data visualization for statistics in social science

Ludecke D, Makowski D, Waggoner P, Patil I (2020) Assessment of Regression Models Performance

Macdonald DW (1980) Patterns of scent marking with urine and faeces amongst carnivore communities. Proc Symp Zool Soc London 45:107–139

Magoun AJ, Copeland JP (1998) Characteristics of Wolverine reproductive den sites. 62:1313–1320. https://doi.org/https://doi.org/10.2307/3801996

Marchand, Peter J (1982) An index for evaluating the temperature stability of a subnivean environment. 46:518–520. https://doi.org/DOI: 10.2307/3808670

Mason C, Macdonald SM (1987a) Seasonal marking in an otter population. Acta Theriol (Warsz) 32:

Mason C, Macdonald SM (1987b) The use of spraint for surveying otter populations. 41:167–177

May R, Gorini L, van Dijk J, et al (2012) Habitat characteristics associated with wolverine den sites in Norwegian multiple-use landscapes. J Zool 287:195–204. https://doi.org/10.1111/j.1469-7998.2012.00907.x

McCarthy M, Després-Einspenner M-L, Samuni L, et al (2018) An assessment of the efficacy of camera-traps for studying demographic composition and variation in chimpanzees (Pan troglodtyes). Am J Primatol 80:

Meek P, Ballard G, Claridge A, et al (2014a) Recommended guiding principles for reporting on camera trapping research. Biodivers Conserv 23:2321–2343. https://doi.org/10.1007/s10531-014-0712-8

Meek P, Ballard G, Fleming P, Falzon G (2016) Are we getting the full picture? Animal responses to camera traps and implications for predator studies. Ecol Evol 6:3216–3225. https://doi.org/10.1002/ece3.2111

Meek P, Ballard G, Fleming PJS (2012) An introduction to camera trapping for wildlife surveys in Australia. Animals Cooperative Research Centre, Canberra, Australia

Meek P, Ballard GA, Fleming PJS, et al (2014b) Camera traps can be heard and seen by animals. PLoS One 9:1–16. https://doi.org/10.1371/journal.pone.0110832

Moorehouse A (1988) Distribution of holts and their utilisation by the European otter (*Lutra lutra*) in a marine environment. MSc thesis. University of Aberdeen

Mori E, Menchetti M, Balestrieri A (2015) Interspecific den sharing: a study on European badger setts using camera traps. Acta Ethol 18:121–126. https://doi.org/10.1007/s10211-014-0197-1

Mugerwa B, Sheil D, Ssekiranda P, et al (2013) A camera trap assessment of terrestrial vertebrates in Bwindi Impenetrable National Park, Uganda. Afr J Ecol 51:21–31. https://doi.org/10.1111/aje.12004

Munoz D, Kapfer J, Olfenbuttel C (2014) Do available products to mask human scent influence camera trap survey results? Wildlife Biol 20:246–252. https://doi.org/10.2981/wlb.00003

Natural England, Department for Environment Food & Rural Affairs (2019) Otters: surveys and mitigation for development project. www.gov.uk/guideance/otters-protection-surveys-and-licences#survey-methods. Accessed 2 Feb 2020

Negrões N, Sollmann R, Fonseca C, et al (2012) One or two cameras per station? Monitoring jaguars and other mammals in the Amazon. Ecol Res 27:639–648. https://doi.org/10.1007/s11284-012-0938-4

Neill LO, Jongh A De, Ozolins J, et al (2007) Minimizing leg-hold trapping trauma for otters with mobile phone technology. J Wildl Manage 71:2776–2780. https://doi.org/10.2193/2006-482

Néill LÓ, Veldhuizen T, de Jongh A, 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. https://doi.org/10.1007/s10344-009-0252-9

Newey S, Davidson P, Nazir S, et al (2015a) Limitations of recreational camera traps for wildlife management and conservation research: A practitioner's perspective. Ambio 44:624–635. https://doi.org/10.1007/s13280-015-0713-1

Newey S, Potts J, Irvine RJ (2015b) Simulation study to inform the design of wildcat camera trap monitoring protocols

Norfolk and Norwich Naturalists Society (1874) Transactions - Norfolk and Norwich Naturalists Society

Norouzzadeh MS, Nguyen A, Kosmala M, et al (2017) Automatically identifying, counting, and describing wild animals in camera-trap images with deep learning. 1–10. https://doi.org/10.1073/pnas.1719367115

NorthConnect (2017) Report on Longhaven Otter Camera Study

Northern Ireland Environment Agency (2017) Otter surveys. NIEA Specific Requirements. https://www.daera-ni.gov.uk/sites/default/files/publications/daera/otter-survey-specifications.pdf

O'Connor KM, Nathan LR, Liberati MR, et al (2017) Camera trap arrays improve detection probability of wildlife: Investigating study design considerations using an empirical dataset. PLoS One 12:1–12. https://doi.org/10.1371/journal.pone.0175684

O'Sullivan WM (1993) The nature and distribution of otter resting sites on part of the River Blackwater catchment, southern Ireland. BiolEnvironProcRIrAcad 93 B:159–162

Ó Néill L, Wilson P, De Jongh A, et al (2008) Field techniques for handling, anaesthetising and fitting radio-transmitters to Eurasian otters (Lutra lutra). Eur J Wildl Res 54:681–687. https://doi.org/10.1007/s10344-008-0196-5

Ottino P, Giller P (2012) Diet and habitat use of the otter in relation to land use in the Araglin Valley, Southern Ireland. Habitat 104:1–17

