

REMOTE CAMERA TECHNOLOGY AND ITS ROLE IN GREY SEAL HAUL-OUT ASSESSMENT



Submitted by William Heaney to the University of Exeter as a thesis for the degree of Master by Research in Biological Sciences in March 2018.

This thesis is available for Library use on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgment.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Student signature:.....

William J. Heaney

ABSTRACT

Remote cameras can permit non-invasive monitoring of marine species and habitats. Using automated time-lapse cameras in combination with human observations and an infrared visitor counter, this project collected data on the daily maximum number of grey seals (*Halichoerus grypus*) hauled-out and daily numbers of visitors at a major grey seal haul-out location in Cornwall, south west England between August 2013 and December 2017. This project assesses the uses of data captured by time-lapse cameras to quantify seasonal patterns of grey seal haul-out abundance and how haul-out patterns might be influenced by environmental conditions, as well as quantifying counts of pups (as pup positive days) during the grey seal pupping season (Chapter 1). Using this knowledge, the project combines data from human-led surveys with time-lapse cameras to quantify the effects of human disturbance at a grey seal haul-out (Chapter 2).

The peak in grey seal haul-out abundance occurred in March and April with median daily maximum grey seal haul-out counts of 103 seals (± 52.00 IQR, range 52 to 188) and 83 seals (± 46.00 IQR, range 25 to 239) respectively. The largest range in daily visitor numbers occurred in April (range 23 to 743) coinciding within the peak period in grey seal abundance but the peak period for visitor numbers at the site occurred in August in 2014 and 2015 with median daily visitor counts of 381 (± 102.00 IQR, range 77-471). Grey seal white-coated pups were observed on a total of 99 days during three seasons of monitoring (2013, 2014, 2017) with the highest number of pup positive days occurring in September (median 15 \pm pup positive days 4.00 IQR) and October (median 13 pup positive days ± 2.50 IQR) each year. 'People on cliff' disturbances were more likely to disturb grey seals into the sea than other stimuli and as such,

reduced the number of grey seals hauled-out on the beach during a disturbance event. This project concludes with a discussion of the potential impacts of disturbance at the haul-out site, with the findings highlighting the value of using time-lapse camera technology in effectively monitoring a pinniped population for a prolonged period and the implications of disturbance and the need for management action.

ACKNOWLEDGEMENTS

I would like to thank my supervisors' Dr Matthew Witt and Dr Lucy Hawkes for their commitment to the project and assistance in developing ideas and techniques. I would also like to thank Sue Sayer and Kate Hockley of the Cornwall Seal Group Research Trust (CSGRT), for their help and enthusiasm in coordinating this project as well providing access to the disturbance data held in CSGRT's database. Without their dedication and passion for researching and conserving grey seals, our research into quantifying the effects of human disturbance would not have been achievable. I thank Dr Anthony Bicknell for his support when the project was in its infancy. Thank you to Dr Phillip Doherty, Bethany Roberts and Owen Greenwood for their assistance with R. I sincerely thank the National Trust Mid-Cornwall Ranger Team for their assistance, commitment and enthusiasm for the project particularly when establishing and maintaining equipment at the field site. Fieldwork would not have been possible without the assistance and support of Steve Sudworth, Nick Holden and Henry Upton. Thank you to my work colleagues at the National Trust for their day to day support and assisting with data collection, even during adverse weather conditions.

Thank you to my parents for their endless love and support over the past few years, there's no doubt that I would not have got through it without them. A huge thank you to my grandparents for their inspiration into the natural world and to my grandad for his endless interest and attention into my tireless pursuit of the animal kingdom.

I must thank Richard Hollis and Calum Laver for their friendship and support in fieldwork throughout the duration of my research. When we weren't outside in howling gales, or on a cliff for hours on end, whether it be day or night, we were laughing and chasing Orcas around Iceland.

Thank you to everyone else who assisted in fieldwork along the way and to the members of the marine vertebrate research group for their insight and for putting up with my endless energy during, and outside of, meetings. Here's my thesis, signed, seal-ed and delivered.

LIST OF CONTENTS

	Page
Abstract.....	2
Acknowledgements.....	4
List of figures and table.....	7
Author's declaration.....	8
General Introduction.....	9
Chapter 1: Using time-lapse camera technology to monitory grey seal haul- outs.....	16
Chapter 2 Assessing the role of cameras in quantifying human disturbance at a grey seal haul-out.....	42
General Discussion.....	69
References.....	76
Supplementary Material.....	99

LIST OF FIGURES AND TABLES

Figures Chapter 1	Page
1. Grey seal haul-out study site location in Cornwall, south west England.	34
2. Grey seal camera trap example images.	35
3. Daily maximum number of grey seals hauled-out (July 2013-October 2015).	36
4. Proportion of pup positive days corrected for camera operation time.	37
5. Hourly counts of hauled-out grey seals corresponding to hourly tidal level.	38
6. Hourly counts of grey seals corresponding to wind chill readings.	39
7. Comparative grey seal counts determined from time-lapse camera images and human observers.	40
Table	
1. Summary of operational camera days and lanugo pup positive days.	41
Figures Chapter 2	
1. Seasonal variance of grey seals and visitors at the haul-out site.	61
2. Correlation between daily number of visitors and daily maximum number of grey seals.	62
3. Distribution of disturbance stimuli recorded by CSGRT.	63
4. Cumulative number of CSGRT surveys and recorded disturbance events.	64
5. Number of hauled-out grey seals during nine 'people on cliff' disturbance events.	65
6. Spatial distributions of grey seals at the haul-out site during a people on cliff disturbance event.	66
7. Thermal images of haul-out beach taken using a FLIR T620.	67
Table	
1. Description of disturbance events observed by CSGRT and summary of camera functioning.	68

AUTHORS' DECLARATION

Data collection was undertaken by William J. Heaney and Dr Anthony J. Bicknell between July 2013 and December 2017. Literature searches, data processing, data analysis and thesis preparation was undertaken by William J. Heaney.

Dr Matthew J. Witt and Dr Lucy Hawkes provided supervision to William J. Heaney throughout data collection, data processing, analysis and thesis preparation.

Sue Sayer from the Cornwall Seal Group Research Trust (CSGRT) provided insight into the study and access to CSGRT disturbance data.

Nick Holden, Henry Upton and Steve Sudworth from the National Trust mid-Cornwall ranger team co-ordinated the implementation of the visitor counter and time-lapse cameras at the field site.

John Prior provided environmental data on behalf of the National Coast Watch Institution in St Ives.

GENERAL INTRODUCTION

To conserve species that may be in decline, it is necessary to identify their core habitats and understand their demography, life history and movements (Hussey *et al.* 2015), which can often require invasive manipulation of individuals (McMahon *et al.* 2012). There are, however, non-invasive methods that may be better used to monitor animal populations. Through monitoring marine vertebrates, estimates of population size and trends can be determined and this information can aid in the prioritisation of conservation strategies and provide insight into spatial and temporal patterns of distribution and behaviour (Wallace *et al.* 2010). This information can yield a deeper understanding of the interactions between marine vertebrates and anthropogenic activities, including associated threats, to better inform conservation of target species (Airoldi *et al.* 2008). Methods that are currently used to monitor marine vertebrates can be largely divided into two categories; invasive and non-invasive.

Invasive methods

Population abundance and survival probability estimates can be derived from invasive capture-mark-recapture (CMR) methods. This is the process through which animals are captured, marked and released with the intention of a portion being re-captured and counted at a later date (Dutton *et al.* 2005). The branding of pinnipeds, where a series of letters and numbers are burned through the coat of a seal to provide a unique identification number, is a controversial example of this (Rand 1950). Brands were considered more suitable than identification tags (1915-1970) when monitoring southern elephant seals (*Mirounga leonina*) as they could be read at greater distances and were longer lasting (Ingham 1967). However, branding had disadvantages when trying to identify individuals in large colonies, as the brand could be hard to observe

when seals laid on top of one another (Ingham 1967). Furthermore, shallow brands, just on the outer coat, can fade with time and deep brands, penetrating through the skin into the blubber, can be difficult to read as they heal and distort (Ingham 1967) and can also injure the animals leaving lesions susceptible to infection (pers.comm. Sue Sayer). Painting seals has also been used in CMR estimates. Cape fur seal pups (*Arctocephalus pusillus*) were painted with white-oil paint for identification, proving useful in identifying individuals until pups began entering the water (Rand 1950).

Flipper tagging has long been used to gather information on the distribution and movements of marine vertebrates, including grey seals (*Halichoerus grypus*) (Pomeroy *et al.* 2000). The use of flipper tags on nesting adult sea turtles, for example, has enabled scientists to gain insights into reproductive behaviour (Miller 1997, Hendrickson 1958) and pre-and post-breeding migrations (Carr *et al.* 1978; Balaz 1980; Limpus *et al.* 1992). Furthermore, flipper tagging of juvenile turtles has provided information on habitat utilisation (Schmid 1995), growth rates (Boulon & Frazer 1990; Limpus & Chaloupka 1997) and ontogenetic migrations (Bjorndal & Bolten 1997; Musick & Limpus 1997). However, flipper tags are not always retained (Troëng *et al.* 2005), can cause drag (Culik *et al.* 1993) and lift (Hazekamp *et al.* 2010) in some species, can lead to infected tagging wounds (Witzell 1998; Leong *et al.* 1989) and contribute to turtles becoming entangled in fishing nets (Nichols *et al.* 1998).

Bio-logging is the process of attaching electronic devices to animals to collect data on movement and habitat use and represents a more recent advance in the use of invasive methods (Block *et al.* 2011, Hussey *et al.* 2015, Viviant *et al.* 2010). Directly gathering observational data of large marine vertebrates is often logistically challenging because many species spend limited time at or near the surface and most of their time underwater (Fedak 2004), restricting the time in which they can be

observed in visual surveys (Witt *et al.* 2012). The use of bio-logging technology has therefore enabled scientists to gain insight into the lives of many marine species (Block *et al.* 2011). A suite of technologies exists to overcome the differing challenges of studying many marine species. Marine vertebrates travel long distances (Block *et al.* 2011), often making it impossible to retrieve tags. Therefore, data have to be transmitted remotely (Hussey *et al.* 2015). This technology can reveal information on migration pathways (Bonfil *et al.* 2017), niche partitioning (Block *et al.* 2011) and multispecies aggregations (Schaefer & Fuller 2013) at locations which are often distant from human view. Furthermore, telemetry data has also enabled the definition of species home ranges (Kelly *et al.* 2010), core habitat use (Jaine *et al.* 2014; Vanbianchi *et al.* 2017) delineated species distributions and assisted in identifying spawning site fidelity (Dean *et al.* 2014).

In recent years, animal borne video and environmental data collection systems (AVEDs) have enabled glimpses of fine-scale behaviours of how individuals act within groups (Moll *et al.* 2007) in species such as sharks (Heithaus *et al.* 2001), sea turtles (Heithaus *et al.* 2002), seabirds (Gremaillet *et al.* 2006), pinnipeds (Davis *et al.* 1999), manatees (Adimey *et al.* 2007) and baleen whales (Williams *et al.* 2000). For many species, fine-scale aspects of behaviour, physiology and ecology “from the animal’s perspective” are poorly understood, if at all (Moll *et al.* 2007; Hays *et al.* 2016). For example, deployments of cetacean-borne video camera and integrated sensor systems on wild dusky dolphins (*Lagenorhynchus obscurus*) off New Zealand have revealed social and environmental parameters such as conspecific body condition, mother-calf spatial positioning, affiliative behaviour, sexual behaviour, sociability, prey and habitat type (Pearson *et al.* 2017). These findings have enabled new perceptions

into the behaviour, socio-ecology, conservation, rehabilitation and welfare of small cetaceans (Pearson *et al.* 2017).

Non-Invasive methods

To minimise the negative effects of invasive methods (Rand 1950, Ingham 1967), non-invasive alternatives are often favoured, particularly when observing fragile or threatened species (Bartel & Sexton 2009). Historically, this was achieved through direct observations (Eberhardt *et al.* 1979) but with miniaturisation of technology and improvements in battery capacity, the methods utilised by human observers are evolving to incorporate, and in some cases being replaced by, remote monitoring techniques involving cameras and acoustic devices (Gucu 2009; Hodgson *et al.* 2013; Bailey *et al.* 2010; Castellote *et al.* 2013).

Marine vertebrates that leave the water present opportunities for human study. As pinnipeds haul-out on land, it has been possible to undertake simple counts for some time (Eberhardt *et al.* 1979). Likewise, adult female marine turtles leave identifying tracks on beaches during nesting events, which can be counted (Witt *et al.* 2009). Counts from land (Hutchinson 1980); from nautical vessels (Würsig *et al.* 1998; Barlow *et al.* 2006; Hutchinson 1980) and aircraft have also been used to non-invasively monitor marine vertebrates, covering large distances in short periods of time (Witt *et al.* 2009; Hutchinson 1980; Koski *et al.* 2009). However, using ships to undertake surveys of marine vertebrates is often prohibitively expensive and in polar regions can be challenging outside of the summer season as winter pack ice can make areas inaccessible (Castellote *et al.* 2013).

Being able to recognise individuals of a study species through the use of natural markings (colours, patterns or shading) is advantageous for population biology and

demographic studies (Marshall & Pierce 2012). Such techniques have been used to study terrestrial (Karanth & Nichols 1998; Kelly 2001; Dixon 2003; Kenyon *et al.* 2009) and marine species (Marshall and Pierce 2012; Buckland 1990; Hammond 1990; Wursig & Jefferson 1990; Stevick *et al.* 2001; Evans & Hammond 2004; Auger-Methe & Whitehead 2007). Photo-ID studies assume that individuals can be reliably distinguished and re-identified over time (Marshall and Pierce 2012). Furthermore, the occurrence of natural identification marks can be a means of permanently 'marking' individuals (Arzoumanian *et al.* 2005; Rowat *et al.* 2009) and can therefore be used for the investigation of population composition (Wilson *et al.* 1999), abundance estimates (Castro & Rosa 2005), residency and movement (Jaquet *et al.* 2003), demography and social behaviours (Marshall & Pierce 2012). For example, the combination of photo-ID and citizen science has enabled scientists to accurately estimate the abundance of whale sharks (*Rhincodon typus*) in the Maldives, using photographs taken by tourists, by a means of modelling mark-recapture estimates (Davies *et al.* 2012).

Remote cameras are an emerging method for monitoring marine ecosystems, from the individual to the population level (Bicknell *et al.* 2016). Baited Remote Underwater Video surveys (BRUVs), comprised of an underwater camera mounted to view a bait bag (Priede & Merrett 1996), sit statically on the sea bed, filming any animals that approach the bait. As any animals moving within the frame are detected by the cameras, the size of the animal does not influence the chance of recording its presence, unlike some more traditional census methods such as experimental fisheries (Cappo *et al.* 2004, 2006). Studies have shown that BRUVs can generate relative abundance and diversity estimates similar to those produced by scientific longline fisheries surveys (Brooks *et al.* 2011) without causing any detrimental impacts

on the species involved. Lightweight cameras can be attached to unmanned aerial vehicles (UAVs) to survey marine vertebrates on land (Monson *et al.* 2013) and in the water (Hodgson *et al.* 2013), to gather data on population estimates (Buckland *et al.* 2012) and develop environmental impact assessments (Thaxter & Burton 2009). Cameras attached to autonomous underwater vehicles (AUVs) can be used to monitor the health of benthic communities and ecosystems (Smale *et al.* 2012), enabling research into previously inaccessible habitats (Singh *et al.* 2004).

Camera traps are being increasingly used to monitor wildlife populations (Henschel & Ray 2003; Silveira *et al.*, 2003). They can be used across terrestrial habitats and more recently have been used to study hauled-out pinnipeds in the Mediterranean (Gucu 2009) and in Finland (Koivuniemi *et al.* 2016). Camera traps provide photographic data that can be used in non-invasive capture-mark recapture studies and can provide information on abundance for endangered (O'Brien *et al.* 2003, Kelly *et al.* 2008) and cryptic species (Bowkett *et al.* 2008). Due to the non-invasive nature of camera traps they can be used to quantify the effects of human disturbance (Foster *et al.* 2016). Marine wildlife tourism is an ever-increasing form of eco-tourism that can provide psychological benefits to the tourists involved (DeMares & Krycka 1998). However, if un-managed, these activities can be detrimental to the species and habitats involved (Wheeller 1992, King & Stewart 1996).

This Research

This thesis sets out to develop an automated time-lapse camera method to monitor pinniped haul-out populations. Firstly, the project uses time-lapse cameras to highlight the seasonal abundance and patterns of grey seals hauled-out at Cornwall's largest onshore haul-out and by combining these data with environmental variables, I describe how grey seals respond to their environment. Secondly, I address the occurrence of human disturbance at the haul-out site. Since 2004, Cornwall Seal Group Research Trust (CSGRT) have been recording disturbances of grey seals at the haul-out and by consulting disturbance data collected by CSGRT in combination with the data from time-lapse cameras and a visitor counter, the project aims to determine which stimuli occur at the site and the frequency and extent to which they disturb hauled-out grey seals.

CHAPTER 1

Using time-lapse camera technology to monitor grey seal haul-outs

William J. Heaney¹, Anthony W.J. Bicknell^{1,2}, Sue Sayer³, Lucy A. Hawkes¹,
Matthew J. Witt^{1,2}

¹ College of Life and Environmental Science, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, United Kingdom.

² Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, United Kingdom.

³ Cornwall Seal Group Research Trust, Copperleaf Cottage, Phillack Hill, Hayle, Cornwall, TR27 5AD, United Kingdom.

Keywords

Remote time lapse cameras, tide, wildlife abundance, pinniped, marine vertebrate

Abstract

Marine vertebrates can act as important indicators of change in the marine environment, particularly those subject to anthropogenic influence. This study uses time-lapse camera systems to monitor a grey seal (*Halichoerus grypus*) haul-out. Data were collected on the north coast of Cornwall, United Kingdom, using camera traps and contemporaneous visual counts from August 2013 to December 2017 to ascertain the efficiency of cameras to provide accurate counts of seals *in-situ*. The median maximum number of individual grey seals hauled-out on the beach at a single time derived from time-lapse cameras was 197 (\pm 60.5 IQR; years 2013, 2014, 2015) although it is not possible to derive estimates of wider population change from these metrics. Time lapse cameras proved to be a useful form of technology to undertake counts throughout the annual cycle of grey seal haul-out activity.

Introduction

Prior to recent technological advances in wildlife monitoring (Hussey et al. 2015), human-led visual surveys were the only means of observing animal populations. The use of time-lapse or motion triggered cameras, where the presence or movement of animals causes the camera to take a photo or start filming, to monitor wildlife populations are a minimally invasive method. These cameras can be utilised with relatively inexpensive equipment and labour costs (Henschel & Ray 2003; Silveira *et al.*, 2003). Camera traps can be used to assess the abundance of many species as well as monitoring activity patterns, habitat use and reproductive data all of which are key components for developing wildlife conservation strategies (Silveira *et al.*, 2003; Trolle & Kéry 2005; O'Connell *et al.*, 2011). Camera traps are a robust and versatile piece of equipment that can be deployed in a variety of environments, causing minimal environmental damage (Rowcliffe *et al.*, 2008). The technology typically integrates a motion activated day/night PIR (passive infrared) sensor and an optical camera, sometimes with infra-red night vision technology enabling recording in low light and night time conditions. Due to their autonomous capabilities, cameras can be left in-situ to monitor animals without the disturbance bias that can sometimes be introduced by direct human-led surveys (Cutler & Swann, 1999). Furthermore, because they can collect continuous data covering periods when human observers cannot be present (e.g. during inclement weather), images can be stored and revisited to undertake repeat counts or other data interrogation (Cutler & Swann, 1999). While the terrestrial applications of camera traps have increased exponentially with the advancement of cheaper and improved digital technology (August *et al.* 2015), the use of autonomous camera systems is still an emerging technique in the study of coastal marine vertebrates.

Marine mammal censuses are often undertaken from ships (Barlow 2010) or aircraft (Jefferson *et al.* 2016, Hammond *et al.* 2013). Ships, however, can influence the distribution of marine mammals through the avoidance or attraction of different species to vessels which can introduce bias (Würsig *et al.*, 1998; Barlow *et al.*, 2006). Aerial surveys using fixed wing aeroplanes (Jefferson *et al.* 2016), helicopters (Scheidat *et al.* 2011) or drones (Hodgson *et al.* 2013) have also been used for direct counts of individuals or indirectly through surveys of presence/activity indicators, such as sea turtle tracks made during nesting events (Witt *et al.*, 2009, SCOS 2015). These surveys can cover large geographic areas in relatively short periods of time but may also have a disturbance effect (Koski *et al.*, 2009). Considering that many marine mammals spend most of their lives submerged at sea, it is difficult to monitor their total spatial distributions in relation to their environment (Hoekendijk *et al.*, 2015). The spatial distribution of some species such as pinnipeds and seabirds, can more easily be assessed, because breeding or resting events often occur on land or ice. Such counts can provide useful indices of abundance (Eberhardt *et al.*, 1979, Lyderson *et al.* 2002), particularly if multiple sites are surveyed and demographic details are well understood (Osterrieder *et al.* 2015), and can be used to estimate population parameters including fecundity, mortality, age structure, migrations, and population growth rates (Harkonen *et al.*, 1999).

Pinnipeds, eared, non-eared seals and walrus, haul-out to rest, warm up, moult, breed and for lactating mothers, feed pups (Weitzman *et al.* 2017, Costa & Gales 2013, Krieger & Barrette 1984, Riedman 1990). Haul-out sites can be used as a convenient means to count individuals, and as such surveys were undertaken historically by seal hunters (Eberhardt *et al.*, 1979) and can be carried out at distance or in extremely

close proximity. However, surveys can cause disturbance to study populations (Boyd & Campbell 1971), sometimes resulting in increased mortality (Eberhardt *et al.*, 1979). Furthermore, seal populations can become habituated to human presence and not disturbed in the conventional sense (Bishop *et al.* 2015). Repeat visits maximise the chance of observing peak numbers and provide more robust data on haul-out population sizes (Eberhardt *et al.*, 1979), but should be carefully timed to coincide with times when variation in activity patterns are at a minimum (Thompson *et al.* 1989). Observer surveys can however, provide information on abundance and distribution during terrestrial haul-outs (Bonner, 1972 & Boveng *et al.*, 2003). Information from observer surveys, such as counts or photographic identification, where individuals can be photographed, reliably distinguished and re-identified over time (Scofield *et al.* 2008), can be essential to inform pinniped conservation management strategies (Osterrieder *et al.*, 2015, Paterson *et al.* 2013, Pomeroy *et al.* 2015). Satellite telemetry can also aid in the assessment of pinniped distribution and behaviour at sea and aid the integration of information from both land and sea to provide a more accurate overview of population size and distribution (Matthiopoulos *et al.*, 2004, Jones *et al.* 2015).