Papacosta P, Linscheid N (2014) The confirmation of the inverse square law using diffraction ratings. Phys Teach 52:243–245. https://doi.org/10.1119/1.4868944

Park HC, Han TY, Kim DC, et al (2011) Individual identification and sex determination of Eurasian otters (*Lutra lutra*) in Daegu city based on genetic analysis of otter spraint. Genes and Genomics 33:653–657. https://doi.org/10.1007/s13258-011-0051-z

Parry GS, Bodger O, McDonald R a., Forman DW (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. https://doi.org/10.1016/j.ecoinf.2012.11.002

Philcox CK, Grogan AL, Macdonald DW (1999) Patterns of otter *Lutra lutra* road mortality in Britain. J Appl Ecol 36:748–761. https://doi.org/10.1046/j.1365-2664.1999.00441.x

Pickles R, Zambrana V, Hoffmann-Heap I, et al (2011) An evaluation of the utility of camera traps in monitoring giant otter populations. IUCN Otter Spec Gr Bull 28:39–45

Prigioni C, Fumagalli R, Schirru L, Carugati C (1995) Sprainting activity of captive otters: its relationship with breeding cycle and number of animals. Hystrix, Ital. J. Mammal. 7:297–301

Prigioni C, Remonti L, Balestrieri A, et al (2006) Estimation of European Otter (Lutra lutra) population size by fecal DNA typing in Southern Italy. J Mammal 87:855–858. https://doi.org/10.1644/05-mamm-a-294r1.1

QGIS Development Team (2018) QGIS Geographic Information System. Open Source Geospatial Foundation Project

Quaglietta L, Fonseca VC, Mira A, Boitani L (2014) Sociospatial organization of a solitary carnivore, the Eurasian otter (*Lutra lutra*). J Mammal 95:140–150. https://doi.org/10.1644/13-MAMM-A-073.1

Quaglietta L, Hájková P, Mira A, Boitani L (2015) Eurasian otter (*Lutra lutra*) density estimate based on radio tracking and other data sources. Mammal Res 60:127–137. https://doi.org/10.1007/s13364-015-0216-2

Randler C, Kalb N (2018) Distance and size matters: A comparison of six wildlife camera traps and their usefulness for wild birds. Ecol Evol 8:7151–7163. https://doi.org/10.1002/ece3.4240

RCore Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rees H, Gough K (2018) Great crested newt eDNA laboratory quality systems, proficiency testing and interpretation of results in Genetic Techniques and Technologies. CIEEM-In Pract

Remonti L, Balestrieri A, Smiroldo G, Prigioni C (2011) Scent marking of key food sources in the Eurasian otter. Ann Zool Fennici 2450:287–294

Rheingantz ML, Leuchtenberger C, Zucco CA, Fernandez FAS (2016) Differences in activity patterns of the Neotropical otter *Lontra longicaudis* between rivers of two Brazilian ecoregions. J Trop Ecol 32:170–174. https://doi.org/10.1017/S0266467416000079

Roos A, Loy A, De Silva P, et al (2015) *Lutra lutra*. The IUCN Red List of Threatened Species 2015: e.T12419A21935287. http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T12419A21935287.en. Accessed 13 Mar 2017

Roper T., Ostler J., Schmid T., Christian S. (2002) Sett use in European badger *Meles meles*. Behaviour 138:173–187. https://doi.org/10.1163/15685390151074366

Roper TJ (1992) Badger *Meles meles* setts–architecture, internal environment and function. Mamm Rev 22:43–53. https://doi.org/10.1111/j.1365-2907.1992.tb00118.x

Rosoux R, Libois RM (1996) Use of day resting places by the european otter (*Lutra lutra*) in the marais Poitevin (France). A radiotracking study. Proc Eur Congr Mammal 199–212

Rovero F, Martin E, Rosa M, et al (2014) Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. PLoS One 9:. https://doi.org/10.1371/journal.pone.0103300

Rovero F, Zimmermann F (eds) (2016) Camera Trapping for Wildlife Research, 1st edn. Exeter:Pelagic Publishing,UK

Rovero F, Zimmermann F, Berzi D, Meek P (2013) “Which camera trap type and how many do I need?” A review of camera features and study designs for a range of wildlife research applications. Hystrix 24:148–156. https://doi.org/10.4404/hystrix-24.2-6316

Rowcliffe MJ (2017) Key frontiers in camera trapping research. Remote Sens Ecol Conserv. https://doi.org/10.1002/rse2.65

Rowcliffe MJ, Carbone C (2008) Surveys using camera traps: are we looking to a brighter future? Anim Conserv 11:185–186. https://doi.org/10.1111/j.1469-1795.2008.00180.x

Rowcliffe MJ, Carbone C, Jansen PA, et al (2011) Quantifying the sensitivity of camera traps: an adapted distance sampling approach. Methods Ecol Evol 2:464–476. https://doi.org/10.1111/j.2041-210X.2011.00094.x

Rowcliffe MJ, Field J, Turvey ST, Carbone C (2008) Estimating animal density using camera traps without the need for individual recognition. J Appl Ecol 45:1228–1236. https://doi.org/10.1111/j.1365-2664.2008.01473.x

Rowcliffe MJ, Jansen PA, Kays R, et al (2016) Wildlife speed cameras: measuring animal travel speed and day range using camera traps. Remote Sens Ecol Conserv 2:84–94. https://doi.org/10.1002/rse2.17

RStudioTeam (2015) RStudio: Integrated Development for R

Ruiz-Olmo J, Batet A, Mañas F, Martínez-Vidal R (2011) Factors affecting otter (*Lutra lutra*) abundance and breeding success in freshwater habitats of the northeastern Iberian Peninsula