Recent advances in satellite imagery and automated camera systems offer additional non-invasive methods to monitor pinniped haul-outs (LaRue *et al.* 2011) and other coastal marine vertebrates (Goebel *et al.* 2015). The use of automated camera systems have proved useful, for example, for monitoring nesting albatrosses (*Thalassarche cauta*), in north west Tasmania, with relatively low labour costs (Lynch *et al.*, 2015). Satellite imagery has proved useful when enumerating elephant seals (*Mirounga leonina*) (McMahon *et al.*, 2014) and detecting the variation in abundance of Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica (LaRue *et al.*,

2011).. Automated camera trap systems have been used to gather estimates of the Mediterranean monk seal (*Monachus monachus*) population size and demographic patterns (Gucu, 2009; Gucu *et al.*, 2004). Similarly, photo-ID images collected by camera traps have also been used to monitor the endangered Saimaa ringed seal (*Phoca hispida saimensis*). These methods could be used to monitor other pinnipeds with well-established terrestrial haul-out sites, such as harbour seals (Cordes & Thompson 2015) and grey seals (Karlsson *et al.*, 2005).

The grey seal is a sexually dimorphic coastal feeding pinniped, feeding on a variety of fish species including gadoids and salmonids, as well as cephalopods and crustacea (Hammill *et al.* 2002, Prime & Hammond 1990). Its distribution in the northern hemisphere can be separated geographically and by the timing of reproduction into three stocks; north west Atlantic, north east Atlantic and Baltic (Bonner 1981). However, the Society for Marine Mammalogy recognises two subspecies, the western Atlantic grey seal (*Halichoerus grypus grypus*) and the eastern Atlantic grey seal (*Halichoerus grypus macrorychus*) (Committee on Taxonomy 2014). The northwest Atlantic has a larger population of 250,000 mature individuals and the northeast Atlantic has a smaller population of 66,000 mature individuals, both of which are apparently increasing (Lonergan *et al.*, 2011; SCOS 2016; IUCN 2016). In 2015, the total UK population of grey seals was estimated at 139,600 (95% CI 116,500–167,100), which represents approximately 36% of the world's population, based on pup production estimates (SCOS 2016). Approximately 0.5% of the total UK grey seal population apparently resides in Cornwall and the Isles of Scilly (Leeney *et al.*, 2010) and the highest proportion of grey seals occurs on the Isles of Scilly, an isolated island archipelago 48 km west of Land's End on the UK mainland. Other significant haul-outs

in the southwest of England Cornwall's north coast, where the three largest mainland haul-out sites have been documented (Leeney *et al.*, 2010) (Figure 1).

Grey seals undergo parturition in caves and on isolated beaches and coves along the Cornish coastline between August and December (SCOS 2015). Female grey seals will spend 18-20 days ashore, giving birth, suckling a single pup and mating again once lactation is complete (Twiss *et al.*, 2003). Grey seal pups are born white, known as 'lanugo' pups, and it takes up to three weeks for them to be weaned off their mother's milk and to fully moult their white coat (Sayer *et al.*, 2012). Five development stages can be used to describe the development of grey seal pups (Boyd *et al.*, 1962): at stage one (days one to three following birth), the pup's umbilical cord is still conspicuous and the fur may be stained yellow in loose folds around the body. At stage two (days four to seven) the umbilicus has atrophied and the skin folds are no longer loose on the body. At stage three, the pup becomes rounded and barrel-shaped and the neck is indistinguishable. At stage four, white natal fur starts to moult revealing yearling pelage and at this point weaning is either imminent or has already occurred. At stage five, the pup is fully moulted and weaned (Radford *et al.*, 1978).

While knowledge on grey seal populations is growing across the Celtic Sea region (Vincent *et al.*, 2005; Gerondeau *et al.*, 2007; Leeney *et al.*, 2010) little information exists in the published literature regarding the size and seasonal dynamics of haul-outs that form within this region. This study employed automated time-lapse camera traps to build an increased understanding of grey seals haul-out dynamics, including seasonality of site use, responses to weather, tide and the role of the site in grey seal reproduction. The study highlights how information from camera-traps may be used to contextualise and enhance existing direct observer surveys.

Material and Methods

Study area

This study was conducted at a National Trust site on the north coast of Cornwall, which hosts the largest grey seal haul-out site in Cornwall (Leeney *et al.*, 2010) (Figure 1). The site, name and location has been redacted under instruction of site owner, it is a Site of Special Scientific Interest (SSSI) and encompasses two haul-out locations 0.7 km apart, one of which is offshore. The primary haul-out location is a crescent shaped cove with a 2.2 km² beach and additional 1.8 km² rocky boulder habitat at low tide (measured using Google Earth Pro; 25th May 2017 on a spring low tide). The secondary, offshore haul-out location is frequented by grey seals in greater numbers through the summer months (Leeney *et al.*, 2010), whereas the primary haul-out cove is a tidally influenced beach visited by grey seals throughout the year, with the upper extremities comprising of sand and shingle and the lower extremity being heavily dominated by rocky boulders. The cove is surrounded by 50 m cliffs, with a coastal footpath fringing the cliff edge, popular with tourists, dog walkers and wildlife watchers, and is close to a National Trust car park.

Time-lapse camera data collection

Two time-lapse camera traps were deployed on land, facing the primary onshore haul-out beach for the period between August 2013 and October 2015. Owing to technological improvements, the specifications of camera technologies used throughout the study changed, but the camera locations did not. At the start of the project in August 2013, two Bushnell HD Colour Max 8 Megapixel cameras (Bushnell, Kansas City, Missouri) were used, but poor weather conditions led to the failure of one

of the cameras in March 2015, and it was not replaced. Between August 2016 and August 2017, the main camera (A) was replaced with a GoPro Hero 4 Silver, housed in a weatherproof pelicase along with a programme scheduler and an external battery pack (CamDo Solutions, Vancouver BC). The programme scheduler was later replaced with a CamDo 'Blink controller' intervalometer. Whilst the pelicase was effective in protecting camera equipment from rain, the camera overheated on five occasions. At the start of September 2017, a Bushnell camera trap was re-deployed on the site for the remainder of the study. The main camera (A) was positioned at a height of approx. 25 m elevation facing north east, looking down onto the primary haul-out beach and out to sea (example image from camera in Figure 2a). The secondary camera (B) was positioned at a height of approx. 40 m elevation on the headland of the cove, facing south east back towards the primary haul-out beach (example image Figure 2b). Cameras were programmed to gather images at 5-minute intervals, every day, during daylight hours. Monthly visits to the cameras were undertaken to replace memory cards and the battery.

Seasonal abundance of grey seals from time-lapse imagery

Due to the volume of data gathered, a technique to identify images with the maximum number of grey seals in each day was developed, termed the 'flipbook' method. Photographs taken each day during the study period (2013 to 2015) were reviewed, and the image with the highest number of grey seals was selected for detailed enumeration using ImageJ (v 1.45). This was achieved by rapidly scrolling through the photos on a computer screen to identify the image with the perceived greatest density of grey seals. To quantify the accuracy of this approach, we randomly selected one day of camera trap data in each of the twelve months in 2014 (n=8) and 2015 (n=4) (whichever had the most complete data) and selected 24 images occurring one hour

either side of the perceived greatest density image. A total of 288 images were analysed across 12 days of data collection with 24 images analysed per day, captured at 5 minute intervals. The number of seals in each photo within this two-hour period was enumerated and compared to the perceived maximum. Only grey seals with at least half their body above the surf line were enumerated. The average discrepancy between the perceived maximum and the maximum count from photos was two grey seals (range zero to nine, representing approximately 4% of the seals hauled-out), and counts derived from images using the 'flipbook' method and the true maximum method were usually five minutes apart from each other, with one example of a 10-minute time difference (Table S.1). Automated object detection techniques were not used because seal pelage was hard to discriminate from the image background at the distance the cameras were located; rocky boulders often look like grey seals and it can be hard to differentiate individuals when grey seals are densely packed together. Storms in January/February 2014 severely damaged the secondary camera (B) due to its exposed position and it was therefore removed from the cliff. The main camera (A) also encountered several periods of failed operation (October 2013, March 2014, April 2014 and all of February 2015). As such, a composite time-series of daily counts was created from pictures taken by the two cameras for the period October 2013 to April 2014 using a correction factor, which was applied to counts from camera B when camera A failed to provide data. This correction factor was developed using 26 days where contemporaneous counts of grey seals were available from both cameras. The photograph with the daily maximum number of hauled-out grey seals was selected for both cameras (A) and (B) and the number of hauled-out seals enumerated using ImageJ. The correction factor showed that, on average, the secondary camera (B) detected three (median \pm 14.29 IQR) more grey seals than the main camera (A).

Grey seal reproduction

The number of white-coated pups (pups hereafter) present on the primary haul-out beach was enumerated from images taken across three autumn-winter periods (2013, 2014, 2017) to determine the utility of cameras in pup detection. Moulded pups were not enumerated as they were difficult to differentiate from other small grey seals. The life stages of pups were also difficult to accurately determine from images, so a sequential pup count was undertaken. It was not possible to count pups in 2015 or 2016 as cameras failed several times during the pupping season due to poor weather and electronic failure. Images between August and January were checked daily using the 'flipbook' method for the presence of one or more pups, and the time and behaviour (alone or in a mother-pup pair) of the pup was recorded. Pups were counted each time they were detected to assess the number of days where pups were present on the beach. The number of pups born in each season could not be determined.

Statistical Analysis of environmental influences

The primary haul-out is a tidal beach and at high tide almost the entire beach is inundated. To determine how environmental conditions, including weather and tide, might influence the number of hauled-out grey seals, hourly seal counts, determined from images, between (18th March – 30th July 2015, n=135 days) were compared to tidal height (POLPRED tidal software; National Oceanography Centre, Liverpool). Measurements of air temperature, wind speed, wind chill, wind direction, and air temperature were provided by a nearby National Coast Watch Institution (St Ives) weather station (distance to station from haul-out 6.3 km). Wind chill was estimated as:

$$\text{Wind Chill} = 35.74 + 0.6215T \times (V^{0.16}) + 0.4275T \times (V^{0.16})$$

Where V is the 10-minute average wind speed in mph and T is the outside air temperature in °F. (NCI, St Ives). A Zero-Inflated Poisson regression model (ZIP) was used ('pscl' package in R) to investigate the relationship between grey seal hourly haul-out count data and environmental conditions recorded at hourly intervals (18th March – 30th July, $n=135$ days). The ZIP modelling framework was adopted due to a high frequency of zero counts in the grey seal abundance data. The response variable was 'count' data (the number of grey seals counted at hourly intervals) and the explanatory variables in the model were, tidal level (in metres) and wind chill. Wind chill values are derived from wind speed and air temperature and as such, wind speed and air temperature were strongly correlated with wind chill and were therefore excluded from the ZIP. Wind direction had no effect so was also excluded from the model.

Ground truthing

To compare grey seal count estimates from the time-lapse cameras with direct counts from *in-situ* observer surveys, contemporaneous counts using both methods were undertaken by one observer sited adjacent to main camera (A) and by one observer stood at a vantage point at the top of the cliff, with a wider field of view. Counts were undertaken every 10 minutes from 14:00 to 16:30 (2.5 hours) on the 21st November 2017. Working from left to right, scanning up and down the beach, an estimate of grey seal haul-out numbers were made with the naked eye and binoculars (NatureTrek 8x42 magnification). Slope test coefficients were used to investigate the relationship between *in-situ* counts and those from camera images.

Results

Time-lapse camera survey effort

Time lapse cameras were deployed for 837 days between August 2013 and October 2015 (Table S.2) and for an additional 153 days between August and December 2017. For the main data collection period between 2013 and 2015, 207,179 photographs were taken (Main camera (A) n=145,209, secondary camera (B) n=61,970). Collectively, the cameras provided 637 days of data, operating for 77% of the study period (August 2013-December 2017), and from this, grey seals were observed on 528 days (i.e. 81% of camera recorded days had grey seals on the beach). During the main data collection period, technical failures were responsible for 200 days of camera inactivity; images were either not gathered due to hardware failure or were impaired by condensation, sun glare or poor weather conditions, which obscured the view of the haul-out. In January and February 2014, the north coast of Cornwall experienced severe storms, and both cameras failed for a combined total of 21 days. The main camera (GoPro and Bushnell Camera Trap) was operational for a total of 79 days during the 2017 pupping season collecting 14,439 images (n=14,439; representing 52% of the total days, Table 1).

Seasonal use of haul-out beach by grey seals

The number of grey seals utilising the haul-out site varied throughout the annual cycle. The period of peak haul-out was in March-April across years 2014 and 2015, with median daily maximum grey seal haul-out counts of 103 (\pm 52.00 IQR, range 52 to 188) and 83 (\pm 46.00 IQR, range 25 to 239) for March and April respectively (Figure 3). With the exception of a single individual, grey seals were absent in June and July 2014 but were present in June (range 0 to 37) and July 2015 (range 0 to 89) with a median daily maximum haul-out count of 6 (\pm 13.00 IQR) and 22 (\pm 22.25 IQR) seals

respectively. In late autumn and boreal winter months (November and December) of 2013 and 2014, there were median daily counts of 56 (\pm 30.00 IQR) and 65 (\pm 54.50 IQR) grey seals hauled-out respectively. The number of grey seals hauled-out peaked in March and April 2015, with median daily counts of 33 (\pm 28.00 IQR) and 1 (\pm 36.00 IQR) grey seals, respectively.

Grey seal reproductive effort

Pups were observed on a total of 99 days during the three seasons of monitoring with the highest number of days in which pups were spotted occurring in September (median 15 pup positive days \pm 4.00 IQR, over three years) and October (median 13 pup positive days \pm 2.50 IQR, over three years) each year (Figure 5, Table 1). Pups were present in 13% of photographs (total $n=2,464$, main camera (A), $n=1,228$; secondary camera (B), $n=1,236$) in the 2013 pupping season, 10% of photographs (total $n= 2,373$, main camera (A), $n=2,212$; secondary camera (B), $n=161$) in the 2014 pupping season, and 12% of photographs (total $n= 1,589$, main camera (A); $n=1,589$) in the 2017 pupping season.

Environmental influences on grey seals

Tide had a significant influence on the number of grey seals hauled-out on the beach (ZIP; $Z=-5.87$, $df=10$, $p < 0.001$), with the greatest number of grey seals hauled-out two hours prior to low tide and the least hauled-out at high tide (approximately six hours before and six hours after low tide) (Figure 5). Wind chill had a significant negative effect on the number of grey seals hauled-out on the beach (Figure 6; ZIP; $Z=-2.14$, $df=10$, $p < 0.001$), such that there was an average loss of 0.17 grey seals (\pm 0.01 s.e.) moving from the beach with a 1-degree ($^{\circ}F$; equivalent to 0.56 $^{\circ}C$) decline in temperature due to wind chill.

Ground-truthing

Counts from the time-lapse camera under-estimated the number of grey seals present on the haul-out by 12 seals, or 5%, (mean value \pm 6 s.d.) compared with the observer counting from a position next to the camera on the single day of observation. In the most ideal observation point, at the top of the cove with a wider field of view, where it was not possible to place a camera, observers recorded 3 more seals, or 2%, (mean value \pm 8 s.d.) above the count produced by the main camera (Figure 7). The main camera and human observer datasets were correlated (main camera (A) and observer sited adjacent to camera; $r=0.97$, $p=0.59$ and main camera (A) and observer stood at the top of the cove; $r=0.95$, $p=0.47$). A human observer sat next to the main camera (A) was more likely to overestimate the number of hauled-out seals, as the restricted field of view made it hard to maintain a reference point of moving grey seals, compared to a human observer stood at the top of the cove, and this resulted in overcounting (Wilcoxon Signed-Rank Test; main camera (A) and observer sited adjacent to the main camera $V = 136$, $p<0.01$; main camera (A) and observed stood at the top of the cliff $V = 107.5$, $p<0.05$). True grey seal numbers enumerated by observers stood at the top of the cliff (Figure S.1).

Discussion

This study used automated time-lapse camera traps to broaden knowledge on the seasonal patterns of grey seal habitat use at a regionally important haul-out site in the south west, UK. Our approach robustly identified the months of peak haul-out, provided insight into the reproductive use of the sites, as well as the responses of grey seals to environmental conditions. Leeney *et al.*, (2010) similarly suggested that grey seal abundance at this location reaches a maximum in March-April and then declines in the summer months when grey seals haul-out on offshore Islands (Leeney *et*

al.,2010). Pups were easily identifiable in images and were most present in October, supporting the findings of Sayer *et al.*, (2012). Results from this study highlighted a tendency for under-counting when using camera traps compared to human observers, with discrepancies of 5% and 2% for an observer sited next to the camera or stood at the top of the cove respectively. This could be due to grey seals moving during counting, the cameras inability to distinguish between grey seals that are on top of each other or huddled next to one another, or a potential for over estimation of hauled-out grey seals by human observers. As such, a density dependent relationship may exist with regards to counting accuracy from photographs. Bajzak & Piatt (1990) highlight that errors such as these in animal counts are common when interpreting photos.

Tidal height significantly influenced the number of grey seals hauled-out on the beach. Grey seal numbers reached their maximum when 75-80% of the beach surface was uncovered but decreased before the tide was at its lowest. The topography of the beach and prey availability at low tide could play a role – grey seals at the haul-out have to move over a series of rocky boulders at low tide that may be energetically costly to navigate (pers. Comm. Sue Sayer). Studies in Perth, Australia, have shown that prey fish move in relation to tides (Wakefield 2010) and may drive Australian sea lions (*Neophoca cinerea*) to leave haul-out sites at low tide to hunt when prey species are easier to target (Osterrieder *et al.*, 2015; Morrison *et al.*, 2002; Ribeiro *et al.*, 2006). Furthermore, the number of grey seals present at the haul-out was lowest at high tide, most likely due to the reduction in available beach area or loss of beach completely on a high spring tide. This movement pattern has also been observed in a Welsh population of grey seals (Westcott and Stringell 2004) and in Australian sea lions (Osterrieder *et al.*, 2015), but harbour seals and other species are more variably

affected (Reder *et al.*, 2003; Thompson *et al.*, 1989). In the present study, grey seals hauled-out less frequently when wind chill was greater. Research into the haul-out patterns of Weddell seals at the Vestfold Hills, Antarctica, showed that wind was significantly related to lower seal abundance in January (Lake *et al.*, 1997). Previous studies investigating the haul-out behaviour of harbour seals have shown that wave intensity (Venables & Venables, 1995), disturbance (van Bommel, 1956) and wind chill (Boulva & Maclaren, 1979) also negatively influence haul-out patterns of pinnipeds.

This study found that observers counting grey seals from a position with a wider field of view at the top of the cove, were more likely to produce counts that were similar to those produced by the main camera than an observer with a restricted field of view. However, more rigorous ground truthing should be incorporated into future studies. The present study has shown that camera traps can collect similar data to human observers, but provides a means by which observers can spend less time at the site, and counts can be reviewed and recounted if necessary (Gucu 2009). Nevertheless, the technique has several disadvantages. First, it is apparent that camera traps can be limiting when undertaking daily counts of grey seals and can fail, for example in poor weather, where human observers would not. Second, while increasing the number of camera locations could reduce blind spots and further minimise the discrepancy in camera and observer counts, this would substantially increase the volume of data requiring analysis. Third, the time-lapse cameras used in this study could not be used to gather haul-out information at all times of day, as their night vision capabilities were inadequate at large distances. However, in the future, thermal infrared cameras could be used to monitor pinniped haul-outs. Finally, when exposed to extreme weather, cameras images were sometimes unusable, and ceased to function when water penetrated the housing. Furthermore, sea spray and sun glare

also reduced the quality of images at times, and over-heating sometimes occurred during the summer months.

This study focused on the primary haul-out beach at the study site which enabled an in-depth survey of the grey seals occupying the beach and how they responded to the environment. However, these individuals are not solely restricted to the north coast of Cornwall. Previous studies have highlighted that grey seals observed in Cornwall and the Isles of Scilly have been identified in other key locations including France, Wales and Ireland (Vincent et al 2005) and are suggested to be part of a meta-population spanning the Celtic Fringe (Leeney *et al.*, 2010). Therefore, it would be interesting to establish camera trap surveys at haul-out beaches elsewhere to facilitate a comparative study of haul-out use and environmental drivers, a suitable beach does exist on the Roseland Peninsula in south east Cornwall. Photo-ID work, which identifies individuals at each site, helping to advance mark-recapture analysis of population parameters and population size (Koivuniemi et al. 2016) is already being carried out at the study site by the Cornwall Seal Group Research Trust and will aid further estimation of individual patterns of behaviour.

The methods used in this study demonstrate that time-lapse cameras can be both time and cost effective for providing extended temporal coverage when direct visual surveys may not be safe or practical to undertake, enabling a longer-term insight into annual grey seal haul-out patterns. The data collected here supports existing research into how tide influences grey seal numbers during an annual cycle (Leeney *et al.* 2010). The combination of both time lapse cameras and photo-ID would provide an in-depth survey technique allowing the collection of fine scale data, such as site fidelity, with the added benefit of a backup of a continuous time series throughout the annual cycle of grey seal haul-out patterns. This study has shown that camera traps are a

viable method to collect population data of hauled-out pinnipeds over prolonged periods

.