Ruiz-olmo J, Gosalbez J (1997) Observations on the sprainting behaviour of the otter *Lutra lutra* in the N E Spain. Acta Theriol (Warsz) 42:259–270

Ruiz-Olmo J, Jiménez J (2009) Diet diversity and breeding of top predators are determined by habitat stability and structure: A case study with the Eurasian otter (*Lutra lutra* L.). Eur J Wildl Res 55:133–144. https://doi.org/10.1007/s10344-008-0226-3

Ruiz-Olmo J, Mañas F, Batet A (2007) Breeding of otters (*Lutra lutra* L.) in the wild in the Mediterranean area. Proc Eur Otter Conf Isle Skye, July 2003

Ruiz-Olmo J, Margalida A, Batet A (2005) Use of small rich patches by Eurasian otter (*Lutra lutra* L.) females and cubs during the pre-dispersal period. J Zool 265:339–346. https://doi.org/10.1017/S0952836905006424

Ruiz-Olmo J, Olmo-vidal JM, Manas S, Batet A (2002) The influence of resource seasonality on the breeding patterns of the Eurasian otter (*Lutra lutra*) in Mediterranean habitats. Can J Zool 80:2178–2189. https://doi.org/10.1139/z02-186

Ruiz-olmo J, Saavedra D, Jiménez J (2001) Testing the surveys and visual and track censuses of Eurasian otters (*Lutra lutra*). J Zool 253:359–369. https://doi.org/10.1017/S0952836901000334

Scottish Government (2020) Scotlands Environment. https://www.environment.gov.scot/data/data-analysis/protected-nature-sites/?pagenumber=1&resetmap=true&siteid=8369. Accessed 15 Dec 2019

Scottish Natural Heritage Standing Advice for Planning Consultations. Protected species: Otter. https://www.nature.scot/sites/default/files/2019-10/Species Planning Advice - otter.pdf

SEPA (2015) Flood Risk Management Strategy: Forth Estuary Local Plan District. Section 3: Supporting information

Shogren AJ, Tank JL, Andruszkiewicz E, et al (2017) Controls on eDNA movement in streams: transport, retention, and resuspension. Sci Rep 7:1–11. https://doi.org/10.1038/s41598-017-05223-1

Si X, Kays R, Ding P (2014) How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. PeerJ 2:e374. https://doi.org/10.7717/peerj.374

Silver SC, Ostro LET, Marsh LK, et al (2004) The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. Oryx 38:148–154. https://doi.org/10.1017/S0030605304000286

Snell T, Cowell R (2006) Scoping in environmental impact assessment: Balancing precaution and efficiency? Environ Impact Assess Rev 26:359–376. https://doi.org/10.1016/j.eiar.2005.06.003

Sollmann R, Kelly MJ (2013) Camera trapping for the study and conservation of tropical carnivores. Raffles Bull Zool 28:21–42

Steel EA, Kennedy MC, Cunningham PG, Stanovick JS (2013) Applied statistics in ecology : common pitfalls and simple solutions. Ecosphere 4:1–13

Strahler AN (1957) Quantitative analysis of watershed geomorphology. Eos, Trans Am Geophys Union 38:913–920. https://doi.org/10.1029/TR038i006p00913

Swann DE, Hass CC, Dalton DC, Wolf SA (2004) Infrared-triggered cameras for detecting wildlife: an evaluation and review. Source Wildl Soc Bull 32:357–365. https://doi.org/10.2307/3784976

Swinnen KRR, Reijniers J, Breno M, Leirs H (2014) A novel method to reduce time investment when processing videos from camera trap studies. PLoS One 9:e98881. https://doi.org/10.1371/journal.pone.0098881

Tabak MA, Norouzzadeh MS, Wolfson DW, et al (2019) Machine learning to classify animal species in camera trap images: Applications in ecology. Methods Ecol Evol 10:585–590. https://doi.org/10.1111/2041-210X.13120

Taylor PS, Kruuk H (1990) A record of an otter (*Lutra lutra*) natal den. J Zool 222:689–692

Thom MD, Johnson DDP, Macdonald DW, Url S (2013) The evolution and maintenance of delayed implantation in the Mustelidae (Mammalia : Carnivora). 58:175–183

Thomson Ecology (2014) Otter Riverbank Survey and Holt Monitoring Survey https://www.northamptonshire.gov.uk/councilservices/environment-and-planning/planning/planning-applications/documents/PDF%20Documents/Road%20Scheme%20Applications/1

4.00086.CCDFUL-ESV2-Appendix12.9.pdf

Tobler MW, Carrillo-Percastegui SE, Leite Pitman R, et al (2008) An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Anim Conserv 11:169–178. https://doi.org/10.1111/j.1469-1795.2008.00169.x

Tobler MW, Zúñiga Hartley A, Carrillo-Percastegui SE, Powell GVN (2015) Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. J Appl Ecol 52:413–421. https://doi.org/10.1111/1365-2664.12399

Trolliet F, Huynen M-C, Vermeulen C, Hambuckers A (2014) Use of camera traps for wildlife studies. A review. Biotechnol Agron Soc Environ 18:466–454

Trowbridge BJ (1983) Olfactory communication in the European otter (*Lutra lutra*). Aberdeen

Usamentiaga R, Venegas P, Guerediaga J, et al (2014) Infrared thermography for temperature measurement and non-destructive testing. Sensors 14:12305–12348. https://doi.org/10.3390/s140712305

Waldemarin HF, Colares EP (2000) Utilization of resting sites and dens by the neotropical river otter (*Lutra longicaudis*) in the south of Rio Grande do Sul state, Southern Brazil. IUCN Otter Spec Gr Bull 17:14–19

Weber J -M (1990) Seasonal exploitation of amphibians by otters (*Lutra lutra*) in north-east Scotland. J Zool 220:641–651. https://doi.org/10.1111/j.1469-7998.1990.tb04740.x

Wegge P, Pokheral CP, Jnawali SR (2004) Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. Anim Conserv 7:251–256. https://doi.org/10.1017/S1367943004001441

Weinberger IC, Muff S, Kranz A, Bontadina F (2019) Riparian vegetation provides crucial shelter for resting otters in a human-dominated landscape. Mamm Biol 98:179–187. https://doi.org/10.1016/j.mambio.2019.09.001

Welbourne DJ, Claridge AW, Paull DJ, Lambert A (2016) How do passive infrared triggered camera traps operate and why does it matter? Breaking down common misconceptions. Remote Sens Ecol Conserv 2:77–83. https://doi.org/10.1002/rse2.20

Wellington K, Bottom C, Merrill C, Litvaitis J a. (2014) Identifying performance differences among trail cameras used to monitor forest mammals. Wildl Soc Bull 38:634–638. https://doi.org/10.1002/wsb.425

Yoxon G, Yoxon P (1990) Otter survey of the Isle of Skye, Scotland (*Lutra lutra*). IUCN Otter Spec Gr Bull 5:70–75

Yoxon P, Yoxon K (2014) Estimating otter numbers using spraints :is it possible ? J Mar Biol 2014:1–6

Yu X, Wang J, Kays R, et al (2013) Automated identification of animal species in camera trap images. Eurasip J Image Video Process 2013:. https://doi.org/10.1186/1687-5281-2013-52

APPENDICES

Appendix I - Model Selection Tables for Chapter 2

Model tables containing all candidate models used for each analysis are presented here with the parameter estimates for each model. We used a threshold of ΔAIC ≤ 2 to indicate models with "substantial support" and the plots of the best supported models (i.e. ΔAIC = 0) are included in the main text. Plots of all other models with ΔAIC ≤ 2 are presented here and are indicated in bold in the following tables.

In the tables below, df = model degrees of freedom, logLik = log likelihood of the model, AIC = Akaike information criterion, Δ_{AIC} = difference in AIC between that model and the model with the lowest AIC; and Wi = Akaike's weight.

Trigger probability models

Variables affecting trigger probability were analysed using generalised linear mixed models using a binomial distribution. Trigger probability was the binary response variable (1 = trigger/ 0 = No trigger) and camera position (CT.POS) was used as a random effect.

Table A1 Model results for Trigger Probability, P(trigger|pass), for (a) badger with Bushnell CT on video setting (b) fox with Bushnell CT on video setting and (c) dry otter from holt with Bushnell CT on video setting, and (d) dry otter from holt with Acorn CT on video setting.

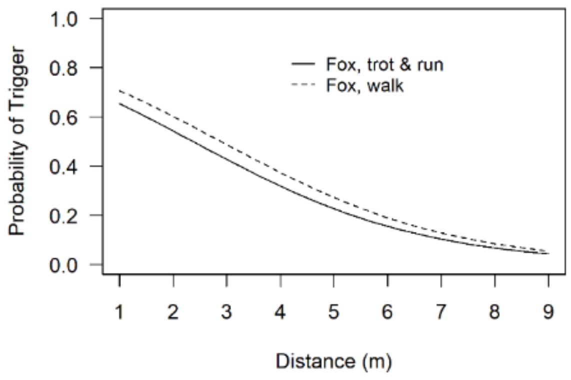
(a) Badger video, Bushnell (n = 249)

			Model Parameters								
Model	df	logLik	Int	DIST	GAIT	LOIT	AIR	DIST: GAIT	AIC	Δ_{AIC}	W_i
GAIT:DIST	**5**	**-130.515**	**0.44**	**-0.111**	**2.351**			**-0.633**	**271.03**	**0.00**	**0.937**
DIST	3	-135.934	1.31	-0.329					277.87	6.84	0.031
GAIT+DIST	4	-135.669	1.21	-0.328	0.230				279.34	8.31	0.015
AIR+DIST	4	-135.931	1.29	-0.330			0.005		279.86	8.83	0.011
LOIT	3	-138.037	0.00			1.006			282.07	11.04	0.004
NULL	2	-140.044	0.09						284.09	13.06	0.001
GAIT	3	-139.728	-0.01		0.250				285.46	14.43	0.001
AIR	3	-139.997	0.20						285.99	14.96	0.001
GAIT+AIR	4	-139.717	0.04		0.241				287.43	16.40	0.000

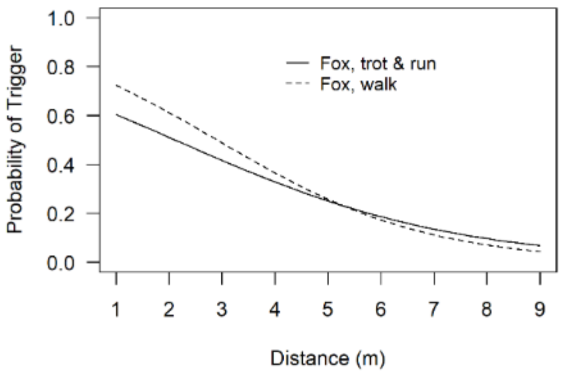
(b) Fox video, Bushnell (n = 454)