FIGURES

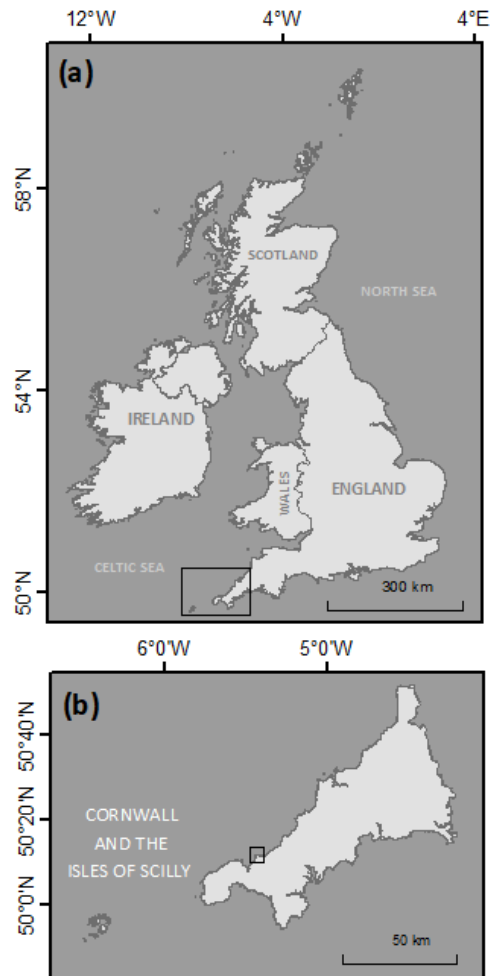


Figure 1. Grey seal haul-out study site location in Cornwall, south west England. (a) United Kingdom and Ireland (b) Cornwall. Black box in 'b' highlights the area in which the study took place. Site name and location has been redacted on instruction of the site owner.

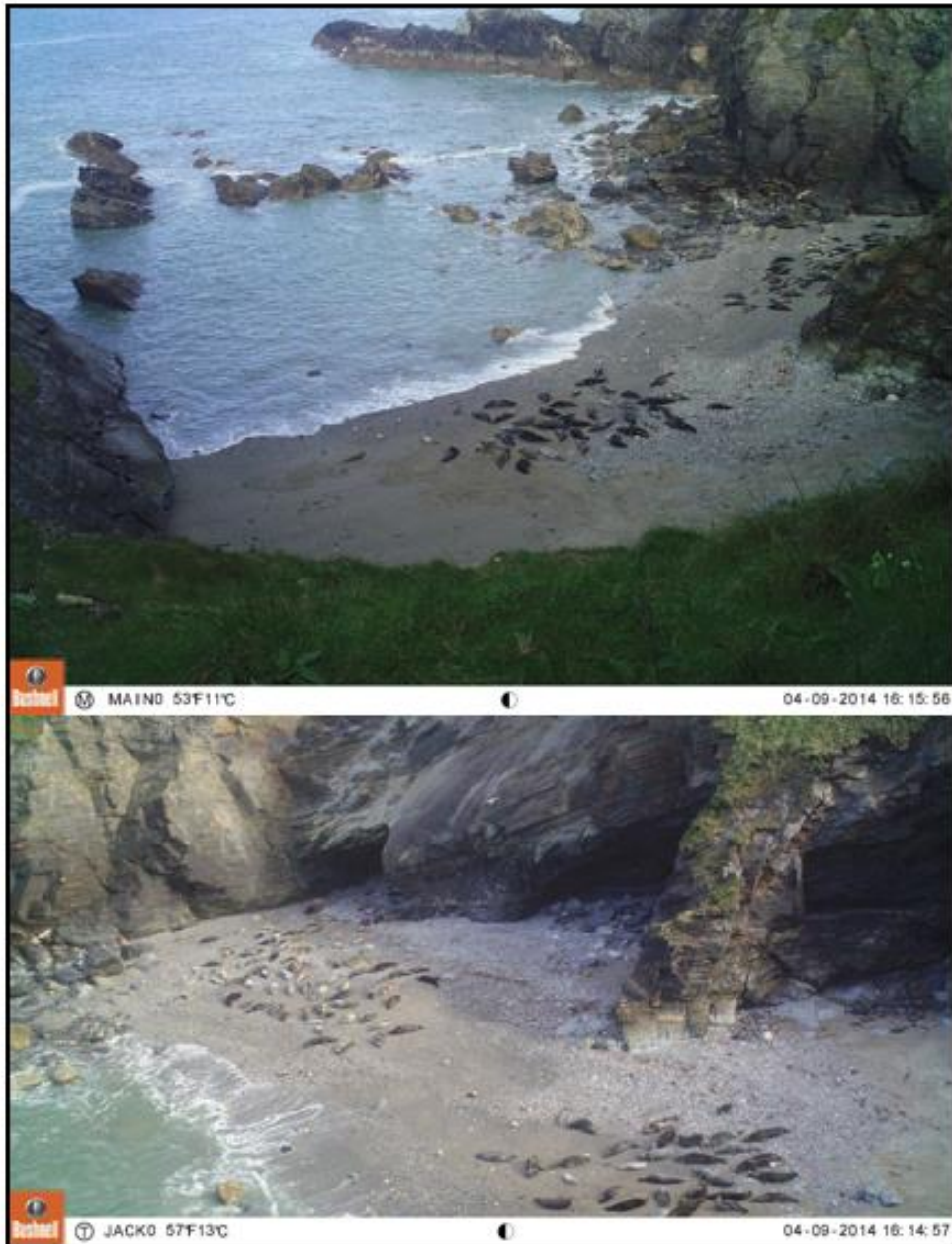


Figure 2. Grey seal camera trap example images. Images captured by camera A and camera B on the 9th April 2014 at 16:15 and 16:14 UTC respectively. Image captured by camera A shows 98 hauled-out grey seals with 130 hauled-out grey seals in the corresponding photo produced by camera B.

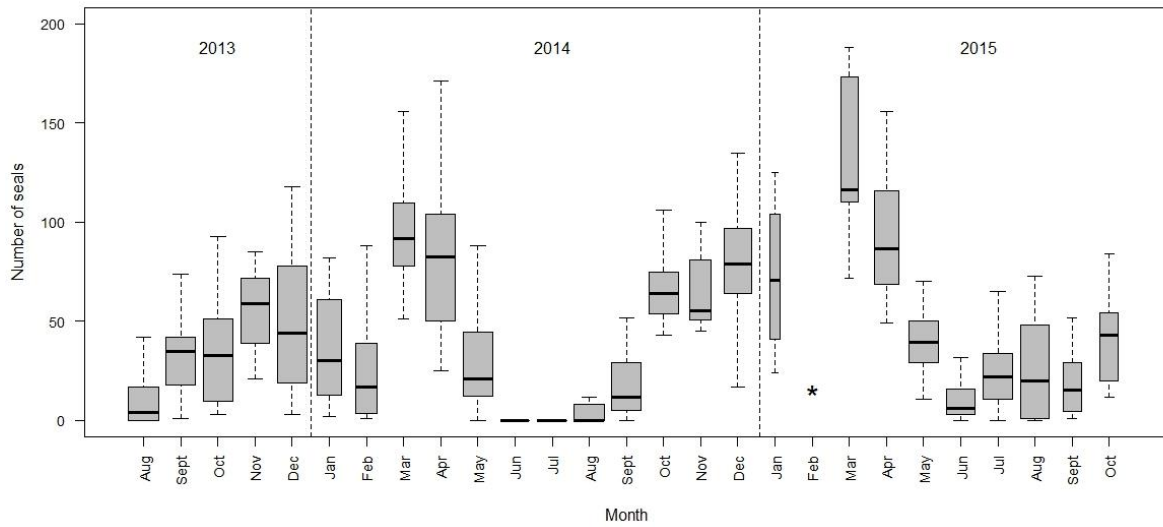


Figure 3. Daily maximum number of grey seals hauled-out as determined from time-lapse camera imagery (Camera A and Camera B; July 2013 to October 2015). Periods of camera failure (n=28 days) are indicated by *. Whiskers represent the highest and lowest count for each month, black lines show the median of each month and the third and first quartiles are represented by the top and bottom of the box respectively. Varying width of boxes indicates the amount of data collected in each month.

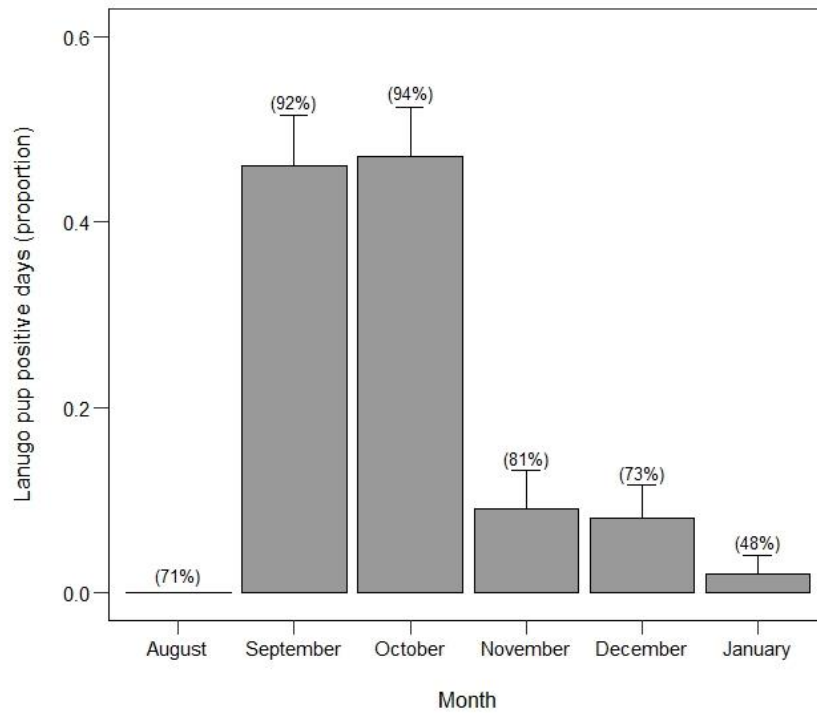


Figure 4. Proportion of pup positive days corrected for camera operation time as determined from a time-lapse camera (Camera A) across three pupping seasons (2013, 2014, 2017). Error bars represent standard error; numbers in parentheses indicate the percentage of operational camera days respective to the days in each combined month.

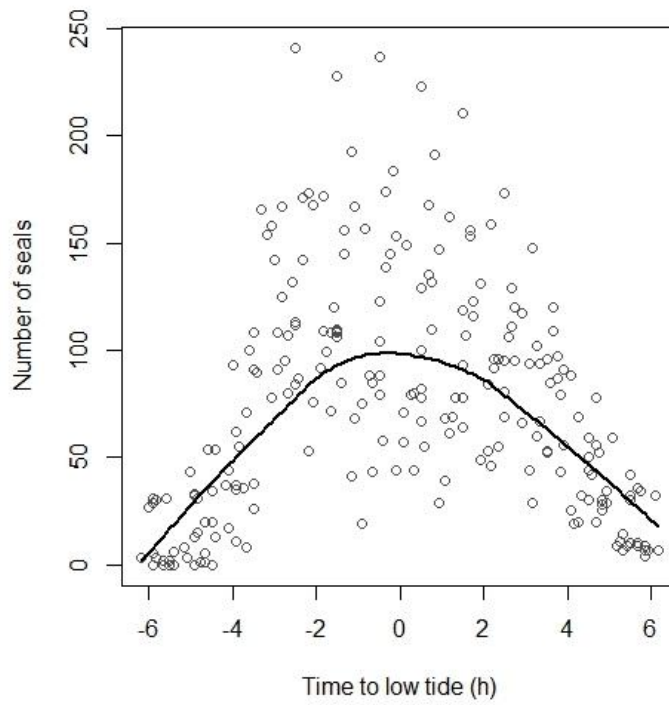


Figure 5. Hourly counts of grey seals hauled out as determined from camera A (18th March – 14th April), corresponding to hourly tidal level (POLPRED) n=234. Lowess smoothing line shown in black.

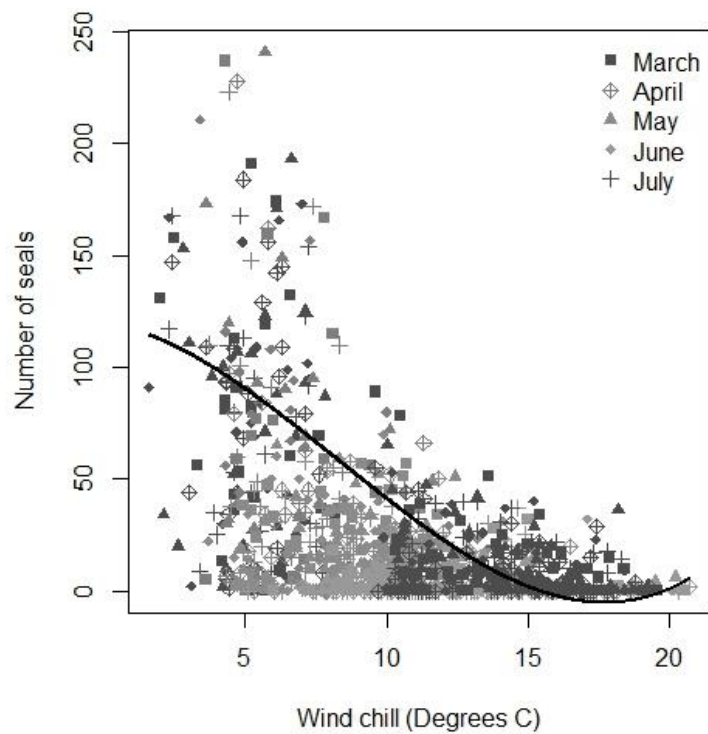


Figure 6. Hourly counts of grey seals hauled-out as determined from Camera A (March 2015 to July 2015), corresponding to wind chill (a proxy for wind speed and temperature) data (n=1221 observations). Black line denotes the cubic linear model fit.

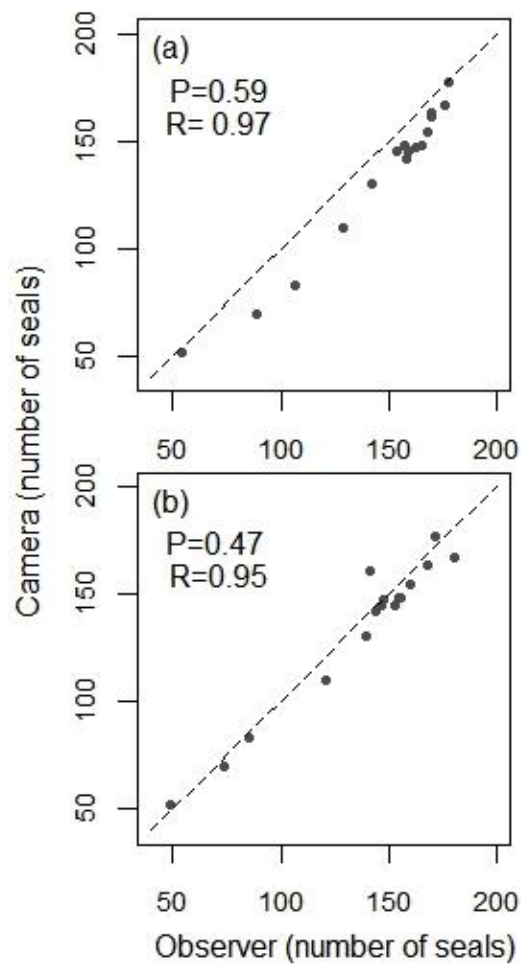


Figure 7. Comparative grey seal counts determined from images collected by Camera A and human observers (n=16 events). Data collected for (a) was undertaken by an observer positioned adjacent to camera A and data collected for (b) was undertaken by an observer stood at an optimal vantage point at the top of the cove. Dashed lines denote the line of equivalence. Slope test outcomes stated on figure.

TABLES

Table 1. Summary table showing the number of days on which seals were recorded by camera A (data from camera B was not incorporated due to the un-reliability of the camera) with respect to the number of operational camera days and total of days in each month. The known pupping season in Cornwall is August-December. January was included in analysis due to the presence of pups.

Month (n days)	Camera operational days			pup positive days		
	2013-14	2014-15	2017	2013-14	2014-15	2017
August (31)	31	31	4	0	0	0
September (30)	30	30	23	9	17	15
October (31)	23	31	30	13	13	18
November (30)	30	27	16	0	7	1
December (31)	5	25	6	0	5	0
January (31)	24	6	NA	0	1	NA

CHAPTER 2

Assessing the role of cameras in quantifying human disturbance at a grey seal haul-out

William J. Heaney ¹, Anthony W.J. Bicknell ^{1,2}, Sue Sayer³, Lucy A. Hawkes ¹,
Matthew J. Witt ^{1,2}

¹ College of Life and Environmental Science, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, United Kingdom.

² Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, United Kingdom.

³ Cornwall Seal Group Research Trust, Copperleaf Cottage, Phillack Hill, Hayle, Cornwall, TR27 5AD, United Kingdom.

Keywords

Remote time lapse cameras, marine wildlife tourism, pinniped, marine vertebrate, human disturbance, grey seal, human observations

Abstract

Marine mammals are a popular attraction for wildlife tourism and have become a growing area of interest for wildlife enthusiasts due to their predictability and reliability at haul-outs. For ecotourism to be sustainable it is important to ensure that activities are not detrimental to the species and or habitats involved. Here, we present a study combining wildlife cameras and recording of tourist visits to quantify the effects of human disturbance events at Cornwall's largest grey seal haul-out. Data were collected using a time-lapse camera trap, infra-red visitor counter system and site observations, between August 2013 to October 2015. People on cliff were more likely to cause a disturbance response, flushing the hauled-out grey seals from the beach into the sea, than other stimuli such as aircraft. The number of tourist visitors was inversely related to the number of grey seals hauled-out on the beach, with the most

visitors and the least grey seals in the summer months (June to August). On average, disturbance to the grey seal haul-out occurred on 39% of days where direct observation was undertaken and 36% of disturbances were caused by tourists, followed by unknown 24%, natural disturbances 17%, aircraft 14%, dogs 4%, boats 4% and unavoidable rescues events by British Divers Marine Life Rescue 1%. Most disturbance events occurred in January, April, May and September. The findings of this research can be utilised by the National Trust in their land management and conservation policies.

Introduction

Marine wildlife tourism is the practice of observing, studying or enjoying marine wildlife (Masters 1998), and is a non-consumptive activity that occurs worldwide (Trave et al. 2017). This tourism takes a variety of forms, including; marine wildlife watching holidays, wildlife boat trips, visiting marine or coastal nature reserves and visiting marine wildlife visitor centres and marine aquaria (Higham & Luck 2007). A wide range of marine vertebrates are subject to marine wildlife watching activities (Higham & Luck 2007), with marine mammals receiving considerable attention (Kovacs & Innes 1990). (Orams 1997; Hughes 2001, Sorice et al. 2006, Barton et al., 1998; Booth 1998; Kirkwood et al., 2003; Scarpaci et al., 2017).

The marine eco-tourism industry can contribute economically to coastal communities (Higham *et al.* 2014) and can provide more revenue than aquaculture and fisheries combined (Hoyt 2005; Hoyt & Hvenegaard 2002). Humans can derive many physical and mental health benefits from wildlife watching activities, including; excitement, novelty, intensity and uniqueness (DeMares & Krycka 1998, Muloin 1998). They can also generate lasting favourable memories (DeMares & Krycka 1998) and promote

educational and conservational or environmental outcomes (Higham 1998; Orams 2000; Schänzel & McIntosh 2000; Tisdell & Wilson 2002, 2005; Luck 2003; Finkler & Higham 2004; Mayes et al. 2004; Hughes & Morrison Saunders 2005; Andersen & Miller 2006), and help develop a sense of environmental well-being, the process of interacting with nature and the observer's personal environment (University of California 2018).

However, eco-tourism can be detrimental to target species. The foraging behaviour, breeding success and activity patterns of hawksbill turtles (*Eretmochelys imbricata*) (Hayes et al. 2017), whale sharks (*Rhincodon typus*) (Quiros 2007), green turtles, (*Chelonia mydas*) (Griffin et al. 2017; Meadows 2004; Jacobson & Lopez 1994) and bottlenose dolphins (*Tursiops truncatus*) (Constantine et al. 2004), Humboldt penguins (*Spheniscus humboldti*) (Ellenberg et al. 2006) have been negatively affected by eco-tourism activities. Increased human presence has also been associated with lower reproductive rates in California sea lions (*Zalophus californianus*), which could ultimately lead to population declines (French et al. 2011).

Pinniped watching has become a popular form of marine wildlife tourism (Granquist & Sigurjonsdottir 2014; Orsini & Newsome, 2005; Kirkwood et al., 2003; Parsons 2003; Curtin et al., 2009). Pinnipeds haul-out on land to reproduce (Weitzman et al. 2017), to recuperate after energy-intensive foraging trips (Costa & Gales 2013; Krieber & Barrette 1984), to socialise with other individuals (Davis & Renouf, 1987) and to moult (Riedman 1990). Due to this amphibious lifestyle, pinnipeds can often easily be observed from land and from the sea making them susceptible to disturbance from a host of tourist related activities such as hiking, picnicking and general recreational beach activities that take place in areas that are important for pinnipeds, including offshore islands that occur in close proximity to more urbanised areas (Higham & Luck

2007). Pinnipeds are susceptible to human disturbance and interference, which can lead to behavioural responses such as displacement, stampedes, flushing, boat strikes and reduced food provisioning (Lewis 1987; Constantine 1999; Shaughnessy 1999, Westcott & Stringell 2003, Strong & Morris 2010). These forms of disturbance have the potential to reduce both the quantity and quality of time spent hauled-out (Orsini et al. 2006) and in extreme cases can result in mothers abandoning their young (French et al. 2011).

Pinniped species such as the harbour seal (*Phoca vitulina*) often haul-out in habitats easily accessible to humans by foot, making them vulnerable to human activities (Acevedo-Gutiérrez and Cendejas-Zarelli 2011; Becker et al. 2011). A recent study demonstrates that harbour seals in Iceland increased their vigilance and preferred to haul-out on rocks further away from the shore when tourist numbers increased in the area (Granquist & Sigurjonsdottir 2014). Similarly, studies have shown that New Zealand fur seals (*Arctocephalus forsteri*) modified their general behaviour in response to tourist activities as well as showing aggression, avoidance and interactive behaviour towards tourists (Boren et al. 2002). However, the consequences of human disturbance posed on pinnipeds can often go undetected (Gerrodette & Gilmartin 1990) due to the erratic nature of pinniped monitoring and because disturbance effects often occur gradually (Curtin et al. 2009).