			Model Parameters								
Model	df	logLik	Int	DIST	GAIT	LOIT	AIR	DIST: GAIT	AIC	Δ_{AIC}	W_i
DIST	**3**	**-280.491**	**1.291**	**-0.471**					**567.0**	**0.00**	**0.401**
GAIT+DIST	**4**	**-279.888**	**1.101**	**-0.465**	**0.242**				**567.8**	**0.79**	**0.269**
GAIT:DIST	**5**	**-279.300**	**0.801**	**-0.378**	**0.664**			**-0.125**	**568.6**	**1.62**	**0.178**
AIR+DIST	**4**	**-280.463**	**1.235**	**-0.471**			**0.010**		**568.9**	**1.94**	**0.152**
LOIT	3	-305.894	-0.302			0.879			617.8	50.81	0.000
GAIT	3	-306.844	-0.494		0.350				619.7	52.71	0.000
NULL	2	-308.278	-0.251						620.6	53.57	0.000
GAIT+AIR	4	-306.841	-0.475		0.349		-0.003		621.7	54.70	0.000
AIR	3	-308.266	-0.215				-0.006		622.5	55.55	0.000

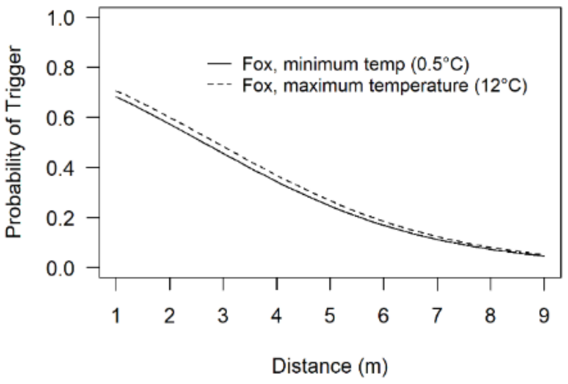
Fox video, Trigger ~GAIT+DIST



Fox video, Trigger ~GAIT:DIST

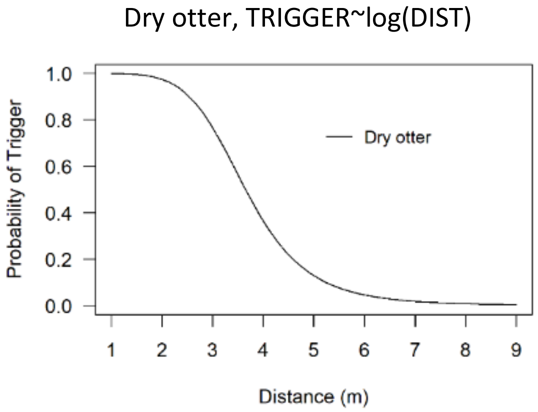


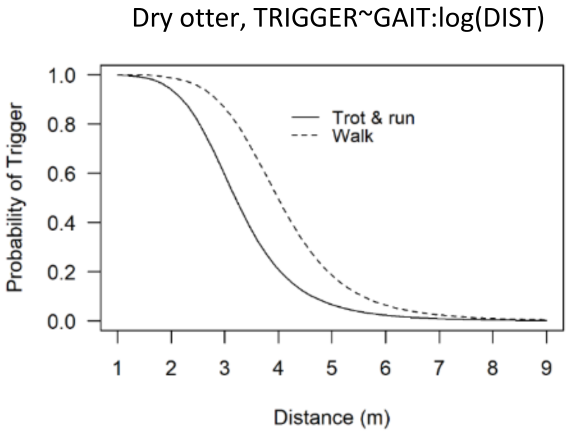
Fox video, Trigger ~AIR+DIST



(c) Dry otter video, from holt, Bushnell (n=111)

			Model Parameters								
Model	df	logLik	Int	Log (DIST)	GAIT	LOIT	AIR	DIST: GAIT	AIC	Δ_{AIC}	W_i
GAIT+log(DIST)	**4**	**-27.543**	**7.215**	**-6.174**	**1.474**				**63.1**	**0.00**	**0.440**
Log(DIST)	**3**	**-29.045**	**7.854**	**-6.065**					**64.1**	**1.00**	**0.266**
GAIT*log(DIST)	**5**	**-27.401**	**6.883**	**-5.924**	**2.191**			**-0.636**	**64.8**	**1.72**	**0.186**
AIR+log(DIST)	4	-28.950	7.292	-5.820			0.045		65.9	2.81	0.108
GAIT	3	-46.350	0.693		1.808				98.7	35.61	0.000
GAIT+AIR	4	-45.373	0.130		1.800		0.087		98.7	35.66	0.000
AIR	3	-50.940	0.792				0.110		107.9	44.79	0.000
NULL	2	-52.344	1.513						108.7	45.60	0.000
LOIT	3	-52.344	1.510			0.024			110.7	47.60	0.000

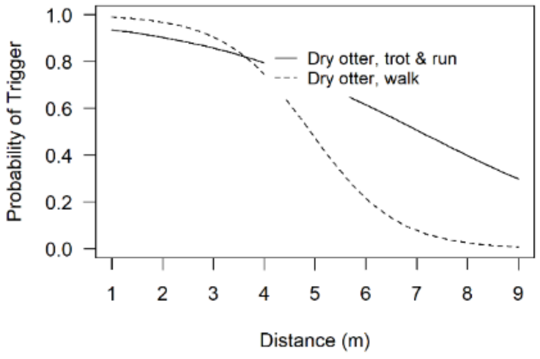

Dry otter, TRIGGER~log(DIST)


Dry otter, TRIGGER~GAIT:log(DIST)

(d) Dry otter video, from holt, Acorn (n = 115)