In 2015, the UK population of grey seals (*Halichoerus grypus*) was estimated at 139,600 (95% CI 116,500-167,100), (SCOS 2016) with 0.5% of the UK population residing in Cornwall and the Isles of Scilly (Leeney et al. 2010) at the southernmost limit of their range. In this region the highest proportion of grey seals occurs on the Isles of Scilly, with considerable numbers occurring on the mainland along Cornwall's north coast (Leeney et al. 2010). Grey seal haul-out sites located in south west

England occur within the most visited region of England, with 22.8% of all domestic tourism occurring in the south west region (United Kingdom Tourism Survey 2004; Curtin *et al.* 2009). In this study, we set out to determine whether the grey seals utilising a haul-out beach in Cornwall, south west England, were subject to human disturbance and to assess the merits of remote technology to improve an understanding of pinniped behaviour during disturbance events.

Methods

Study area

This study took place at an onshore grey seal haul-out on the north coast of Cornwall, south west England, between August 2013 and October 2015. The site, name and location has been redacted on instruction of the site owner, is a tidal cove with a beach, backed by cliffs, that was used by grey seals year-round in 2015 and can be viewed by visitors from along a coastal path fringing the cliff top (see chapter 1 for more details regarding the haul-out site). The haul-out is within a Site of Special Scientific Interest (SSSI) and is managed by the National Trust. Visitors can access the site at any time of day and as such, the site is one of the most popular National Trust properties in the UK with approximately 194,000 cars visiting in 2015 (pers.comm. National Trust).

CSGRT Disturbance data

Since 2004, data on grey seal disturbance events occurring at the haul-out site were gathered by the Cornwall Seal Group Research Trust (CSGRT). Whilst conducting photo identification research, trained observers from CSGRT gathered information on the date, time and cause of disturbances. Using these data, putative disturbance stimuli were generalised into seven categories; (i) people on cliff, (ii) aircraft, (iii) dogs (without owners), (iv) nautical, (v) natural, (vi) rescues and (vii) unknown. 'People on

cliff' disturbances referred to either single or groups of people observing seals. Aircraft were defined as helicopters, planes, microlights and drones. Dog disturbances were dogs running and barking at the observation point. Nautical disturbance were boats, kayaks and jet skis. Natural disturbances included; a dominate 'beach master' male asserting his status at the haul-out, other seal behaviour, rock falls and weather. Rescue disturbances were caused by the British Divers Marine Life Rescue during efforts to free seals from entanglement in fishing net or pups ostensibly separated from their mothers. Remaining disturbance events caused by undetermined stimuli were grouped as unknown. To determine in which month grey seals are more likely to be disturbed, the number of disturbance events observed in surveys (often more than one) was noted to determine the frequency of disturbance per month to give an indication of the time of year when grey seals are more prone to disturbance.

Time-lapse camera

A Bushnell Camera trap (Bushnell HD Colour Max 8 Megapixel) with time-lapse capabilities was deployed at the haul-out site throughout the duration of the study (Aug 2013 – Oct 2015). The camera was operational for 852 days, collecting 145,209 photographs and was configured to gather a photograph at 5-minute intervals every day, during daylight hours. The camera was installed at the site in July 2013 and was positioned facing north east, observing the haul-out beach with an elevation of approximately 25m. Data collection began in August 2013. Monthly visits to the site were undertaken to collect recorded data and replace camera batteries.

Visitor counter

A thermal infra-red visitor counter (LineTop; Blaenau Gwent, Wales) was integrated into an existing fence post, at waist height, marking the main footpath leading to the

grey seal observation area. The visitor counter was comprised of an infrared-sensor and data management system. The visitor counter was activated when warm objects, such as people, passed through the infra-red sensor beam, and the time at which activations occurred was recorded and data extracted at 1-second intervals. The visitor counter was not specific to human thermal signatures and so large dogs could also trigger the visitor counter, although the height of the sensor was such that all but the largest dogs would go undetected.

Data analysis

Seasonal patterns of visitors and seals

Photographic images gathered by the time-lapse camera were used to determine the maximum number of seals using the haul out each day (see Chapter 1 for description of procedure). Data from the visitor counter were processed to determine: (i) daily total number of visitors at the haul-out site, and (ii) estimates of the number of visitors present at the haul-out site during disturbance events. Daily visitor totals were calculated by summing the number of sensor activations and dividing those by two to account for a visitors return trip past the counter. Estimates of visitors present during a disturbance event were enumerated by summing the total number of activations, divided by two, that occurred during a disturbance event. These data provided a conservative estimate of visitor numbers using the main access point, visitors could also use other minor routes to access the haul out site, it was, however, not logistically feasible to monitor these.

Disturbance events supported by time-lapse camera observations

For periods where time-lapse cameras produced images of suitable quality for analysis (i.e. when poor weather, condensation, electronics failure did not prevent usable data

from being gathered), these images were organised into bouts corresponding to the times of disturbance events recorded by CSGRT (Table 1). A Bias Reduction Binomial Logistic Regression (BRGLM in R) modelling procedure was conducted to assess disturbance. The binary response variables were 'disturbance' and 'no disturbance'. Events with grey seal flushing (where seals move rapidly into the sea) visible in the images were categorised as 'disturbance' and events without obvious grey seal flushing were categorised as 'no disturbance'. Micro disturbance responses to disturbance were not included as they could not be distinguished from images. Explanatory variables in the model were; disturbance stimuli (i.e. 'people on cliff' | aircraft | natural; Table 1), number of visitors (present during disturbance events), tidal level in metres, wind direction (radians) and the number of grey seals hauled-out 30 minutes prior to disturbance. Natural disturbances were caused by other wildlife, rockfalls and grey seals. Only disturbance stimulus types with a minimum of nine events were used to ensure sample sizes of stimuli were comparable with each other. Wind data were provided by a National Coast Watch Institution (NCI St Ives) weather station (distance to station from haul-out 6.3 km). Spatio-temporal relevant tide level data (determined at the start of each disturbance event) were obtained from POLPRED (National Oceanography Centre, Liverpool). Of the 132 CSGRT recorded disturbance events between July 2013 and October 2015, 44 were incorporated into the BRGLM. Equipment failure, of either the camera or visitor counter, accounted for the exclusion of 80 disturbance events from the BRGLM analysis. A further 12 disturbance events were excluded from the BRGLM as the number of events recorded for dog, nautical, rescue and unknown stimuli did not reach the minimum requirement of nine disturbance events for BRGLM analysis. Data for a further nine known non-disturbance events, referred to as 'reference events', determined from time-lapse data

on days following people on cliff disturbance incidents were also incorporated in to the model as a 'stimulus'. The model was relevelled so that 'reference events' were the first level in the model and as such used as the reference level for interpreting the effect of the remaining stimuli.

Spatial dynamics of disturbance

The spatial dynamics of grey seals during 'people on cliff' disturbance events were investigated. Only disturbance events that resulted in grey seals flushing into the sea (n=9 events; n=381 photographs) and had corresponding visitor counter data were analysed. Smaller seal movements such as head turning or increased vigilance were not easily identified (Table 1), and so these events were not incorporated. Each disturbance event consisted of a sequence of images, and from this sequence the image containing the main flushing event (termed T0) was selected and then the remaining number of hauled-out grey seals were enumerated in subsequent images. Images from one hour before and one hour after the disturbance event were also identified and grey seals were enumerated at 15-minute intervals (nine counts in total termed T-60, T-45, T-30, T-15, T+15, T+30, T+45, T+60). A reference dataset of non-disturbance events was also created using the above procedure. This dataset was created from images gathered on the day following each recorded disturbance event (offset by 45 minutes to account for tide).

Pinnipeds communally haul-out, so disturbance events can influence groups of individuals, including the spatial pattern of hauled-out seals. To examine this response, photographs from the time-lapse camera were geo-referenced and ortho-rectified using the British National Grid (BNG) coordinate system in ArcMap (v. 10.3.1). ImageJ was then used to digitise the positions (easting and northings, metres) of grey

seals in each image. These data were used to calculate inter-phocid distance (IPD) of hauled-out individuals and the total beach area (minimum concave polygon; metres squared) occupied by grey seals for each of the nine timesteps for a disturbance event. This process was repeated for images for each of the nine non-disturbance reference events occurring the following day. Mean IPD distance among hauled out grey seals and their nearest neighbours was calculated in R (R core team; v 3.2.3). Non-parametric Wilcoxon signed-rank tests were used to compare differences between disturbance and reference events; quantifying (i) the change in the number of hauled-out seals, (ii) the change in the IPD (iii) the change in the beach area (polygon) occupied by grey seals and (iv) the density of hauled-out grey seals.

Results

Seasonal patterns of visitors and seals

The annual peak in grey seal abundance occurred in March and April (Figure 1), with recorded median daily maximum grey seal counts in 2014 and 2015 of 103 (\pm 52.00 IQR) and 83 (\pm 46.00 IQR) respectively (Figure 1; March: range 52 to 188; April: range 25 to 239). During this peak period there were median daily visitor counts of 86 people (\pm 61.25 IQR) and 203 people (\pm 151.75 IQR) for March and April respectively (Figure 1; March range 6 to 249). An increase in the number of visitors was correlated with a decrease in the number of hauled-out grey seals ($r_s=-0.33$, $n=744$, $p < 0.001$) (Figure 2). The peak for visitor numbers at the site occurred in August in 2014 and 2015 with median daily visitor counts of 381 people (\pm 102.00 IQR, range 77-471), coinciding with school summer holidays. Visitor numbers were also high during September and October (2014 and 2015), particularly during school half term which coincided with the grey seal reproductive season and peak grey seal pup abundance. Median daily visitor

counts for September and October were 291 people (± 111.50 IQR) and 205 people (± 122.50 IQR) respectively (Figure 1; September: range 178 to 520; October: range 61 to 431). For this same period, median daily maximum grey seal counts were 13 seals (± 24.00 IQR) and 59 seals (± 23.50 IQR) for September and October respectively (Figure 8; September: range 0 to 52; October: range 17 to 106).

Disturbance events

Observers from CSGRT visited the haul-out site between 4-10 times a month (July 2013-October 2015), undertaking 195 surveys, of which 76 (39%) documented disturbance of hauled-out grey seals. Multiple disturbance events were often observed during single visits, with a total 132 disturbance events recorded at the haul-out site. Time-lapse cameras were operational for 63 of these events (48%). Disturbance events can affect different numbers of grey seals hauled-out on the beach. Disturbances documented by CSGRT were categorised into seven groups (Figure 3). People on cliff disturbance events were the most common stimulus, representing 36% (n=47) of all disturbances. Disturbances with unknown stimuli accounted for 24% (n=32) of disturbance events, with the remainder of disturbance events as follows; natural disturbances 17% (n=23), aircraft 14% (n=19), dogs 4% (n=5), nautical 4% (n=5) and rescues 1% (n=1). High number of disturbance events (regardless of cause), occurred in January, April, May and September. In January (2014 and 2015), there were 16 surveys, half of which (n=8) documented a total of 17 disturbances (Figure 4a). There was a total of 14 survey days in April (2014 and 2015 combined), 13 of which documented 33 disturbances. In May (2014 and 2015 combined) there was a total of 15 surveys, 7 of which documented 21 cases of disturbance. There was a total of 24 survey days in September (2013, 2014, 2015), 11 of which documented 17 cases of disturbance. The frequency of 'people on cliff' disturbance events (caused

by people shouting, moving or otherwise creating stimuli that disturbed the seals) was bimodally distributed, with modes occurring in April and September (Figure 4b). People on cliff disturbance events were most frequent in spring (March; n=13 and April; n=17 disturbance events), coinciding with the peak haul-out season for grey seals at the site, and during autumnal months (September; n=9 and October; n=5), coinciding with the grey seal reproductive season. Highlighting, that grey seals are more prone to disturbance during important moulting periods (March-April) and reproductive periods (September and October).

A BGRLM was used to investigate the effect of disturbance stimuli on grey seals. People on cliff disturbance events were more likely to disturb grey seals (BRGLM; $Z=1.97$, $df=14$, $p=0.049$) than aircraft (BRGLM; $p=0.275$) or natural stimuli (BRGLM; $p=0.108$). Wind direction (BRGLM; $p=0.15$), tidal level (BRGLM; $p>0.05$), number of grey seals, (BRGLM; $p=0.681$), nor the number of people (BRGLM; $p=0.340$) explained disturbance of grey seals as covariates in the model.

Spatial dynamics of disturbance

Spatial responses to disturbance were analysed for nine people on cliff disturbance events. The median number of grey seals present on the haul-out beach 30-minutes prior to T0 was 49 seals (± 12 IQR) and 30-minutes after T0 was 24 seals (± 12 IQR). During reference events when no disturbance occurred, the median number of grey seals present on the beach 30-minutes prior to T0 was 47 seals (± 26 IQR) and 30 minutes after T0 was 33 seals (± 29 IQR). All but one disturbance event occurred on a falling tide when grey seals typically leave the haul-out. For 88% of events (8 of 9) the number of grey seals on the haul-out was less 30 minutes after disturbance than for respective reference events. A median average of 9 grey seals were disturbed off

the beach during disturbance events when benchmarked against corresponding reference events with no disturbance (Figure 5). This change in the number of grey seals using the haul out was statistically significant (Wilcoxon signed-rank test; $Z=-2.37$, $p\text{-value}=0.02$). The decline in grey seal numbers was steeper and more acute during disturbance events compared to the change in grey seal numbers during reference events (Figure 5).

IPD analysis of hauled-out grey seals during disturbance events revealed a median IPD of 9.5 m (± 3.34 IQR) 30-minutes prior to T0 and a median IPD of 10 m (± 4.61 IQR) 30-minutes after T0. A median increase of 0.8 m, indicating seals were less aggregated but not significantly. Median IPD of hauled-out grey seals for reference events was 9.8 m (± 7.69 IQR.) 30-minutes prior to 'T0' and 12 m (± 5.34 IQR) 30-minutes after T0, a median increase of 1.2 m. The observed change in IPD between disturbance and reference events was not significantly different (Wilcoxon signed-rank test; $Z=-0.53$, $p\text{-value}=0.65$).

Beach area occupied by grey seals during disturbance events at 30-minutes prior to T0 was 139 m² (median ± 110.3 IQR, $n = 9$), in comparison to 75 m² (median ± 71.2 IQR, $n= 9$) 30-minutes after T0. There was median decrease in beach area occupied of 94 m² (Figure 6). Total beach area analysis during reference events revealed a median beach area occupation of 170.6 m² (± 133.8 IQR) 30-minutes prior to T0 and a median beach occupation of 135.5 m² (± 110.2 IQR) 30-minutes after T0. A median decrease in beach occupation of 35 m². Area occupied for disturbance and non-disturbance events were not significantly different (Wilcoxon signed-rank test; $Z=-1.24$, $p\text{-value}=0.25$).

The density of grey seals during disturbance events at 30-minutes prior to T0 was 0.38 m² (median ± 0.16 IQR, n = 9), in comparison to 0.32 m² (median ± 0.10 IQR, n= 9) 30-minutes after T0. There was median decrease in density of 0.06 m² (Figure 6). Density analysis of reference events revealed a median density of 0.28 m² (± 0.08 IQR) 30-minutes prior to T0 and a density of 0.32 m² (± 0.10 IQR) 30-minutes after T0. A median increase in density of 0.04 m². Density for disturbance and non-disturbance events were not significantly different (Wilcoxon signed-rank test; Z=-0.77, p-value=0.49)

Discussion

The use of time-lapse cameras throughout an annual cycle enabled an extensive photo data collection documenting the seasonal abundance of hauled-out grey seals and enabled an unobtrusive means of continuously surveying these animals. The combination of visitor counts and photo-based enumeration of grey seal numbers allowed for an in-depth study into the seasonal trends of grey seals and visitors at the site, and responses to disturbance.

This study highlighted that surveys documenting disturbance were more prevalent in April and that people on cliff disturbances were a significant disturbance stimulus at the haul-out site leading to grey seal displacement. The number of hauled-out grey seals did not significantly influence the disturbance response, suggesting that this may not be a density dependant effect although this requires further investigation. Visitor activity occurs year-round at the site with the largest range of visitors occurring in April, coinciding with the annual peak of grey seal haul-out activity during March and April and the spring school holidays, but peaks in August during the school summer

holidays. There was also a large range of visitors to the site in October coinciding with peak grey seal pup presence at the site and the October half term school holiday.

Camera data and visitor counter data revealed that an increase in the number of visitors was correlated to a decrease in the number of grey seals hauled-out, suggesting that higher visitor presence might result in lower grey seal haul-out numbers. However, the behaviour of a single visitor can be as disruptive to hauled-out grey seals as a large group (pers.comm. Sue Sayer). Due to the nature of visitor counter data collection, group sizes of visitors aggregating at haul-out could not be assessed in this analysis.

Analysis of disturbance revealed that people on cliff disturbance events caused significantly more disturbance to grey seals than any other recorded stimulus at the site, suggesting that grey seals are potentially more open to disturbance in the presence of visitors at the site than, they are to aircraft and natural disturbances. Visitors at the site can view grey seals from a distance of approximately 50-75 metres (approx. line of sight distance from clifftop to beach). Osinga *et al.* (2012) found that the presence of visitors less than 50 metres from a harbour seal haul-out, would always result in disturbance but that visitors viewing seals from 50-200 metres were less likely to cause disturbance. Aircraft disturbances were less frequent in our study but still resulted in grey seal disturbance. Studies have shown that aircraft disturbances to hauled-out seals are less frequent but can be disruptive due to the sound of the aircraft (Osinga *et al.* 2012). Furthermore, Born *et al.* (1999) showed that the helicopters caused a stronger escape response in ringed seals (*Phoca hispida*) than fixed-wing aircraft.

Spatial analysis revealed that there was a significant difference in the change in the number of grey seals hauled-out during disturbance and reference events and that this resulted in declines in grey seal haul-out numbers. There was no significant difference in the change in IPD, beach area occupancy or density between disturbance events or reference events. Other studies however, have shown that the spatial distribution and behaviour of harbour seals were affected by the presence and behaviour of tourists (Granquist & Sigurjonsdottir 2014).

As the camera was unable to detect fine scale behavioural changes, photo analysis focused on obvious flushing events detecting acute responses to disturbance. However, previous studies have shown that pinnipeds do not always respond to disturbance with extreme changes in their behaviour (Curtin et al. 2009, Osinga et al. 2012, Stafford-Bell et al. 2012, Hoover-Miller et al. 2013) and that they can also exhibit fine scale changes that are not detected in photographs. Increased vigilance in response to the presence of humans, be they on land or onboard vessels, is a common behaviour documented by human observers in a variety of pinniped species including; southern elephant seals (*Mirounga leonina*) (Engelhard et al. 2002), harbour seals (Granquist & Sigurjonsdottir 2014; Henry & Hammill 2001), harp seals (*Pagophilus groenlandicus*) (Kovacs & Innes 1990) and New Zealand and Australian fur seals (*Arctocephalus forsteri*, *Arctocephalus pusillus*) (Shaughnessy et al. 2008). Furthermore, Granquist and Sigurjonsdottir (2014) showed that vigilance in harbour seals increased when the number of tourists in the area increased and behaved in an active way. Such responses are highly likely in the grey seals monitored in this study, despite the camera not being able to provide information on grey seal vigilance.

Marine wildlife tourism may have detrimental effects on pinnipeds resulting from chronic disturbance. Increased vigilance is a time consuming acute response to

human disturbance which can result in chronic effects such as reduced resting, feeding and rearing success (Kovacs & Innes 1990; Dyck & Baydack 2004; Dans *et al.* 2008). Studies have shown that at Donna Nook, England, maternal grey seals gave birth later in the season in areas of higher disturbance. This resulted in a diminished lactation period with possible detrimental effects on pup growth rates (Lidgard 1996). In Port Philip Bay, Australia, Australian fur seals (*Arctocephalus pusillus doriferus*) increased their haul-out behaviour during the presence of human swimmers (Stafford-Bell *et al.* 2012) and in the Mediterranean, mass tourism has led to population declines of the Mediterranean monk seal (*Monachus monachus*) (Johnson & Lavigne 1999).

Pinnipeds are reluctant to move into the sea whilst hauled-out at a rookery, but the cumulative effects of repeat human disturbance can result in species abandoning it permanently (Peterson and Bartholomew 1967). Furthermore, Australian sea lions have shown to heighten their level of vigilance due to low level, but on-going, high frequency repetitive disturbances from human presence, ultimately leading to physiological stress responses (Orsini *et al.* 2006).

The haul-out site in our study is situated in a harsh coastal environment, exposing the camera to sea spray damage which often impaired the reliability of the camera, and as such compromised the quality of the images captured. Nonetheless, large scale disturbance events resulting in grey seals returning to the sea were successfully captured by the time-lapse camera. Disturbance events that caused grey seals to suddenly move closer to the shoreline or to flush completely off the beach were easily identifiable. Finer scale changes in behaviour such as increased vigilance or subtle body re-orientation, however, were not detectable using images taken at 5-minute intervals. Using consumer grade electronics, rugged enough for long-term deployment

in coastal areas to count seals from over 20 m is challenging as grey seals are easily camouflaged against the sandy and rocky substrate

Technology in marine environments is often prone to failure. Cameras are liable to stop recording during deployments as shown in bird-borne video-cameras studies (Tremblay *et al.* 2014), leading to failure in capturing interesting behaviours and insights into animal behaviour.

The challenges of detection of disturbance in this study, where automated techniques could not be used, meant a reliance on observer surveys to first indicate times at which disturbance occurred. The scope of the disturbance study was further limited by periods of camera failure and/or photograph impairment.. The use of the visitor counter and environmental data also had limitations. Due to the existing infrastructure at the site the deployment of the visitor counter system was restricted to a single fence post. There are several paths and routes that can be taken to reach the grey seal haul-out observation point and the visitor counter was positioned on the most direct and commonly used route.. In future studies the visitor counter counted be sited nearer to the observation point or a human observer could work at the site to manually record the number of visitors at fixed intervals. The data provided by the NCI, was consistent and reliable. However, as the NCI was situated 6.3 km south west from the haul-out site, it is possible that wind direction and wind speed differed to those occurring at the haul-out site.

The incorporation of thermal camera technology would aid in the automation of grey seal counting in future studies (Figure 7), as thermal thresholds can be applied to images to remove any confusion between camouflaged animals and their habitats (Steen *et al.* 2012). Not only would thermal technology allow for automated algorithms

but the use of thermal video could aid in detecting fine scale behaviours in response to disturbance events.

This study identified that people on cliff disturbances were a significant disturbance stimulus at the haul-out site and that grey seals were displaced because of such events. Visitor activity occurs year-round at the site peaking in August with large levels occurring in April and October, coinciding with the annual peak of grey seal haul-out activity during March and April and the peak grey seal pup presence in October. Educating the public about conservation is a crucial part of ecotourism as it helps raise awareness about environmental issues and wildlife wellbeing. However, if unmanaged, ecotourism activities, including marine wildlife tourism, can negatively impact wildlife populations (Kruger 2005). We propose that the monitoring of both grey seals and people at the haul-out site continues, incorporating new thermal infrared technology video and revised people counting techniques, to better understand the fine scale behaviour changes emitted by hauled-out grey seals.

FIGURES

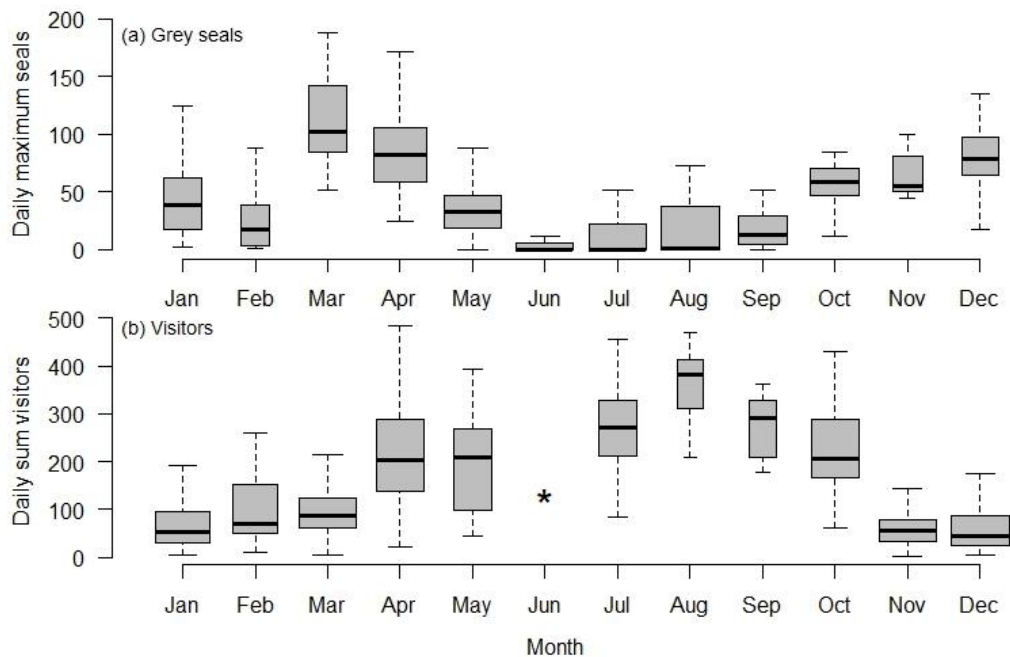


Figure 1. Boxplots describing the seasonal variance of (a) Grey seals and (b) Visitors at the haul-out site across two years (2014 and 2015). Data gathered from the visitor counter and time-lapse camera respectively. * indicates a period of technology failure. Note that Y axis lengths in plots 'a' and 'b' differ for better visualisation of the data. Whiskers represent the highest and lowest count for each month, black lines show the median of each month and the third and first quartiles are represented by the top and bottom of the box respectively. Outliers have been removed from figure.

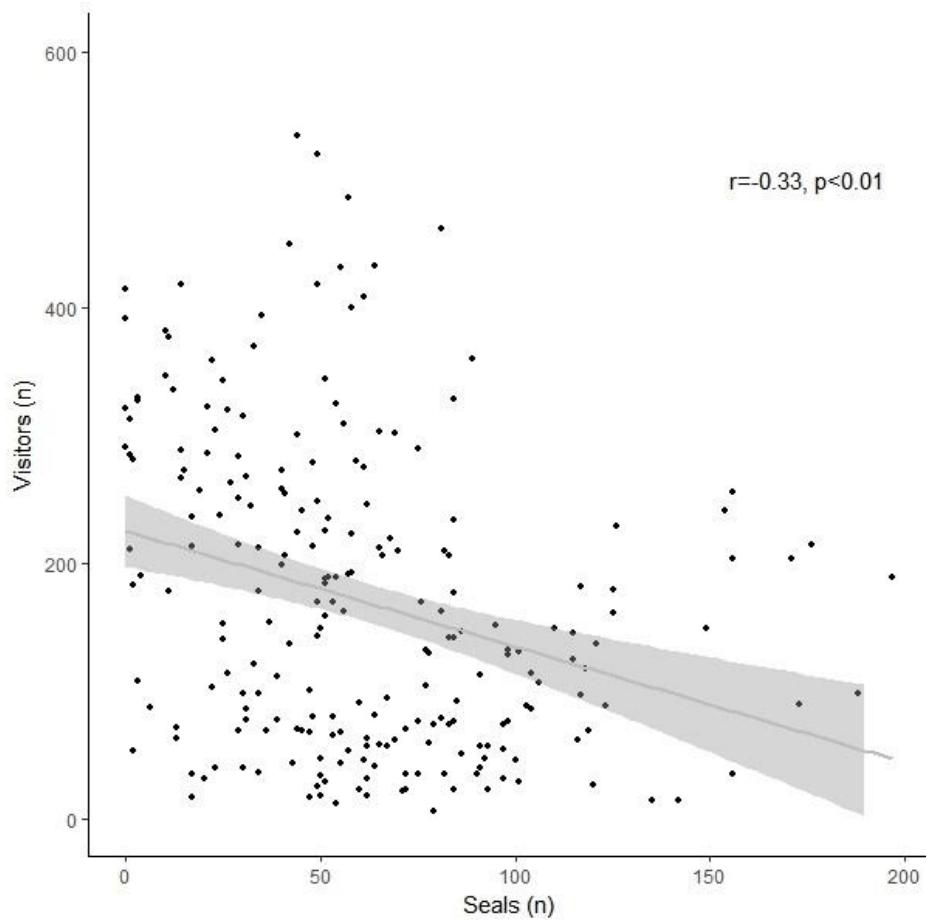


Figure 2. Scatterplot of the daily number of visitors at the observation site against daily maximum number of grey seals hauled-out (2013, 2014 and 2015, $n = 744$ days). Data gathered from the people counter and time-lapse camera respectively.

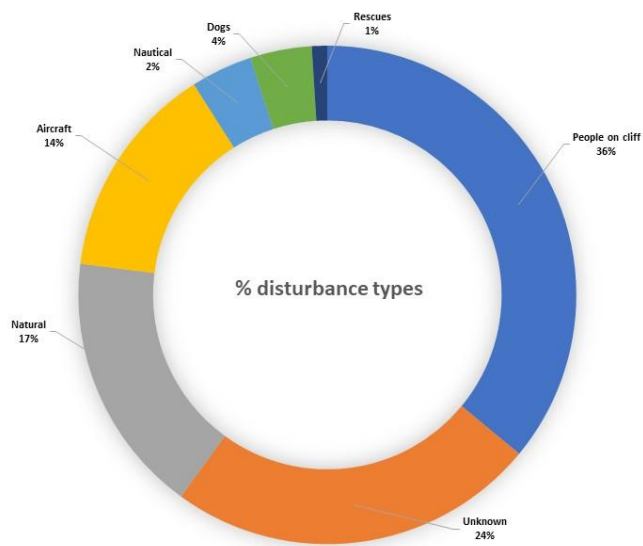


Figure 3. Distribution of disturbance stimuli recorded by CSGRT at the grey seal haul-out (July 2013-October 2015; n=132 disturbance events). Events with grey seal flushing visible in the images were categorised as 'disturbance' and events without obvious grey seal flushing were categorised as 'no disturbance'

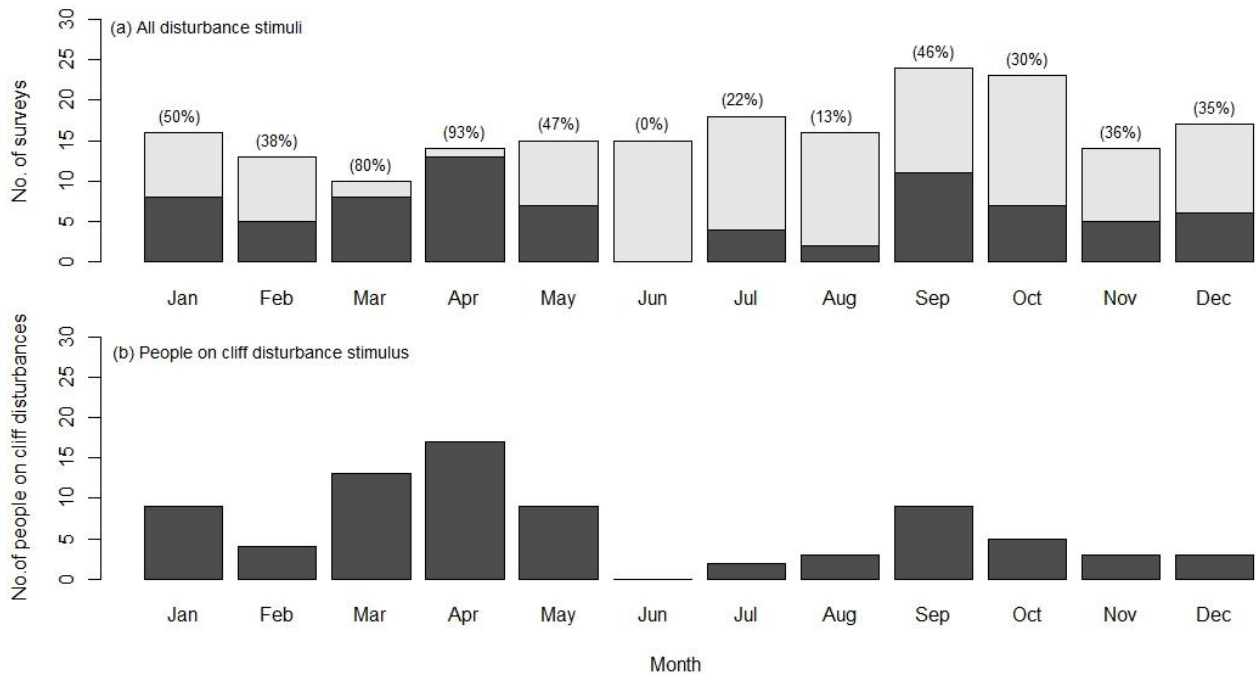


Figure 4. Stacked bar plots showing (a) Total number of surveys per month reporting grey seal disturbance at the haul-out site; surveys documented disturbance from CSGRT (July 2013 and October 2015). Dark grey bars indicate the number of surveys where disturbance was observed and light grey bars indicate the number of surveys where no disturbance was observed. Numbers above bars indicate the percentage of surveys with disturbance. (b) Seasonal abundance of people on cliff disturbances recorded by CSGRT (July 2013-October 2015).

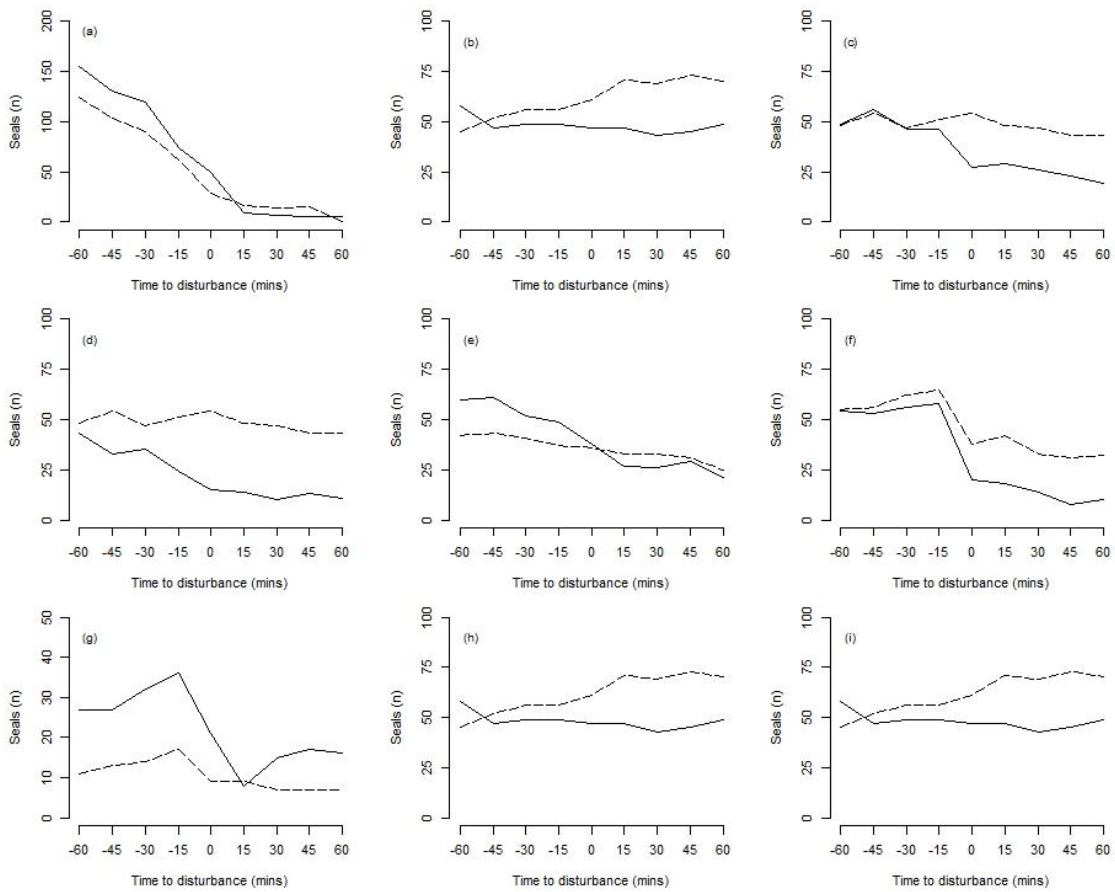


Figure 5. Plots showing the change in the number of hauled-out grey seals observed at 15-minute intervals during nine ‘people on cliff’ disturbance events (a-i: black solid line). For reference, the black broken line shows the change in the number of hauled-out grey seals for a period where there was no disturbance. Note that Y axes differ for plots a and g.

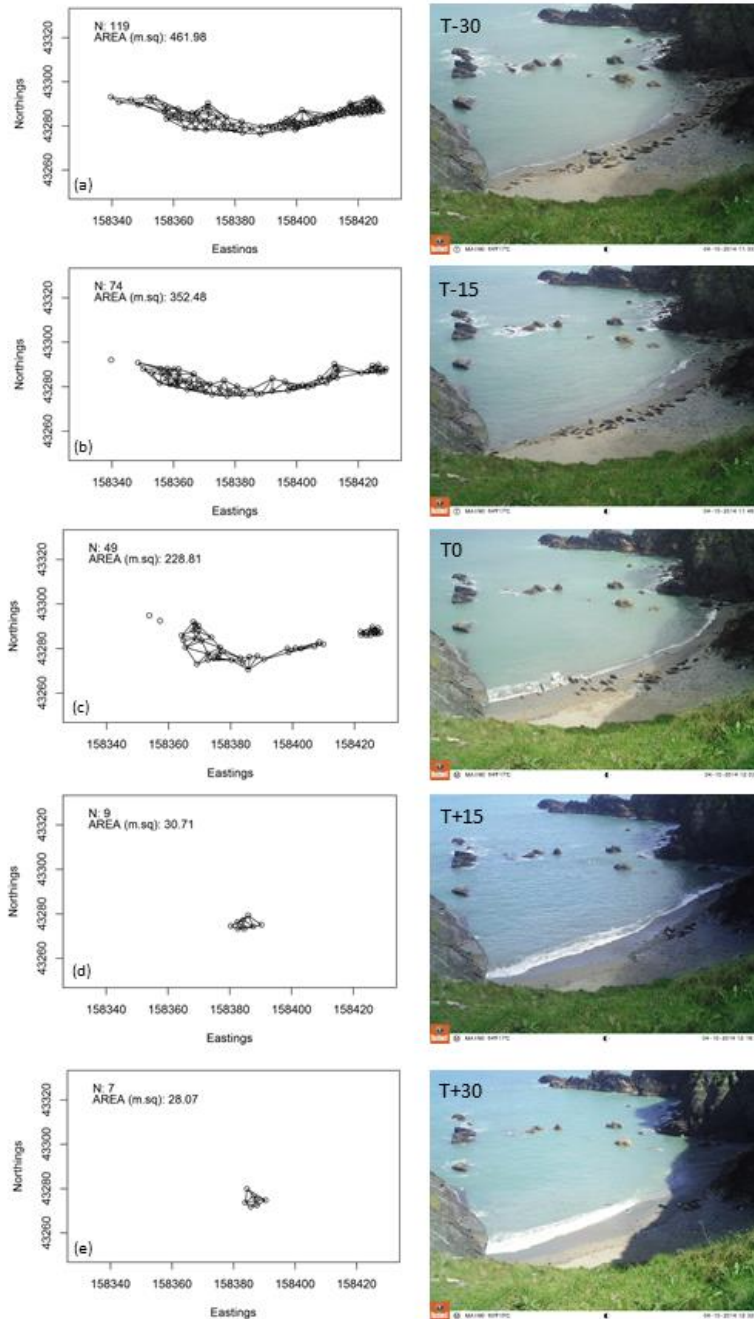


Figure 6. Spatial distribution of grey seals at the haul-out, before, during and following a people on cliff disturbance event occurring on a rising tide. The number of grey seals and the total beach area occupied by grey seals is illustrated by a series of plots produced in R. (a) 30-minutes before disturbance, (b) 15-minutes before disturbance (c) as disturbance occurs, (d) 15-minutes following disturbance event, (e) 30-minutes following disturbance.

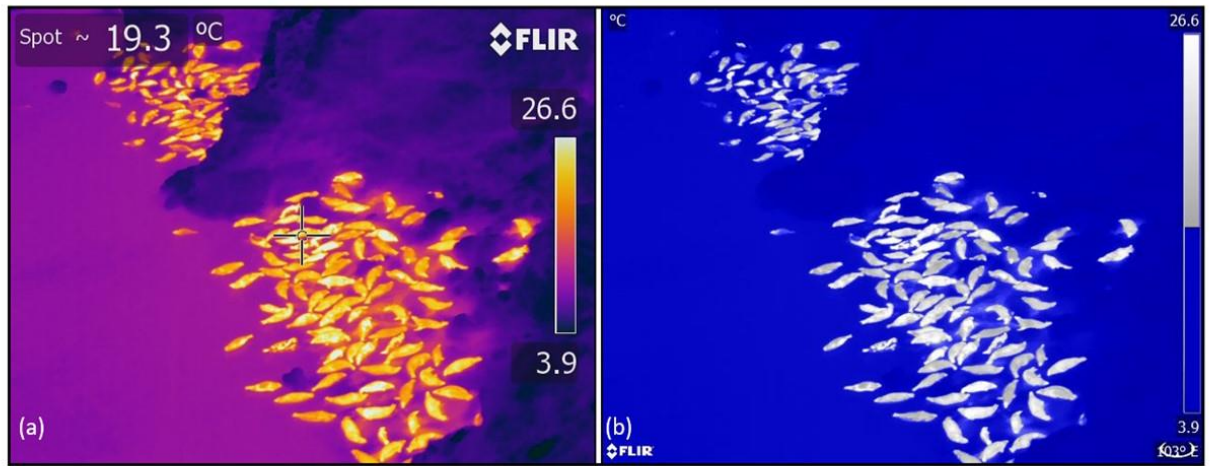


Figure 7. Photos of haul-out beach taken using a FLIR T620. Photo (a) is a standard thermography (b) the thermal threshold has been set at 12 degrees Celsius.

Table 1.

Description of disturbance events observed by CSGRT (July 2013-October 2015; 195 surveys, n=132 disturbance events). and summary of corresponding functioning of time-lapse camera and visitor counter.

Disturbance stimuli	Observed disturbances	Camera operational	Camera non-operational	Condensation	Sun-glare	No disturbance detected by camera	Available photo data sets	Data sets with functional visitor counter
People on cliff	47	32	15	1	2	16	13	9
Aircraft	19	13	6	0	1	10	2	2
Dogs	5	3	2	0	1	2	0	0
Nautical	5	3	2	1	0	1	1	0
Natural	23	9	14	0	0	7	2	2
Rescues	1	1	0	0	0	0	1	1
Unknown	32	2	30	0	0	2	0	0

GENERAL DISCUSSION

This research

The use of time-lapse cameras allowed the project to investigate the seasonal relative abundance of grey seals at a haul-out site on the north coast of Cornwall. Using the technology alongside environmental parameters, we were able to determine how grey seal haul-outs potentially respond to environmental influences, including tide and wind chill. Such understandings were vital in enabling a study into how grey seals respond to human disturbance at the site. The disturbance study incorporated novel technologies and human observations to investigate the potential for human disturbance at Cornwall's largest onshore haul-out. The research presented here delivers a time-saving method that can be used to gain an insight into the haul-out dynamics of grey seals at an onshore haul-out and the incorporation of human observations in conjunction with cameras, provides an understanding of how grey seals respond to human disturbance. The methods utilised in this project can be expanded upon and utilised to study other onshore pinniped haul-outs across the globe.

The findings presented in chapter 1 provide a visual understanding of the seasonal patterns and relative abundance of a grey seal haul-out with respect to environmental influences. Furthermore, the nature of the technology and methodology used in chapter 1 has enabled a vast archive of photos to be collected across multiple years. In chapter 2, the project focused on human disturbance stimuli at the site and how grey seals respond in such situations. The findings here can be used by the National Trust to inform tourists visiting the site, ultimately helping to manage people observing seals.