			Model Parameters								
Model	df	logLik	Int	DIST	GAIT	LOIT	AIR	DIST: GAIT	AIC	Δ_{AIC}	W_i
AIR+DIST	**4**	**-34.870**	**3.076**	**-0.636**			**0.135**		**77.7**	**0.00**	**0.387**
GAIT:DIST	**5**	**-34.210**	**3.124**	**-0.442**	**2.669**			**-0.738**	**78.4**	**0.68**	**0.275**
DIST	**3**	**-36.333**	**4.036**	**-0.652**					**78.7**	**0.93**	**0.243**
GAIT+DIST	**4**	**-36.272**	**4.209**	**-0.668**	**-0.225**				**80.5**	**2.80**	**0.095**
AIR	3	-47.923	0.442				0.192		101.8	24.11	0.000
GAIT+AIR	4	-47.703	0.277		0.364		0.187		103.4	25.67	0.000
NULL	2	-51.611	1.619						107.2	29.48	0.000
GAIT	3	-51.186	1.349		0.494				108.4	30.63	0.000
LOIT	3	-51.599	1.602			0.107			109.2	31.46	0.000

Trigger~GAIT:DIST



Trigger~DIST

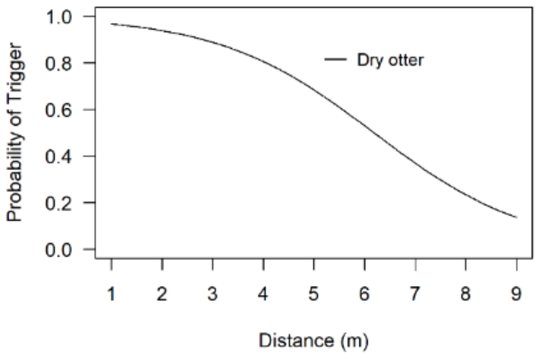
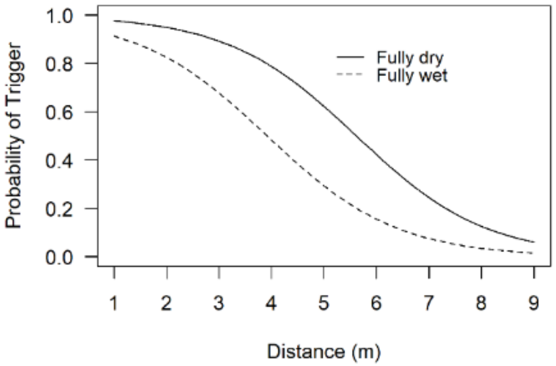


Table A 2 Model results for Trigger Probability, P (T|P), including the variable WET.DRY, using (a) Bushnell video setting and (b) Acorn video setting. Generalised Linear Mixed models, using trigger probability as a response variable and binomial distribution. CT.POS is used as fixed effect.

(a) Coat wetness, Bushnell video (n = 190)

			Model Parameters											
Model	df	logLik	Int	DIST	GAIT	LOIT	AIR	WET.DRY	DIST: WET. DRY	WET. DRY: GAIT	AIR: WET. DRY	AIC	Δ_{AIC}	W_i
wet.dry:DIST	**5**	**-75.645**	**5.670**	**-1.077**				**-3.613**	**0.574**			**161.29**	**0.00**	**0.606**
wet.dry+DIST	**4**	**-77.545**	**4.556**	**-0.811**				**-1.378**				**163.09**	**1.80**	**0.246**
AIR+DIST	4	-78.463	5.572	-0.872			-0.180					164.93	3.64	0.098
GAIT+DIST	4	-79.187	3.044	-0.773	1.146							166.37	5.08	0.048
DIST	3	-83.442	3.700	-0.792								172.88	11.59	0.002
wet.dry:AIR	5	-94.808	0.915				0.092	3.316			-0.533	199.62	38.33	0.000
wet.dry+GAIT	4	-96.537	0.766		1.590			-1.558				201.07	39.78	0.000
wet.dry:GAIT	5	-96.398	0.693		1.808			-1.386		-0.389		202.80	41.51	0.000
GAIT	4	-103.465	0.965		1.432		-0.106					214.93	53.64	0.000
GAIT	3	-106.441	0.150		1.382							218.88	57.59	0.000
wet.dry+AIR	4	-105.779	2.044				-0.071	-1.258				219.56	58.27	0.000
wet.dry	3	-106.955	1.515					-1.388				219.91	58.62	0.000
wet.dry+LOIT	4	-106.158	1.443			0.550		-1.446				220.32	59.03	0.000
AIR	3	-112.456	1.670				-0.095					230.91	69.62	0.000
NULL	2	-114.661	0.907									233.32	72.03	0.000
LOIT	3	-114.328	0.847			0.345						234.66	73.37	0.000

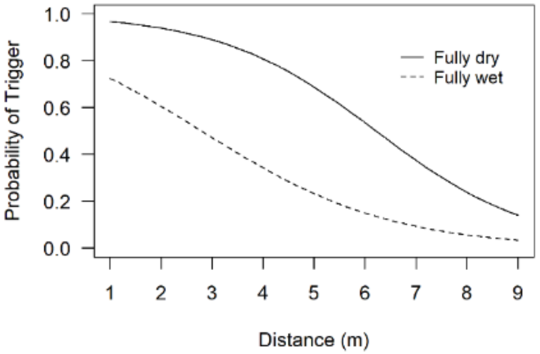
Trigger~wet.dry+DIST



(b) Coat wetness, Acorn video (n = 193)