Future of camera technology in monitoring wildlife

Camera technology is rapidly developing and is being incorporated into scientific research across disciplines, including; microscopy, earth and space science, botany and health (Park et al. 2015, Alberton et al. 2017, Lin et al. 2017, Gunn & Cousins 2018) . In conservation, cameras have been deployed to remotely monitor cryptic and endangered species, such as big cats (Karanth *et al.* 2006; Maffei et al. 2004), and have also been used more directly being attached to animals to gain an insight into their behaviour and social dynamics (Sakamoto et al. 2009, Pearson et al. 2017). To successfully conserve nature, we need to accurately monitor the distribution and abundance of animal species over time (Buckland *et al.* 2001; Buckland *et al.* 2004). In the past, this involved direct counts of animals and also indirect counts of their signs, including nests, dung and calls. Such methods are time consuming, costly and logistically challenging, especially in remote areas (van Gemert *et al.* 2014). Previous studies undertaking ground surveys of orangutan (*Pongo spp*) populations in Sumatra, Indonesia, have cost up to \$250,000 over a three-year period. As such, surveys are not conducted regularly enough to acquire sufficient statistical analysis of population trends and many remote areas of forest are still to be surveyed (van Gemert *et al.* 2014). The use of small planes or helicopters can be used to overcome some of the logistical problems but they too are costly, risky to use in forested areas and are often unavailable (van Gemert *et al.* 2014). The use of cameras can provide time saving and cheaper alternatives, but with limited spatial coverage. Cameras are also prone to failure and require large amounts of post processing and investment. The use of unmanned aerial vehicles (UAVs) are frequently being used to determine animal abundance and their associated threats (Jones *et al.* 2006; Koh & Wich 2012). As they are relatively inexpensive to build, drones

can be utilised by researchers working in developing countries. Drones can undertake automated flights to gather high resolution photographs and videos that can be used to not only detect large animal species, including orangutans, elephants, rhinos and whales, but animal tracks too, such as ape nests and turtle tracks. Furthermore, drones can detect signs of human activity which can be used to better inform conservation measures (Hodgson *et al.* 2013; Koski *et al.* 2009; Vermeulen *et al.* 2013; Malisiewicz *et al.* 2011).

Thermal imaging is a novel approach that has previously been used to detect human activity (Dai *et al.* 2007; Fernández-Caballero *et al.* 2010; Sun *et al.* 2011; Castillo *et al.* 2009). In terms of surveying wildlife, previous applications of thermal imagery have been used to; estimate cervid population densities (Ditchkoff *et al.* 2005; Gill *et al.* 1997), to detect and census birds (Boonstra *et al.* 1995), aerial survey mammal populations (Havens *et al.* 1998; Wiggers & Beckerman 1993), gain an insight into night-time behaviour of grey partridges (*Perdix perdix*) (Tillmann 2009) and to detect migrating birds around offshore wind farms (Desholm 2003). Adaptive thresholding, where the threshold value (temperature) is based on the maximum pixel value of the current image compared to the mean value of maximum pixel values of previous images (Gonzalez *et al.* 2001), can be applied to images and videos taken by thermal imaging cameras which enables better discrimination of animals from the background (Steen *et al.* 2012). When an animal is present in an image, the maximum values increase significantly and this rapid increase can be used to detect individuals (Steen *et al.* 2012). Furthermore, algorithms can be applied to enhanced images to automate counts.

Evaluating the effectiveness of conservation management activities is a challenging process. It is also difficult to monitor populations rapidly, effectively and at low cost (Dajun *et al.* 2006). The use of remote cameras to monitor vertebrate populations is a repeatable process that can provide a quantifiable measure of effectiveness, particularly when monitoring animals within reserves, as the distribution of mammals relative to management efforts is a swift way in assessing reserve effectiveness (Dajun *et al.* 2006). Furthermore, using spatial capture-recapture models with data collected by cameras, we can improve density estimates for elusive carnivores (Sollmann *et al.* 2011) and in remote rainforest habitats, automated camera systems can be utilised to estimate species richness of large and medium sized mammals (O'Brien 2008).

Moreover, knowledge from camera surveys can be used to engage local communities providing them with information regarding wildlife populations and animal movements, informing communities and land managers about natural areas, helping to minimize human-wildlife conflicts and making science accessible in the classroom (Patterson 2012). Self-triggering wildlife cameras are non-invasive and provide valuable data that is available and engaging to students (Patterson 2012). This can help inspire future generations to continue conservation work and help protect endangered species.

Limitations

Remote cameras have the added benefit of collecting data that can be reviewed *ex-situ*, enabling in-depth analysis into the collected data, a component which can be absent from human observations. However, cameras can be limiting when investigating fine scale behaviours of animals and their responses to disturbance,

as highlighted in this study, and can fail when exposed to extreme weather. Camera failure for prolonged periods and unusable data, caused by photo impairment, also resulted in a large loss of usable data. In addition, reviewing data collected from remote cameras is time consuming and requires a large volume of *ex-situ* analysis. Cameras were unable to detect fine scale changes in grey seal behaviour and so photo analysis was restricted to obvious flushing events where acute responses to disturbance could be detected. Furthermore, well camouflaged animals can be tricky to detect in optical photographs, but the development and incorporation of thermal imaging cameras into wildlife studies could provide the solution.

The use of the visitor counter and environmental data also had limitations. In future studies, it would be worth re-positioning the visitor counter closer to the observation point to collect a more accurate representation of footfall. Furthermore, as the NCI was situated 6.3 km south west from the haul-out site, it is possible that wind direction and wind speed differed to those occurring at the haul-out site. As such, it could be useful to insert an anemometer at the site to gather accurate wind data for analysis.

Eco-Tourism

Ecotourism focuses on delivering environmentally sustainable forms of tourism with minimal ecological and socio-cultural impacts and it is one of the fastest growing sectors within the tourism industry (Coles *et al.* 2015). For example, whale-watching occurs on every continent (Orams 2000) and is arguably the most demanded form of marine wildlife tourism within the industry, exceeding revenues of \$2.0 billion a year, creating 13,000 jobs and attracting 13 million whale-watchers a year (O'Connor *et al.* 2009). Whale watching provides a motive for

conservation whilst providing income for local communities in and around protected areas (Das & Chatterjee 2015). Furthermore, ecotourism promotes local livelihoods, an important policy instrument for biodiversity conservation (Cattarinich 2001, Lai & Nepal 2006, Scheyvens 2008), and contributes to poverty eradication and the conservation of natural resources (Surendran & Sekar 2011). Engaging individuals and communities with the environment is a benefit of marine wildlife tourism, with the conservation benefits gained from wildlife tourism including; wildlife management and research, finances for conservation of species, socio-economic benefits and the education of visitors which can potentially result in more conservation focused behaviour and support (Higginbottom & Tribe 2004).

Tourists seek interactions with marine wildlife to gain personal rewards and benefits whilst escaping from their daily routines (Higham & Luck 2007). A study in New Zealand found that visitors to a penguin watching tourism attraction reported feelings of enhanced environmental awareness and mood benefits as well as eliciting feelings of exploration and privilege (Schänzel & McIntosh 2000). These types of responses to wildlife tourism are reputed to generate environmental actions that could result in conservation benefits for both marine wildlife and the natural environment (Higham & Luck 2007). However, unsustainable practices and the development of infrastructure can have detrimental effects on biodiversity conservation (Ritchie 2013). Research into a population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in western Australia has shown that there was a significant average decline in dolphin abundance due to the increase in wildlife tour boats and unsustainable practices (Bejder et al. 2006).

Achieving sustainable marine wildlife tourism is a trade-off between the environmental wellbeing of humans and the detrimental effects the industry poses on the species involved. Studies have shown that human presence can have cumulative and substantial negative impacts on wildlife and their habitats if inappropriately managed (Marion & Reid 2007). Examples of these negative/adverse impacts include; injury, death, stress, alteration in foraging, nesting or breeding behaviour, habituation to humans, the destruction or changes to habitat and variation in animal feeding due to provisioning of food, whether it is deliberate or unintentional (Chin et al. 2000; Glick 1991; Green & Higginbottom 2000; Shackley 1996). The effects of tourism on wildlife and associated habitats need to be understood and efforts to reduce negative impacts through implementing appropriate management strategies need to be exhibited to ensure the long term sustainability of the industry (Trave et al. 2017; Higginbottom 2004, Newsome *et al.*, 2004, Rodger *et al.*, 2007, Strong & Morris 2010).

Managing visitors taking part in wildlife tourism activities is vital as it helps prevent disturbance and other detrimental impacts on species. A passive form of managing tourists is the development and implementation of interpretation signs in wildlife areas. A study by Marschall *et al.* (2017) found that signage is an effective method in modifying visitor behaviour at a seal watching site in Iceland. In addition, teleological information (instructions with explanation) was more effective than ontological information (instructions without explanation). Ultimately, if managed appropriately, wildlife tourism can ensure that the needs of wildlife and tourists do not conflict. This can be achieved by maximising positive visitor experience and minimising impacts posed on wildlife (Ballantyne *et al.* 2009).

Conclusions

The project assessed the efficiency of low cost time-lapse camera equipment to monitor pinniped haul-outs and how this knowledge can be utilised to improve field surveys. Furthermore, in conjunction with human observations, we have demonstrated how cameras can be used to detect and document disturbance of grey seals. Using this information, we can inform and implement better management strategies, through the development of improved signage for instance, at the site to help mitigate and reduce disturbance events. The combination of ecotourism and conservation can help protect this species and their associated habitats. The monitoring and conservation of marine wildlife needs to continue to better understand human-wildlife interactions and how activities can be managed to prevent biodiversity loss. Sustainable co-existence between wildlife and people must be the definitive goal when managing wildlife tourism (Marschall *et al.* 2017).

REFERENCES

- Acevedo-Gutiérrez A (2011) Nocturnal Haul-Out Patterns of Harbor Seals (*Phoca vitulina*) Related to Airborne Noise Levels in Bellingham, Washington, USA. *Aquat Mamm* 37:167–174
- Adimey N, Abernathy K, Gaspard JC III, Marshall G (2007) Meeting the manatee challenge: the feasibility of using CRITTERCAM on wild manatees. *Mar Technol Soc J* 41:14–18. doi:10.4031/002533207787442015
- Airoldi L, Balata D, Beck MW (2008) The Gray Zone: Relationships between habitat loss and marine diversity and their applications in conservation. *J Exp Mar Bio Ecol* 366:8–15
- Alberton B, Torres R da S, Cancian LF, Borges BD, Almeida J, Mariano GC, Santos J dos, Morellato LPC (2017) Introducing digital cameras to monitor plant phenology in the tropics: applications for conservation. *Perspect Ecol Conserv* 15:82–90
- Andersen MS, Miller ML (2006) Onboard marine environmental education: Whale watching in the San Juan Islands, Washington. *Tour Mar Environ* 2:111–118
- Arzoumanian Z, Holmberg J, Norman B (2005). An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus*. *Journal of Applied Ecology* 42, 999–1011
- Auger-Methe, M, Whitehead H (2007). The use of natural markings in studies of long-finned pilot whales (*Globicephala melas*). *Marine Mammal Science* 23, 77–93
- August T, Harvey M, Lightfoot P, Kilbey D, Papadopoulos T, Jepson P (2015) Emerging technologies for biological recording. *Biol J Linn Soc* 115:731–749
- Bailey H, Clay G, Coates, Elizabeth A, Lusseau D, Senior B, Thompson, Paul M (2010) Using T-PODs to assess variations in the occurrence of coastal bottlenose dolphins and harbour porpoises. *Aquat Conserv Mar Freshw Ecosyst* 20:150–158
- Bajzak D, Piatt PDE, (1990). Computer-aided procedure for counting waterfowl on aerial photographs. *Wildlife Society Bulletin*. 18:125-129.
- Balazs GH (1980) Synopsis of the biological data on the green turtle in the Hawaiian Islands. NOAA Tech Memo NMFS SWFC-7, Honolulu
- Ballantyne R, Packer J, Hughes K (2009) Tourists' support for conservation messages and sustainable management practices in wildlife tourism experiences. *Tour Manag* 30:658–664
- Barlow J (2010) Cetacean abundance in the California Current estimated from a 2008 ship-based line-transect survey.
- Barlow J, Ferguson M, Perrin W, Gerrodette T, Joyce G, Macleod C, Mullin K, Palka D, Waring G (2006) Abundance and densities of beaked and bottlenose whales (family *Ziphiidae*). *J Cetacean Res Manag* 7:263–270

- Barstow R (1986) Non-consumptive utilization of whales. *Ambio* 15(3), 155–163
- Bartel RA, Sexton JO (2009) Monitoring habitat dynamics for rare and endangered species using satellite images and niche-based models. *Conserv Biol* 23:888–896
- Barton K, Booth K, Simmons DG, Fairweather JR (1998) Tourist and New Zealand Fur Seal Interactions Along the Kaikoura Coast. Education Centre Report No. 9. Lincoln University, Lincoln, New Zealand.
- Battersby JE, Greenwood JJD (2004) Monitoring terrestrial mammals in the UK: past, present and future, using lessons from the bird world. *Mammal Rev.*, Volume 34, Issue 1-2, pp 3-29
- Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: A threat to global biodiversity. *Mar Policy* 27:313–323
- Becker BH, Press DT, Allen SG (2011) Evidence for long-term spatial displacement of breeding and pupping harbour seals by shellfish aquaculture over three decades. *Aquat Conserv Mar Freshw Ecosyst* 21:247–260
- Bejder L, Samuels A, Whitehead H, Gales N, Mann J, Connor R, Heithaus M, Watson-Capps J, Flaherty C, Krützen M (2006) Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conserv Biol* 20:1791–1798
- Bicknell AW, Godley BJ, Sheehan E V, Votier SC, Witt MJ (2016) Camera technology for monitoring marine biodiversity and human impact. *Front Ecol Environ* 14:424–432
- Biodiversity Steering Group (1995) Biodiversity: the UK Steering Group report. Two volumes. HMSO, London.
- Bishop, A., Pomeroy, P., Twiss, S.D. (2015) Breeding male grey seals exhibit similar activity budgets across varying exposures to human activity. *Mar Ecol Prog Ser* 527:247-259.
- Bjorndal KA, Bolten AB (1997) Developmental migrations of juvenile green turtles in the Bahamas. In: Keinath JA, Barnard DE, Musick JA, Bell BA (compilers) *Proc 15th Annu Symp Sea Turtle Biol Conserv*. NOAA Tech Memo NMFS-SEFSC-387, US Dept Commerce, Miami, FL, p 338
- Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison AL, Ganong JE, Swithenbank A, Castleton M, Dewar H, Mate BR, Shillinger GL, Schaefer KM, Benson SR, Weise MJ, Henry RW, Costa DP (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* 475:86–90
- Bonfil R, Meyer M, Scholl MC, Johnson R, Brien O, Oosthuizen H, Swanson S, Kotze D, Paterson M, Bonfil R, Meyer M, Scholl MC, Johnson R, Brien SO, Oosthuizen H, Swanson S, Kotze D, Paterson M (2017) *Transoceanic Migration, Spatial Dynamics, and Population Linkages of White Sharks* Published by: American Association for the Advancement of Science.
- Bonner N (1972). The grey seal and common seal in European waters. *Oceanogr Mar Biol.*, 10: 461–507

- Bonner WN (1981). Grey seal *Halichoerus grypus* Fabricius, 1791. In: S. H. Ridgway and R. Harrison (eds), Handbook of marine mammals, Vol. 2: Seals, pp. 111-144. Academic Press
- Boonstra R, Eadie JM, Krebs CJ, Boutin S (1995) Limitations of Far Infrared Thermal Imaging in Locating Birds (Limitaciones en el Uso de Imágenes Termales con Radiación Infraroja Extrema Para Localizar Aves). *J F Ornithol* 66:192–198
- Booth K (1998) The tourist experience of New Zealand fur seals along the Kaikoura coast, New Zealand. In: Kandampully, J. (ed.) New Zealand Tourism and Hospitality Research Conference 1998: Advances in Research Part 2. Lincoln University, Canterbury, New Zealand.
- Boren LJ, Gemmell NJ, Barton KJ, Boren LJ, Gemmell NJ, Barton KJ (2002) Tourist disturbance on New Zealand Fur seals *Arctocephalus forsteri*. *Australian Mammalogy*. 24: 85-95.
- Born EW, Riget FF, Dietz R, Andriashek D (1999) Escape responses of hauled out ringed seals (*Phoca hispida*) to aircraft disturbance. *Polar Biol* 21:171–178
- Boulva J, Maclaren I. (1979). Biology of the harbour seal *Phoca vitulina*, in eastern Canada. *Bull. Fish. Res. Bd. Canada.*, 200:1-24.
- Boveng PL, Bengtson JL, Withrow DE, Cesarone JC, Simpkins MA, Frost KJ, Burns JJ. (2003) The abundance of harbour seals in the Gulf of Alaska. *Mar Mammal Sci.*, 19: 111–127.
- Bowkett AE, Rovero F, Marshall AR (2008) The use of camera-trap data to model habitat use by antelope species in the Udzungwa Mountain forests, Tanzania. *Afr J Ecol* 46:479–487
- Boyd JM, Lockie JD, Hewer HR (1962) The breeding colony of Grey seals at North Rona. *Proceedings of the Zoological Society of London*, 138, 257-277.
- Boyd JM, Campbell RN (1971) The Grey seal (*Halichoerus grypus*) at North Rona, 1959 to 1968. *J Zool* 164:469–512
- Brooks EJ, Sloman KA, Sims DW, Danylchuk AJ (2011) Validating the use of baited remote underwater video surveys for assessing the diversity, distribution and abundance of sharks in the Bahamas. *Endanger Species Res* 13:231–243
- Buckland ST (1990). Estimation of survival rates from sightings of individually identifiable whales. Report of the International Whaling Commission Special Issue 12, 149–153
- Buckland ST, Anderson D, Burnham K, Laake J, Borchers D, Thomas L (2001) Introduction to distance sampling estimating abundance of biological populations.
- Buckland ST, Newman KB, Thomas L, Koesters NB (2004) State-space models for the dynamics of wild animal populations. *Ecol Modell* 171:157–175
- Buckland ST, Burt ML, Rexstad EA, Mellor M, Williams AE, Woodward R (2012)

- Aerial surveys of seabirds: The advent of digital methods. *J Appl Ecol* 49:960–967
- Cadotte MW, Carscadden K, Mirotnick N (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. *J Appl Ecol* 48:1079–1087
- Cappo M, Speare P, De'ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *J Exp Mar Biol Ecol* 302:123–152
- Cappo M, Harvey E, Shortis M (2006) Counting and measuring fish with baited video—an overview. In: Lyle JM, Furlani DM, Buxton CD (eds) Cutting-edge technologies in fish and fisheries science. Australian Society for Fish Biology Workshop. Australian Society of Fish Biology, Hobart, p 101–115
- Caro T, Stankowich T, Mesnick SL, Costa DP, Beeman K (2012) Pelage coloration in pinnipeds: Functional considerations. *Behav Ecol* 23:765–774
- Carr AF, Carr MH, Meylan AB (1978) The ecology and migrations of sea turtles 7, the west Caribbean green turtle colony. *Bull Am Mus Nat Hist* 162:1–48
- Castellote M, Leeney RH, O'Corry-Crowe G, Lauhakangas R, Kovacs KM, Lucey W, Krasnova V, Lydersen C, Stafford KM, Belikov R (2013) Monitoring white whales (*Delphinapterus leucas*) with echolocation loggers. *Polar Biol* 36:493–509
- Castillo JC, Serrano-Cuerda J, Fernández-Caballero A, López MT (2009) Segmenting Humans from Mobile Thermal Infrared Imagery. In: Springer, Berlin, Heidelberg, p 334–343
- Castro ALF, Rosa RS (2005) Use of natural marks on population estimates of the nurse shark, *Ginglymostoma cirratum*, at Atol das Rocas Biological Reserve, Brazil. *Environ Biol Fishes* 72:213–221
- Cattarinich X (2001) Pro-poor tourism initiatives in developing countries : Analysis of secondary case studies. *Pro-Poor Tour*:1–91
- Chin CLM, Moore SA, Wallington TJ, Dowling RK (2000) Ecotourism in bako national park, borneo: Visitors' perspectives on environmental impacts and their management. *J Sustain Tour* 8:20–35
- Coles T, Polandb RHC, Clifton J (2015) Ecotourism in an educational context: Promoting learning opportunities through travel. *J Biol Educ* 49:213–217
- Committee on Taxonomy. (2014). List of marine mammal species and subspecies. Society for Marine Mammalogy. Available at: <https://www.marinemammalscience.org/species-information/list-of-marine-mammal-species-subspecies/>. (Accessed: 3 January 2018).
- Constantine R (1999) Effects of tourism on marine mammals in New Zealand. Department of Conservation. Wellington, New Zealand.
- Constantine R, Brunton DH, Dennis T (2004) Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biol Conserv* 117:299–307

Cordes LS, Thompson PM (2015) Mark-resight estimates of seasonal variation in harbour seal abundance and site fidelity. *Popul Ecol* 57: 467–472

Corkeron PJ (2004) Whale watching, iconography, and marine conservation. *Conservation Biology* 18(3), 847–849.

Costa DP, Gales NJ (2013) Energetics of a Benthic Diver : Seasonal Foraging Ecology of the Australian Sea Lion , *Neophoca cinerea*. *Ecological Monographs*. 73:27–43

Culik BM, Wilson RP, Bannasch R (1993) Flipper-bands on penguins: what is the cost of a life-long commitment? *Mar Ecol Prog Ser* 98:209–214

Cunningham L, Baxter JM, Boyd IL, Duck CD, Lonergan M, Moss SE, McConnell B(2008) Harbour seal movements and haul-out patterns: implications for monitoring and management. *Aquat Conserv.*, Volume 19, Issue 4, pp 398-407

Curtin S, Richards S, Westcott S (2009) Tourism and grey seals in south Devon: Management strategies, voluntary controls and tourists' perceptions of disturbance. *Curr Issues Tour* 12:59–81

Cutler TL, Swann DE (1999) Using Remote Photography in Wildlife Ecology: A Review. *Wildlife Soc B.*, Vol. 27, No. 3 pp. 571-581

Dai C, Zheng Y, Li X (2007) Pedestrian detection and tracking in infrared imagery using shape and appearance. *Comput Vis Image Underst* 106:288–299

Dajun W, Sheng L, McShea WJ, Fu LM (2006) Use of remote-trip cameras for wildlife surveys and evaluating the effectiveness of conservation activities at a nature reserve in Sichuan Province, China. *Environ Manage* 38:942–951

Dans SL, Crespo EA, Pedraza SN, Degradi M, Garaffo G V. (2008) Dusky dolphin and tourist interaction: Effect on diurnal feeding behavior. *Mar Ecol Prog Ser* 369:287–296

Das M, Chatterjee B (2015) Ecotourism: A panacea or a predicament? *Tour Manag Perspect* 14:3–16

Davis M, Renouf D (1987). Social behaviour of harbour seals. *Phoca vitulina*, on haulout grounds at Miqueulon. *Canadian Field Naturalist*, 101(1), 1–5

Davis RW, Fuiman LA, Williams TM, Collier SO, Hagey WP, Kanatous SB, Kohin S, Horning M (1999) Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 283:993– 996. doi:10.1126/science.283.5404.993

Davies TK, Stevens G, Meekan MG, Struve J, Rowcliffe JM (2012) Can citizen science monitor whale-shark aggregations? Investigating bias in mark-recapture modelling using identification photographs sourced from the public. *Wildl Res* 39:696–704

Dean MJ, Hoffman WS, Zemeckis DR, Armstrong MP (2014) Fine-scale diel and gender-based patterns in behaviour of Atlantic cod (*Gadus morhua*) on a spawning ground in the Western Gulf of Maine. *ICES J Mar Sci J du Cons* 71:1474–1489

DeMares R, Krycka K (1998) Wild-animal triggered peak experiences:

Transpersonal aspects. *J Transpers Psychol* 30:161–177

Desholm M (2003) Thermal Animal Detection System (TADS). Development of a method for estimating collision frequency of migrating birds at offshore wind turbines. Natl Environ Res Institute, Denmark 27 pp - NERI Tech Rep No 440:27

Ditchkoff SS, Raglin JB, Smith JM, Collier B a (2005) From the field: capture of white-tailed deer fawns using thermal imaging technology. *Wildl Soc Bull* 33:1164–1168

Dixon DR (2003). A non-invasive technique for identifying individual badgers *Melesmeles*. *Mammal Review* 33, 92–94

Duffus DA, Dearden P (1993) Recreational Use, Valuation, and Management, of Killer Whales (*Orcinus orca*) on Canada's Pacific Coast. *Environ Conserv* 20:149

Dutton DL, Dutton PH, Chaloupka M, Boulon RH (2005) Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. *Biol Conserv* 126:186–194

Dyck MG, Baydack RK (2004) Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill , Manitoba , Canada. 116:343–350

Eberhardt LL, Chapman DG, Gilbert JR (1979) A review of marine mammal census methods. *Wildlife Monographs*. 63:3-46

Ellenberg U, Mattern T, Seddon PJ, Jorquera GL (2006) Physiological and reproductive consequences of human disturbance in Humboldt penguins: The need for species-specific visitor management. *Biol Conserv* 133:95–106

Engelhard GH, Baarspul AN., Broekman M, Creuwels JC., Reijnders PJ. (2002) Human disturbance, nursing behaviour, and lactational pup growth in a declining southern elephant seal (*Mirounga leonina*) population. *Can J Zool* 80:1876–1886

Evans PGH, Hammond PS (2004). Monitoring cetaceans in European waters. *Mam- mal Review* 34, 131–156

Evans PGH, Wang J (2003) Re-examination of distribution data for the harbour porpoise around Wales and the UK with a view to site selection for this species. Report to Countryside Council for Wales. Sea Watch Foundation, Oxford. 115pp

Fedak M (2004) Marine animals as platforms for oceanographic sampling: a “win / win ” situation for biology and operational oceanography. *Mem Natl Inst Polar Res Spec Issue*:133–147

Fernández-Caballero A, Castillo JC, Martínez-Cantos J, Martínez-Tomás R (2010) Optical flow or image subtraction in human detection from infrared camera on mobile robot. *Rob Auton Syst* 58:1273–1281

Finkler W, Higham J (2004) The Human Dimensions of Whale Watching: An Analysis Based on Viewing Platforms. *Hum Dimens Wildl* 9:103–117

- Foster RJ, Harmsen BJ, Doncaster CP (2016) Habitat Use by Sympatric Jaguars and Pumas Across a Gradient of Human Disturbance in Belize. *Association for Tropical Biology and Conservation*. 42:724–731
- Fraser WR, Carlson JC, Duley PA, Holm EJ, Patterson L (1999) Using Kite-Based Aerial Photography for Conducting Adélie Penguin Censuses in Antarctica *Water birds: Waterbirds*., Vol. 22, No. 3, pp. 435-440
- French SS, González-Suárez M, Young JK, Durham S, Gerber LR (2011) Human disturbance influences reproductive success and growth rate in California sea lions (*Zalophus californianus*). *PLoS One* 6:e17686
- Gaston AJ, Pelletier M, Eberl C, Mallory ML (2014) Incubation shifts of northern fulmars *Fulmarus glacialis* in the Canadian high Arctic determined by digital photography. *Polar Biol* 37:261–267
- Gerondeau M, Barbraud C, Ridoux V, Vincent C, (2007) Abundance estimate and seasonal patterns of grey seal (*Halichoerus grypus*) occurrence in Brittany, France, as assessed by photo-identification and capture–mark–recapture. *Journal of the Marine Biological Association of the United Kingdom*, 87, 365–372
- Gerrodette T, Gilmartin WG (1990) Demographic Consequences of Changed Popping and Hauling Sites of the Hawaiian Monk Seal. *Conserv Biol* 4:423–430
- Gill RMA, Thomas ML, Stocker D (1997). The use of portable thermal imaging for estimating deer population density in forest habitats. *Journal of Applied Ecology* 34: 1273- 1286.
- Glick D (1991). Tourism in Greater Yellowstone: maximising the good, minimising the bad, eliminating the ugly. In T. Whelan (Ed.), *Nature tourism: Managing for the environment* (pp. 58–74). Washington, DC: Island Press.
- Goebel ME, Perryman WL, Hinke JT, Krause DJ, Hann NA, Gardner S, LeRoij DJ (2015) A small unmanned aerial system for estimating abundance and size of Antarctic predators. *Polar Biol* 38:619–630
- Gonzalez RC, Woods RE (2001) *Digital Image Processing*, 2nd ed.; Addison-Wesley Longman Publishing Co., Inc.: Boston, MA, USA
- Granquist SM, Sigurjonsdottir H (2014) The effect of land based seal watching tourism on the haul-out behaviour of harbour seals (*Phoca vitulina*) in Iceland. *Appl Anim Behav Sci* 156:85–93
- Green RJ, Higginbottom K. (2000). The effects of non-consumptive wildlife tourism on free ranging wildlife: a review. *Pacific Conservation Biology*, 6, 183–197
- Grémillet D, Enstipp MR, Boudiffa M, Liu H (2006) Do cormorants injure fish without eating them? An underwater video study. *Mar Biol* 148:1081–1087
- Griffin LP, Brownscombe JW, Gagné TO, Wilson ADM, Cooke SJ, Danylchuk AJ (2017) Individual-level behavioral responses of immature green turtles to snorkeler disturbance. *Oecologia* 183:909–917
- Gucu AC, Gucu G, Orek H. (2004) Habitat use and preliminary demographic evaluation of the critically endangered Mediterranean monk seal (*Monachus*

- monachus*) in the Cilician Basin (Eastern Mediterranean). *Biol Conserv.*, 116:417–431
- Gucu A (2009) Preliminary study on the effects of photo traps used to monitor Mediterranean monk seals *Monachus monachus*. *Endanger Species Res* 10:281–285
- Gunn MD, Cousins CR (2018) mars surface context cameras past, present, and future. *Earth and Space Science*.pp144-162.
- Hammill MO, Stenson GB (2000) Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. *J Northwest Atl Fish Sci* 26:1–23
- Hammond PS (1990). Heterogeneity in the Gulf of Maine? Estimating humpback whale population size when capture probabilities are not equal. In *Individual Recognition of Cetaceans: Use of Photo-identification and Other Techniques to Estimate Population Parameters* (Hammond, P. S., Mizroch, S. A. & Donovan, G. P., eds), pp. 135–139. Cambridge: International Whaling Commission
- Hammond, P.S., Macleod, K., Berggren, P., Borchers, D.L., Burt, L., Canadas, A., Desportes, G., Donovan, G.P., Gilles, A., Gillespie, D., Gordon, J., Hiby, L., Kuklik, I., Leaper, R., Lehnert, K., Leopold, M., Lovell, P., Oien, N, Vasquez, J.A. (2013) Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. *Biol Conserv.* 164:107-122.
- Harkonen T, Harding KC, Lunneryd G. (1999) Age and sex specific behaviour in harbour seals *Phoca vitulina* leads to biased estimates of vital population parameters. *Journal of Applied Ecology.* 36, pp-825-841.
- Harting A, Baker J, Becker B (2004). Non-metrical digital photo-identification system for the Hawaiian monk seal. *Marine Mammal Science* 20, 886–895
- Havens KJ, Sharp EJ, Havens KJ, Shabp EJ (1998) Using Thermal Imagery in the Aerial Survey of Animals Published by : Wiley on behalf of the Wildlife Society Using thermal imagery in the aerial survey of animals. *Wildl Soc Bull* 26:17–23
- Hayes CT, Baumbach DS, Juma D, Dunbar SG (2017) Impacts of recreational diving on hawksbill sea turtle (*Eretmochelys imbricata*) behaviour in a marine protected area. *J Sustain Tour* 25:79–95
- Hays GC, Bradshaw CJA, James MC, Lovell P, Sims DW (2007) Why do Argos satellite tags deployed on marine animals stop transmitting? *J Exp Mar Bio Ecol* 349:52–60
- Hazekamp AAH, Mayer R, Osinga N (2010) Flow simulation along a seal: The impact of an external device. *Eur J Wildl Res* 56:131–140
- Heithaus MR, Marshall GJ, Buhleier BM, Dill LM (2001) Employing Crittercam to

- study habitat use and behavior of large sharks. *Mar Ecol Prog Ser* 209:307–310
- Heithaus MR, McLash JJ, Frid A, Dill LM, Marshall GJ (2002) Novel insights into green sea turtle behaviour using animal-borne video cameras. *J Mar Biol Assoc UK* 82:1049–1050. doi:10.1017/S0025315402006689
- Hendrickson J (1958). The green sea turtle, *Chelonia mydas* (Linn.) In Malaya and Sarawak. In: Proceedings of the Zoological Society of London 130, 455–535.
- Henry E, Hammill MO (2001) Impact of small boats on the haulout activity of harbour seals in Metis Bay, Saint Lawrence Estuary, Quebec, Canada. *Aquat Mamm.* 27.2,140-148
- Higginbottom K, Tribe A (2004) Contributions of Wildlife Tourism to Conservation. Common Ground Publishing, Australia. pp 99–123
- Higham JES (1998) Tourists and albatrosses: the dynamics of tourism at the Northern Royal Albatross Colony, Taiaroa Head, New Zealand. *Tour Manag* 19:521–531
- Higham JES, Bejder L, Williams R (2014) Whale-watching : sustainable tourism and ecological management.
- Higham JES, Luck M (2007) Marine Wildlife Tourism Management: Insights from the Natural and Social Sciences (JES Higham and M Luck, Eds.). CABI International, Oxfordshire
- Hodgson A, Kelly N, Peel D, Fenton B (2013) Unmanned Aerial Vehicles (UAVs) for Surveying Marine Fauna: A Dugong Case Study. *PLoS One* 8
- Hoekendijk JPA, Vries J de, Bolt K van der, Greinert J, Brasseur S, Camphuysen KCJ, Aarts G (2015) Estimating the spatial position of marine mammals based on digital camera recordings. *Ecol Evol* 5:578–589
- Hoover-Miller A, Bishop A, Prewitt J, Conlon S, Jezierski C, Armato P (2013) Efficacy of voluntary mitigation in reducing harbor seal disturbance. *J Wildl Manage* 77:689–700
- Hoyt E (2005) Sustainable Ecotourism on Atlantic Islands, With Special Reference To Whale Watching, Marine Protected Areas and Sanctuaries for Cetaceans Sustainable Ecotourism on Atlantic Islands, With Special Reference To Whale Watching, Marine Protected Areas and San. *Proc R Irish Acad* 105:141–154
- Hoyt E, Hvenegaard GT (2002) A review of whale-watching and whaling with applications for the Caribbean. *Coast Manag* 30:381–399
- Hughes P (2001) Animals, values and tourism - structural shifts in UK dolphin tourism provision. *Tour Manag* 22:321–329
- Hughes M, Morrison Saunders A (2005) Interpretation, activity participation and environmental attitudes of visitors to Penguin Island, Western Australia. *Society and Natural Resources*, 18. 7:611-624.
- Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Flemming JEM, Whoriskey FG (2015) Aquatic animal telemetry: A panoramic window into the underwater world.

Science (80-) 348:1255642

Hutchinson, Alan E (1980) Estimating Numbers of Colonial Nesting Seabirds : A Comparison of Techniques. Proc Colon Waterbird Group, 3:235–244

Ingham SE (1967) Branding elephant seals for life history studies. Polar Rec (Gr Brit) 13:447–449

IUCN (2016). The IUCN Red List of Threatened Species. Version 2016-1. Available at: www.iucnredlist.org. (Accessed: 3 January 2018).

Jacobson, Susan. K ., Lopez AF (1994) Biological Impacts of Ecotourism : Tourists and Nesting Turtles in Tortuguero National Park , Costa Rica. Wildl Soc Bull 22:414–419

Jaine FRA, Rohner CA, Weeks SJ, Couturier LIE, Bennett MB, Townsend KA, Richardson AJ (2014) Movements and habitat use of reef manta rays off eastern Australia: Offshore excursions, deep diving and eddy affinity revealed by satellite telemetry. Mar Ecol Prog Ser 510:73–86

Jaquet N, Gendron D, Coakes A (2003) Sperm whales in the Gulf of California: Residency, movements, behavior and the possible influence of variation in food supply. Mar Mammal Sci 19:545–562

Jefferson TA, Smultea MA, Courbis SS, Campbell GS (2016) Harbor porpoise (*Phocoena phocoena*) recovery in the inland waters of Washington: estimates of density and abundance from aerial surveys, 2013–2015. Can J Zool 94:505–515

Johnson WM, Lavigne DM (1999) Mass tourism and the Mediterranean monk seal. The role of mass tourism in the decline and possible future extinction of Europe's most endangered marine mammal, *Monachus monachus*. Monachus Guard 2:62–81

Jones GP, Pearlstine LG, Percival HF (1973) An Assessment of Small Unmanned Aerial Vehicles for Wildlife Research. Source Wildl Soc Bull 34:750–758

Jones, E.L., McConnell, B.J., Smout, S. et al. (2015) Patterns of space use in sympatric marine colonial predators reveal scales of spatial partitioning. Marine Ecology Progress Series, 534, 235–249

Karanth KU, Nichols JD, Kumar NS, Hines JE (2006) Assessing tiger population dynamics using photographic capture-recapture sampling. Ecology 87:2925–2937

Karlsson O, Hiby L, Lundberg T, Jussi M, Jussi I, Helander B (2005) Photo-identification, site fidelity, and movement of female gray seals (*Halichoerus grypus*) between haul-outs in the Baltic sea. Ambio 34, 628–634.

Kelly MJ (2001). Computer-aided photograph matching in studies using individual identification: an example from Serengeti cheetahs. Journal of Mammalogy 82, 440–449.

Kelly BP, Badajos OH, Kunnsaranta M, Moran JR, Martinez-Bakker M, Wartzok D, Boveng P (2010) Seasonal home ranges and fidelity to breeding sites among

ringed seals. *Polar Biol* 33:1095–1109

Kelly MJ, Noss AJ, Bitetti MS Di, Maffei L, Arispe RL, Paviolo A, Angelo CD De, Blanco YE Di (2008) Estimating Puma Densities from Camera Trapping across Three Study Sites: Bolivia, Argentina, and Belize. *J Mammal* 89:408–418

Kenyon N, Phillott AD, Alford RA (2009). Evaluation of the photographic identification method (PIM) as a tool to identify adult *Litoria genimaculata* (Anura: Hylidae) *Herpetological Conservation and Biology* 4, 403–410

King DA, Stewart WP (1996) Ecotourism and commodification: protecting people and places. *Biodivers Conserv* 5:293–305

Kirkwood R, Boren L, Shaughnessy P, Szteren D, Mawson P, Hückstädt L, Hofmeyr G, Oosthuizen H, Schiavini A, Campagna C, Berris, M. (2003) Pinniped-focused tourism in the Southern Hemisphere: a review of the industry. In: Gales, N., Hindell, M. and Kirkwood, R. (eds) *Marine Mammals: Fisheries, Tourism and Management Issues*. CSIRO Publishing, Collingwood, Victoria, pp. 245–264

Klinck H, Nieukirk SL, Mellinger DK, Klinck K, Matsumoto H, Dziak RP (2012) Seasonal presence of cetaceans and ambient noise levels in polar waters of the North Atlantic. *J Acoust Soc Am* 132:EL176-EL181

Koh LP, Wich SA (2012) Dawn of drone ecology: low-cost autonomous aerial vehicles for conservation. *Mongabay.com Open Access J -Tropical Conserv Sci* Mongabay.com Open Access J -Tropical Conserv Sci Trop Conserv Sci 55

Koivuniemi M, Aitulla M, Niemi M, Levanen R, Kunnasranta M (2016) Photo-ID as a tool for studying and monitoring the endangered Saimaa ringed seal. *Endanger Species Res:Vol. 30: 29-36*

Koski WR, Allen T, Ireland D, Buck G, Smith PR, Macrender AM, Halick MA, Rushing C, Sliwa DJ, McDonald TL (2009) Evaluation of an unmanned airborne system for monitoring marine mammals. *Aquat Mamm* 35:347–357

Kovacs KM, Innes S (1990) The impact of tourism on harp seals (*Phoca groenlandica*) in the Gulf of St. Lawrence, Canada. *Appl Anim Behav Sci* 26:15–26

Kriebler M, Barrette C (1984) Aggregation Behaviour of Harbour Seals at Forillon National Park, Canada Source. *J Anim Ecol* 53:913–928

Krüger O (2005) The role of ecotourism in conservation: Panacea or Pandora's box? *Biodivers Conserv* 14:579–600

Lai PH, Nepal SK (2006) Local perspectives of ecotourism development in Tawushan Nature Reserve, Taiwan. *Tour Manag* 27:1117–1129

Lake SE, Burton HR, Hindell MA, (1997) Influence of time of day and month on Weddell seal haul-out patterns at the Vestfold Hills, Antarctica. *Polar Biol.* 18: 319–324

Landres PB, Verner J, Thomas JW, Landres PB, Verner J (1988) Society for Conservation Biology Ecological Uses of Vertebrate Indicator Species : A Critique Ecological Uses of Vertebrate Indicator Species : A Critique. 2:316–328

- LaRue MA, Rotella JJ, Garrott RA, Siniff DB, Ainley DG, Stauffer GE, Porter CC, Morin PJ (2011) Satellite imagery can be used to detect variation in abundance of Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica. *Polar Biol.* Volume 34 pp 1727-1737.
- Leeney RH, Broderick AC, Mills C, Sayer S, Witt MJ, Godley BJ (2010) Abundance, distribution and haul-out behaviour of grey seals (*Halichoerus grypus*) in Cornwall and the Isles of Scilly, UK.
- Leong, Jorge K, Smith, David L, Revera, Dickie B, Clary III, Lt. John C, Lewis DH, Scott, Janis L, DiNuzzo, Anthony R (1989) Health care and diseases of captive reared sea turtles.pdf. Proc First Int Symp Kemp's ridley sea Turt Biol Conserv Manag TAMU-SG-89-105
- Leprieur F, Hickey MA, Arbuckle CJ, Closs GP, Brosse S, Townsend CR (2006) Hydrological disturbance benefits a native fish at the expense of an exotic fish. *J Appl Ecol* 43:930–939
- Lewis JP (1987) An evaluation of a census-related disturbance of Stellar sea lions. MSc thesis, University of Alaska, Fairbanks, Alaska.
- Lidgard DC (1996) The effects of human disturbance on the maternal behaviour and performance of grey seals (*Halichoerus grypus*) at Donna Brook, Lincolnshire, England. Preliminary Report to the British Ecological Society, UK.
- Limpus CJ, Miller JD, Parmenter CJ, Reimer D, McLachlan N, Webb R (1992) Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from Eastern Australian rookeries. *Wildl Res* 19:347–358
- Limpus CJ, Chaloupka M (1997) Nonparametric regression modelling of green sea turtle growth rates (southern Great Barrier Reef). *Mar Ecol Prog Ser* 144:1–12
- Lin R, Clowsley AH, Jayasinghe ID, Baddeley D, Soeller C (2017) Algorithmic corrections for localization microscopy with sCMOS cameras - characterisation of a computationally efficient localization approach. *Opt Express* 25:11701
- Lindsey PA, Alexander RR, Toit JT Du, Mills MGL (2005) The potential contribution of ecotourism to African wild dog *Lycaon pictus* conservation in South Africa. *Biol Conserv* 123:339–348
- Lonergan M, Duck CD, Thompson D, Moss S, McConnell BJ (2011). British grey seal (*Halichoerus grypus*) abundance in 2008: an assessment based on aerial counts and satellite telemetry. *ICES J. Mar. Sci.* 68. 2201–2209.
- Luck M (2003) Education on marine mammal tours as agent for conservation—but do tourists want to be educated? *Ocean Coast Manag* 46:943–956
- Lydersen C, Krafft BA, Andersen M, Kovacs KM (2002) Marine mammals in the Bellsund- Van Mijenfjorden - Van Keulenfjorden area. New investigations and status of knowledge. Norsk Polarinstitut.
- Lynch PT, Alderman R, Hobday JA (2015) A high resolution panorama camera system for monitoring colony-wide seabird nesting behaviour. *Methods Ecol Evol*

- Macdonald DW, Tattersall F, (2001) *Britain's Mammals: The Challenge for Conservation*. People's Trust for Endangered Species, London.
- Maffei L, Cuéllar E, Noss A (2004) One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *262:295–304*
- Malisiewicz T, Gupta A, Efros A (2011) Ensemble of Exemplar-SVMs for Object Detection and Beyond.
- Marion JL, Reid SE (2007) Minimising Visitor Impacts to Protected Areas: The Efficacy of Low Impact Education Programmes. *J Sustain Tour 15:5–27*
- Marschall S, Granquist SM, Burns GL (2017) Interpretation in wildlife tourism: Assessing the effectiveness of signage on visitor behaviour at a seal watching site in Iceland. *J Outdoor Recreat Tour 17:11–19*
- Marshall AD, Pierce SJ (2012) The use and abuse of photographic identification in sharks and rays. *J Fish Biol 80:1361–1379*
- Masters D (1998) *Marine Wildlife Tourism: Developing a Quality Approach in the Highlands and Islands*. [Report] Tourism and Environment Initiative and Scottish Natural Heritage, Inverness, Scotland.
- Martín-López B, Montes C, Benayas J (2007) The non-economic motives behind the willingness to pay for biodiversity conservation. *Biol Conserv 139:67–82*
- Matson PA a, Parton WJJ, Power AGG, Swift MJJ (1997) Agricultural intensification and ecosystem properties. *Science 277:504–509*
- Matthiopoulos J, McConnell B, Duck C, Fedak M(2004) Using satellite telemetry and aerial counts to estimate space use by grey seals around the British Isles. *J. Appl. Ecol., Volume 41, Issue 3, pp 476-491*
- Mayes G, Dyer P, Richins H (2004) Dolphin-human Interaction: Pro-environmental Attitudes, Beliefs and Intended Behaviours and Actions of Participants in Interpretation Programs: A Pilot Study. *Ann Leis Res 7:34–53*
- McMahon CR, Hindell MA, Harcourt RG (2012) Publish or perish: Why it's important to publicise how, and if, research activities affect animals. *Wildl Res 39:375–377*
- McMahon CR, Howe M, van den Hoff J, Alderman R, Brotsma H, Hindell M (2014) Satellites, the All-Seeing Eyes in the Sky: Counting Elephant Seals from Space. *PlosOne*.
- Meadows D. (2004). Behavior of green sea turtles in the presence and absence of recreational snorkellers. *Marine Turtle Newsletter, 103,1?4. R*
- Miller JD (1997) Reproduction in sea turtles. In: Lutz PL, Musick JA (eds) *Biology of sea turtles*. CRC Press, Boca Raton, FL, p 51–81
- Miller PJO, Biassoni N, Samuels A, Tyack PL (2000) Whale songs lengthen in response to sonar. *Nature 405, 903*
- Moll RJ, Millspaugh JJ, Beringer J, Sartwell J, He Z (2007) A new 'view' of ecology and conservation through animal-borne video systems. *Trends Ecol Evol 22:660–668*.