			Model Parameters											
Model	df	logLik	Int	DIST	GAIT	LOIT	AIR	WET. DRY	DIST: WET. DRY	WET. DRY: GAIT	AIR: WET. DRY	AIC	Δ_{AIC}	W_i
wet.dry+DIST	**4**	**-83.694**	**3.918**	**-0.620**				**-2.128**				**175.4**	**0.00**	**0.715**
wet.dry:DIST	**5**	**-83.612**	**4.041**	**-0.650**				**-2.534**	**0.111**			**177.2**	**1.84**	**0.285**
GAIT+DIST	4	-97.793	3.180	-0.607	-0.652							203.6	28.20	0.000
DIST	3	-99.354	2.656	-0.564								204.7	29.32	0.000
AIR+DIST	4	-99.340	2.582	-0.562			0.009					206.7	31.29	0.000
wet.dry:AIR	5	-99.202	0.416				0.177	-0.659			-0.169	208.4	33.02	0.000
wet.dry+LOIT	4	-100.340	1.448			0.953		-1.958				208.7	33.29	0.000
wet.dry+AIR	4	-100.421	0.860				0.105	-2.056				208.8	33.45	0.000
wet.dry	3	-102.546	1.562					-1.836				211.1	35.70	0.000

Trigger~wet.dry:DIST



Registration probability models

Only passes of mammal where the CTs triggered were used in these models, thus the registration probability is conditional on there being a trigger.

Variables affecting registration probability were analysed using generalised linear mixed models using a binomial distribution. Registration probability was the binary response variable (1 = animal registered / 0 = no animal registered) and camera position (CT.POS) was used as a fixed effect.

Table A3 Model results for Registration Probability P (C/T), for (a) badger, Bushnell video (b) fox, Bushnell video (c) otter (all passes), Bushnell video and, (d) otter (all passes), Acorn video.

(a) Badger video (n = 140)

			Model Parameters								
	df	logLik	Intercept	DIST	GAIT	LOIT	AIR	DIST: GAIT	AIC	Δ_{AIC}	W_i
LOIT+GAIT+DIST	**5**	**-78.262**	**-1.970**	**0.243**	**1.632**	**1.375**			**166.5**	**0.00**	**0.727**
GAIT	3	-82.364	-0.962		1.502				170.7	4.20	0.089
GAIT+DIST	4	-81.481	-1.785	0.247	1.639				171.0	4.44	0.079
GAIT+AIR	4	-81.758	-0.456		1.424		-0.091		171.5	4.99	0.060
GAIT:DIST	5	-81.106	-1.973	0.300	2.256			-0.249	172.2	5.69	0.042
LOIT	3	-86.414	-0.572			1.413			178.8	12.30	0.002
LOIT+DIST	4	-86.405	-0.651	0.026		1.411			180.8	14.29	0.001
AIR	3	-88.469	0.375				-0.144		182.9	16.42	0.000
NULL	2	-90.160	-0.379						184.3	17.80	0.000
AIR+DIST	4	-88.245	0.059	0.123			-0.156		184.5	17.97	0.000
DIST	3	-90.136	-0.504	0.041					186.3	19.75	0.000

(b) Fox video (n = 199)

			Model Parameters								
Model	df	logLik	Intercept	DIST	GAIT	LOIT	AIR	DIST: GAIT	AIC	Δ_{AIC}	W_i
LOIT+GAIT+DIST	**5**	**-106.985**	**-1.576**	**0.060**	**0.953**	**1.807**			**224.0**	**0.00**	**0.513**
LOIT	**3**	**-109.598**	**-0.696**			**1.985**			**225.2**	**1.23**	**0.278**
LOIT+DIST	4	-109.597	-0.712	0.006		1.985			227.2	3.22	0.102
GAIT	3	-111.308	-1.412		1.120				228.6	4.65	0.050
GAIT+DIST	4	-111.213	-1.586	0.054	1.156				230.4	6.46	0.020
GAIT+AIR	4	-111.292	-1.333		1.114		-0.012		230.6	6.61	0.019
GAIT:DIST	5	-110.692	-2.287	0.222	2.027			-0.236	231.4	7.41	0.013
NULL	2	-115.196	-0.542						234.4	10.42	0.003
AIR	3	-115.131	-0.400				-0.023		236.3	12.29	0.001
DIST	3	-115.192	-0.514	-0.010					236.4	12.41	0.001
AIR+DIST	4	-115.119	-0.338	-0.019			-0.025		238.2	14.27	0.000

Registration~LOIT

(c) Otter Bushnell video (n = 220)

			Model parameters								
Model	df	logLik	Intercept	DIST	GAIT	LOIT	AIR	DIST: GAIT	AIC	Δ_{AIC}	W_i
LOIT+GAIT+DIST	**5**	**-127.152**	**-2.202**	**0.273**	**1.852**	**1.347**			**264.3**	**0.00**	**0.996**
GAIT+DIST	4	-134.191	-1.893	0.263	1.895				276.4	12.08	0.002
GAIT:DIST	5	-133.625	-1.387	0.098	1.205			0.250	277.2	12.95	0.002
GAIT	3	-137.110	-1.136		1.737				280.2	15.92	0.000
GAIT+AIR	4	-137.021	-1.261		1.713		0.018		282.0	17.74	0.000
LOIT	3	-143.350	-0.231			1.404			292.7	28.40	0.000
LOIT+DIST	4	-142.504	-0.561	0.130		1.420			293.0	28.71	0.000
NULL	2	-152.265	0.091						308.5	44.23	0.000
DIST	3	-151.564	-0.199	0.116					309.1	44.82	0.000
AIR	3	-152.123	-0.072				0.020		310.2	45.94	0.000
AIR+DIST	4	-151.460	-0.332	0.113			0.017		310.9	46.62	0.000

(d) Otter Acorn video (n = 201)

			Model parameters								
Model	df	logLik	Intercept	DIST	GAIT	LOIT	AIR	DIST: GAIT	AIC	Δ_{AIC}	W_i
LOIT+GAIT+DIST	**5**	**-107.963**	**-1.173**	**-0.017**	**2.041**	**1.296**			**225.9**	**0.00**	**0.906**
GAIT	3	-113.080	-0.957		2.086				232.2	6.23	0.040
GAIT+AIR	4	-112.324	-1.436		2.107		0.056		232.6	6.72	0.031
GAIT+DIST	4	-113.053	-1.045	0.027	2.114				234.1	8.18	0.015
GAIT:DIST	5	-112.794	-1.259	0.081	2.624			-0.183	235.6	9.66	0.007
LOIT+DIST	4	-123.109	0.425	-0.209		1.433			254.2	28.29	0.000
LOIT	3	-124.782	-0.135			1.357			255.6	29.64	0.000
DIST	3	-130.418	0.604	-0.158					266.8	40.91	0.000
NULL	2	-131.497	0.164						267.0	41.07	0.000
AIR	3	-130.803	-0.260				0.049		267.6	41.68	0.000
AIR+DIST	4	-129.809	0.196	-0.154			0.046		267.6	41.69	0.000

Appendix II – Table of bedding collection behaviour for Chapter 4

Table A4 Details of all bedding collection recorded by camera-traps, incidents where more than one otter collect bedding are highlighted.

Site	Date	Duration of bedding collection events (min)			Group or single otter	Sex	Duration of rest (min)	Nocturnal (N) or Diurnal (D) Rest	
		Event 1	Event 2	Event 3					
LEARMOUTH	29/03/2018	<1			SINGLE	U	19	N	PAIR
LEARMOUTH	10/03/2019	<1			SINGLE	U	944	D	PAIR
GORDON	17/09/2016	<1			SINGLE	U			
GORDON	18/09/2016	<1			GROUP	U			
GORDON	18/09/2016	<1			GROUP	U			
GORDON	28/10/2016	<1			GROUP	U			IN
GORDON	24/11/2016	12			GROUP	U			IN
GORDON	24/11/2016	4			GROUP	U			IN
GORDON	05/01/2017	11			GROUP	U	230	N	PAIR
GORDON	10/01/2017	1	3	1	GROUP	U	354	N	PAIR
GORDON	10/01/2017	1	3	1	GROUP	U	354	N	PAIR
GORDON	21/01/2017	6			GROUP	F	88		PAIR
GORDON	21/01/2017	6			GROUP	M	88		PAIR
GORDON	03/02/2017	1			SINGLE	U			IN
GORDON	04/02/2017	1			GROUP	U			IN
GORDON	04/02/2017	1			GROUP	U			IN
GORDON	11/02/2017	3			GROUP	U			IN
GORDON	11/02/2017	3			GROUP	U			IN
GORDON	16/02/2017	<1			GROUP	U	756	D	PAIR
GORDON	16/02/2017	<1			GROUP	U	756	D	PAIR
FROGDEN1	09/04/2015	<1			GROUP	F	137	N	PAIR
FROGDEN1	18/01/2017	1			GROUP	U	322	N	PAIR
FROGDEN1	26/01/2017	6			GROUP	U	970	D	PAIR
FROGDEN1	17/01/2018	<1			SINGLE	U	622	D	PAIR
FROGDEN1	28/01/2018	7			SINGLE	M			IN
FROGDEN1	03/02/2018	<1			SINGLE				
FROGDEN1	05/02/2018	4			SINGLE	M	326		PAIR
FROGDEN1	08/02/2018	1			SINGLE	NONE	249	N	PAIR
FROGDEN1	12/02/2018	2			SINGLE	U	652		PAIR
FROGDEN1	05/04/2018	<1			SINGLE	U	392		PAIR
FROGDEN1	01/05/2018	<1			SINGLE	M			IN
FROGDEN1	11/05/2018	<1			SINGLE	M	491		PAIR
NENTHORN	05/12/2018	1			SINGLE	U			
TORQUHAN	09/02/2017	<1			GROUP	F	779	N	PAIR
TORQUHAN	16/02/2017	4			SINGLE	U	583	N	PAIR
TORQUHAN	23/02/2017	1			GROUP	U	560	N	PAIR
TORQUHAN	02/03/2017	<1			SINGLE	U	149	N	PAIR
TORQUHAN	15/03/2017	1			SINGLE	M	60		PAIR

Site	Date	Duration of bedding collection events (min) Event 1	Event 2	Event 3	Group or single otter	Sex	Duration of rest (min)	Nocturnal (N) or Diurnal (D) Rest	
TORQUHAN	23/04/2017	<1			SINGLE	U	479	N	PAIR
TORQUHAN	28/04/2017	<1			SINGLE	U			OUT
TORQUHAN	11/03/2018	3			GROUP	F	154	N	PAIR
CRAILING	27/04/2017	<1			SINGLE	M	1038		PAIR
CRAILING	12/02/2018	6			SINGLE	U			IN

Appendix III – Published chapters

Chapter 2:

Findlay MA, Briers RA, White PJC (2020) Component processes of detection probability in camera-trap studies: understanding the occurrence of false-negatives. Mammal Res 167–180. doi: 10.1007/s13364-020-00478-y

Chapter 3:

Findlay MA, Briers RA, Diamond N, White PJC (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. doi: 10.1007/s10344-017-1143-0