- Monson DH, Udevitz MS, Jay C V. (2013) Estimating Age Ratios and Size of Pacific Walrus Herds on Coastal Haulouts using Video Imaging. *PLoS One* 8
- Morrison MA, Francis MP, Hartill BW, Parkinson DM, (2002) Diurnal and tidal variation in the abundance of the fish fauna of a temperate tidal mudflat. *Estuar Coast Shelf Sci* 54: 793–807
- Muloin S (1998). Wildlife tourism: The psychological benefits of whale watching. *Pacific Tourism Review*, 2, 199– 213.
- Musick JA, Limpus CJ (1997) Habitat utilisation and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*. CRC Press, Boca Raton, FL, p 137–165
- Musyl MK, Domeier ML, Nasby-Lucas N, Brill RW, McNaughton LM, Swimmer JY, Lutcavage MS, Wilson SG, Galuardi B, Liddle JB (2011) Performance of pop-up satellite archival tags. *Mar Ecol Prog Ser* 433:1–28
- Nichols WJ, Seminoff JA, Resendiz, A. (1998). Plastic "Roto-tags" may be linked to sea turtle bycatch. *Marine Turtle Newsletter*, 79, 20-21.
- O'Brien TG (2008) On the use of automated cameras to estimate species richness for large- and medium-sized rainforest mammals. *Anim Conserv* 11:179–181
- O'Brien TG, Kinnaird MF, Wibisono HT (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Anim Conserv* 6:131–139
- O'Connell, Allan F, Nichols, James D, Ullas Karanth K *Camera Traps in Animal Ecology*.
- O'Connor S, Campbell R, Cortez H, Knowles T (2009) Whale watching worldwide: tourism numbers, expenditures and expanding economic benefits. a Spec Rep from Int Fund Anim Welf:295
- Orams MB (1997) Historical accounts of human-dolphin interaction and recent developments in wild dolphin based tourism in Australasia. *Tour Manag* 18:317–326
- Orams MB (2000) Tourists getting close to whales, is it what whale-watching is all about? *Tour Manag* 21:561–569
- Orsini J-P and DN (2005) Human perceptions of hauled out Australian sea lions (*Neophoca cinerea*) and implications for management: A case study from Carnac Island, Western Australia. *Tour Mar Environ* 2(1)23-37
- Orsini J-P, Shaughnessy PD, Newsome D (2006) Impacts of human visitors on Australian Sea Lions (*Neophoca cinerea*) at Carnac Island, Western Australia: Implications for tourism management. *Tour Mar Environ* 3:101–115
- Osinga N, Nussbaum SB, Brakefield PM, Udo de Haes HA (2012) Response of common seals (*Phoca vitulina*) to human disturbances in the Dollard estuary of the Wadden Sea. *Mamm Biol* 77:281–287
- Osterrieder S, Salgado Kent C, Robinson R (2015) Variability in haul-out

- behaviour by male Australian sea lions *Neophoca cinerea* in the Perth metropolitan area, Western Australia. *Endanger Species Res* 28:259–274
- Park B-K, Lumeng JC, Lumeng CN, Ebert SM, Reed MP (2015) Child body shape measurement using depth cameras and a statistical body shape model. *Ergonomics* 58:301–309
- Parsons ECM (2003) Seal Management in Scotland: Tourist Perceptions and the Possible Impacts on the Scottish Tourism Industry. *Curr Issues Tour* 6:540–546
- Paterson, W.D., Redman, P., Hiby, L.A., Moss, S.E.W., Hall, A.J., Pomeroy, P. (2013) Pup to adult photo-ID: Evidence of pelage stability in grey seals. *Marine Mammal Science*. 29: 537-541.
- Patterson B (2012) Communities, Cameras and Conservation. *The Science Teacher*. Pages 40–45
- Pearson HC, Jones PW, Srinivasan M, Lundquist D, Pearson CJ, Stockin KA, Machovsky-Capuska GE (2017) Testing and deployment of C-VISS (cetacean-borne video camera and integrated sensor system) on wild dolphins. *Mar Biol* 164:1–8
- Peterson, R. S. and Bartholomew, G. A. J. (1967) Natural history and behaviour of the California sea lion. *American Society of Mammalogists Special Publication* 1.
- Pomeroy PP, Twiss SD, Redman P (2000) Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology* 106:899–919
- Pomeroy, P., O'Connor, L., Davies, P. (2015) Assessing use of and reaction to unmanned aerial systems in grey and harbour seals during breeding and moulting in the UK. *Journal of Unmanned Vehicle Systems*. 3:102-113.
- Priede IG, Merrett NR (1996) Community Studies: Part II Estimation of abundance of abyssal demersal fishes ; a comparison of data from trawls and baited cameras. *J Fish Biol* 49:207–216
- Prime JH, Hammond PS (1990) The Diet of Grey Seals from the South-Western North Sea Assessed from Analyses of Hard Parts Found in Faeces. *J Appl Ecol* 27:435–447
- Pyenson ND, Vermeij GJ, Norris R, Turner SK, Hull P, Ridgwell A, Vermeij G, Vermeij G, Sarko D, Domning D, Marino L, Reep R, Clementz M, Hoppe K, Koch P, Muizon C de, McDonald H, Salas R, Urbina M, Pyenson N, Sponberg S, Domning D, Vélez-Juarbe J, Fleming A, Clark C, Calambokidis J, Barlow J, Evans A, Churchill M, Clementz M, Kohno N, Pyenson N, Jacobs D, Haney T, Louie K, Bolton J, Villafaña J, Rivadeneira M, Pyenson N, Herman F, Seward D, Valla P, Carter A, Kohn B, Willett S, Ehlers T, Vermeij G, Friedman M, Shimada K, Martin L, Everhart M, Liston J, Maltese A, Triebold M, Parham J, Pyenson N,

- Klug C, Baets K de, Kröger B, Bell M, Korn D, Payne J (2016) The rise of ocean giants: maximum body size in Cenozoic marine mammals as an indicator for productivity in the Pacific and Atlantic Oceans. *Biol Lett* 12:492–498
- Quiros AL (2007) Tourist compliance to a Code of Conduct and the resulting effects on whale shark (*Rhincodon typus*) behavior in Donsol, Philippines. *Fish Res* 84:102–108
- Radford PJ, Summers CF, Young KM, (1978) A Statistical procedure for estimating Grey seal pup production from a single census. *Mammal rev.* Vol 8, Nos. 1 and 2, 34-42
- Rae BB (1968) The food of seals in Scottish waters. *Mar Res.* 2:23.
- Rand RW (1950) Branding in Field-Work on Seals. *J Wildl Manage* 14:128–132
- Reder S, Lydersen C, Arnold W, Kovacs KM (2003) Haul-out behaviour of High Arctic harbour seals (*Phoca vitulina vitulina*) in Svalbard, Norway. *Polar Biol* 27: 6–16
- Ribeiro J, Bentes L, Coelho R, Gonçalves JMS (2006) Seasonal, tidal and diurnal changes in fish assemblages in the Ria Formosa lagoon (Portugal). *Estuar Coast Shelf Sci* 67: 461–474
- Riedman M (1990) The pinnipeds : seals, sea lions, and walruses. University of California Press
- Ritchie EG (2013) Conservation: relaxed laws imperil Australian wildlife. *Nature* 498:434
- Rodger K, Moore SA, Newsome D (2007) Wildlife Tours in Australia: Characteristics, the Place of Science and Sustainable Futures. *J Sustain Tour* 15:160–179
- Rowat D, Speed CW, Meekan MG, Gore M (2009). Population abundance and apparent survival of the Vulnerable whale shark, *Rhincodon typus*, in the Seychelles aggregation. *Oryx* 43, 591–598.
- Rowcliffe JM, 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
- Sayer S, Hockley C, Witt MJ, (2012). Monitoring grey seals (*Halichoerus grypus*) in the Isles of Scilly during the 2010 pupping season. Natural England Commissioned Reports, Number 103.
- Sakamoto KQ, Takahashi A, Iwata T, Trathan PN (2009) From the Eye of the Albatrosses: A Bird-Borne Camera Shows an Association between Albatrosses and a Killer Whale in the Southern Ocean (RL Earley, Ed.). *PLoS One* 4:e7322
- Scarpaci C, Nuggeoda D, Corkeron PJ (2017) Tourists' Perspectives on Dolphin Watching in Bocas Del Toro, Panama. *Tour Mar Environ* 12:79–94
- Schaefer KM, Fuller DW (2013) Simultaneous behavior of skipjack (*Katsuwonus pelamis*), bigeye (*Thunnus obsesus*), and yellowfin (*T. albacares*) tunas, within large multi-species aggregations associated with drifting fish aggregating devices (FADs) in the equatorial eastern Pacific Ocean. *Mar Biol* 160:3005–

Schänzel HA, McIntosh AJ (2000) An Insight into the Personal and Emotive Context of Wildlife Viewing at the Penguin Place, Otago Peninsula, New Zealand. *J Sustain Tour* 8:36–52

Scheffer M, Carpenter S, Young B de (2005) Cascading effects of overfishing marine ecosystems. *Trends Ecol Evol* 20:577–579

Scheidat M, Friedlaender A, Kock KH, Lehnert L, Boebel O, Roberts J, Williams R (2011) Cetacean surveys in the Southern Ocean using icebreaker-supported helicopters. *Polar Biol* 34:1513–1522

Scheyvens R (2008) Current Issues in Tourism Exploring the Tourism-Poverty Nexus Exploring the Tourism-Poverty Nexus. *Curr Issues Tour* 3500:37–41

Schmid JR (1995) Marine turtle populations on the east- central coast of Florida: results of tagging studies at Cape Canaveral, Florida, 1986–1991. *Fish Bull* 93:139–151

Schofield G, Katselidis KA, Dimopoulos P, Pantis JD (2008) Investigating the viability of photo-identification as an objective tool to study endangered sea turtle populations. *J Exp Mar Bio Ecol* 360:103–108

SCOS (2016). Scientific Advice on Matters Related to the Management of Seal Populations: 2016. SCOS, Sea Mammal Research Unit161.

SCOS (2015) Grey seal and harbour seal indicators for the Marine Strategy Framework Directive. SCOS, Sea Mammal Research Unit161.

Sears R, Williamson JM, Wenzel FW, Berube M, Gendron D, Jones P (1990). Photographic identification of the blue whale (*Balaenoptera musculus*) in the Gulf of St. Lawrence, Canada. Report of the International Whaling Commission 1990, 335–342.

Sedberry GR, Loefer JK (2001) Satellite telemetry tracking of swordfish, *Xiphias gladius*, off the eastern United States. *Mar Biol* 139:355–360

Shackley M (1996). Wildlife tourism. London: International Thomson Business Press.

Shaughnessy PD, Nicholls AO, Briggs S V. (2008) Do Tour Boats Affect Fur Seals at Montague Island, New South Wales? *Tour Mar Environ* 5:15–27

Silveira L, Jacomo ATA, Diniz-Filho JAF (2003) Camera trap, line transect census and track surveys: a comparative evaluation. *Biol. Conserv.*, 114, 351–355.

Singh H, Can A, Eustice R, Lerner S, McPhee N, Pizarro O, Roman C (2004) Seabed AUV Offers New Platform for High-Resolution Imaging. *Eos (Washington DC)* 85:160

Skibins JC, Powell RB, Hallo JC (2013) Charisma and conservation: Charismatic megafauna's influence on safari and zoo tourists' pro-conservation behaviors. *Biodivers Conserv* 22:959–982

Smale DA, Kendrick GA, Harvey ES, Langlois TJ, Hovey RK, Niel KP Van, Waddington KI, Bellchambers LM, Pember MB, Babcock RC, Vanderklift MA, Thomson DP, Jakuba M V., Oscar Pizarro⁶ and SBW (2012) Regional-scale benthic monitoring for ecosystem-based fisheries management (EBFM) using an autonomous underwater vehicle (AUV). *ICES J Mar Sci* 69:1108–1118

Smith EA(1964). A seals symposium: 63-74. Mimeographed Proceedings. Edinburgh: Nature Conservancy

Sollmann R, Furtado MM, Gardner B, Hofer H, Jácomo ATA, Tôrres NM, Silveira L (2011) Improving density estimates for elusive carnivores: Accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biol Conserv* 144:1017–1024

Sorice MG, Shafer CS, Ditton RB (2006) Managing endangered species within the use-preservation paradox: The Florida manatee (*Trichechus manatus latirostris*) as a tourism attraction. *Environ Manage* 37:69–83

Springer AM, Estes JA, van Vliet GB, Williams TM, Doak DF, Danner EM, Forney KA, Pfister B (2003). Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences USA* 100:12223–12228. Strange, I. 1979. Sealion survey in the Falklands. *Oryx* 15:175– 184.

Stafford-Bell R, Scarr M, Scarpaci C (2012) Behavioural responses of the Australian Fur Seal (*arctocephalus pusillus doriferus*) to vessel traffic and presence of swimmers in port phillip bay, Victoria, Australia. *Aquat Mamm* 38:241–249

Steen KA, Villa-Henriksen A, Therkildsen OR, Green O (2012) Automatic Detection of Animals in Mowing Operations Using Thermal Cameras. *Sensors* 12:7587–7597

Stevick PT, Palsbøll PJ, Smith TD, Bravington MV, Hammond PS (2001). Errors in identification using natural markings: rates, sources, and effects on capture–recapture estimates of abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 1861–1870.

Strong, P. and Morris, S.R. (2010). Grey seal (*Halichoerus grypus*) disturbance, ecotourism and the Pembrokeshire Marine Code around Ramsey Island. *Journal of Ecotourism*, 9:2, 117-132.

Summers CF (1974) The Grey Seal (*Halichoerus grypus*) in Cornwall and the Isles of Scilly. *Biol Conserv* 6:285–291

Sun H, Wang C, Wang B, El-Sheimy N (2011) Pyramid binary pattern features for real-time pedestrian detection from infrared videos. *Neurocomputing* 74:797–804

Surendran A, Sekar C (2011) A Comparative Analysis on the Socio-economic Welfare of Dependents of the Anamalai Tiger Reserve (ATR) in India. *Margin J Appl Econ Res* 5:361–379

Thaxter CB, Burton NHK (2009) High Definition Imagery for Surveying Seabirds and Marine Mammals: A Review of Recent Trials and Development of

Protocols.

Thompson PM, Fedak MA, McConnell BJ, Nicholas KS (1989) Seasonal and Sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *J Appl Ecol* 26:521–535

Tisdell C, Wilson C (2005) Perceived Impacts of Ecotourism on Environmental Learning and Conservation: Turtle Watching as a Case Study. *Environ Dev Sustain* 7:291–302

Trave C, Brunnschweiler J, Sheaves M, Diedrich A, Barnett A (2017) Are we killing them with kindness? Evaluation of sustainable marine wildlife tourism. *Biol Conserv* 209:211–222

Tremblay Y, Thiebault A, Mullers R, Pistorius P (2014) Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. *PLoS One* 9

Troëng S, Evans DR, Harrison E, Lagueux CJ (2005) Migration of green turtles *Chelonia mydas* from Tortuguero, Costa Rica. *Mar Biol* 148:435–447

Trolle M, Kéry M (2005) Camera-trap study of ocelot and other secretive mammals in the northern Pantanal. *Mamm.* 69:3,405-412

Twiss SD, Duck C, Pomeroy PP (2003) Grey seal (*Halichoerus grypus*) pup mortality not explain by local breeding density on North Rona, Scotland. *J. Zoo.,Lond.* 259, 83-91

Tillmann J (2009) Fear of the Dark : Night-Time Roosting and Anti-Predation Behaviour in the Grey Partridge (*Perdix perdix L .*) *Behaviour.* 146.7:999-1023

United Kingdom Tourism Survey. (2004). Retrieved January 1st, 2018, from <http://www.tourismtrade.org.uk/MarketIntelligenceResearch/DomesticTourismStatistics/UKTS/UKTS.asp>

University of California, Davis One Shields Avenure, Davis, CA 95616 [Internet] Definition of Environmental Wellness [cited 2018 Feb 9]. Available: <https://shcs.ucdavis.edu/wellness/environmental>

Vale TR, Vale GR, Journal S, Jun N, Vale TR, Vale GR (2016) Suburban Bird Populations in West-Central California. *Journal of Biogeography*:3:157–165

Van Bommel ACV (1956). Planning a census of the harbour seal (*Phoca vitulina*) on the coasts of the Netherlands. *Beaufortia*, 54:121-132

Vanbianchi C, Gaines WL, Murphy MA, Pither J, Hodges KE (2017) Habitat selection by Canada lynx: making do in heavily fragmented landscapes. *Biodivers Conserv* 26:3343–3361

van Gemert JC, Verschoor CR, Mettes P, Epema K, Koh LP, Wich S, others (2014) Nature Conservation Drones for Automatic Localization and Counting of Animals. *ECCV Work*:255–270

Vanhatalo J, Vetemaa M, Herrero A, Aho T, Tiilikainen R. (2014) By-Catch of Grey Seals (*Halichoerus grypus*) in Baltic Fisheries—A Bayesian Analysis of Interview Survey. *PLoS ONE* 9(11)

- Venables VM, Venables LSV. (1955). Observation on a breeding colony of the seal, *Phoca vitulina*, in Shetland. Proc. Zool. Soc. London, 125:521-532.
- Vermeulen E, Cammareri A, Holsbeek L (2012) Alteration of southern right whale (*Eubalaena australis*) behaviour by human-induced disturbance in Bahía San Antonio, Patagonia, Argentina. Aquat Mamm 38:56–64
- Vermeulen C, Lejeune P, Lisein J, Sawadogo P, Bouché P (2013) Unmanned Aerial Survey of Elephants (AL Roca, Ed.). PLoS One 8:e54700
- Vincent C, Fedak MA, McConnell BJ, Meynier L, Saint-Jean C, Ridoux V (2005) Status and conservation of the grey seal, *Halichoerus grypus*, in France. Biol. Conserv. 126, 62–73
- Viviant M, Trites AW, Rosen DAS, Monestiez P, Guinet C (2010) Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. Polar Biol 33:713–719
- Wagner D, Kurina L (1997) The influence of ants and water availability on oviposition behaviour and survivorship of a facultatively ant-tended herbivore. Ecol Entomol 22:352–360
- Wakefield CB (2010) Annual, lunar and diel reproductive periodicity of a spawning aggregation of snapper *Pagrus auratus* (Sparidae) in a marine embayment on the lower west coast of Australia. J Fish Biol 77: 1359–1378
- Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM, Bolten AB, Chaloupka MY, Hutchinson BJ, Alberto Abreu-Grobois F, Amorocho D, Bjorndal KA, Bourjea J, Bowen BW, Dueñas RB, Casale P, Choudhury BC, Costa A, Dutton PH, Fallabrino A, Girard A, Girondot M, Godfrey MH, Hamann M, López-Mendilaharsu M, Marcovaldi MA, Mortimer JA, Musick JA, Nel R, Pilcher NJ, Seminoff JA, Troëng S, Witherington B, Mast RB (2010) Regional Management Units for Marine Turtles: A Novel Framework for Prioritizing Conservation and Research across Multiple Scales. PLoS One 5:1–11
- Weitzman J, Heyer C den, Bowen DW (2017) Factors influencing and consequences of breeding dispersal and habitat choice in female grey seals (*Halichoerus grypus*) on Sable Island, Nova Scotia. Oecologia 183:367–378
- Westcott, S.M. and Stringell, T.B.(2004) Grey seal distribution and abundance for North Wales, 2002-2003. Bangor,CCW Marine Monitoring Report No: 13. 80pp
- Westcott SM, Stringell TV (2005) Field observations on the disturbance of grey seals in North Wales, 2003, Bangor,UK: Countryside Council for Wales. Marine Monitoring Report No 15
- Wheeller B (1992) Is progressive tourism appropriate? Tour Manag 13:104–105
- Whitfield Gibbons J, Scott DE, Ryan TJ, Buhlmann KA, T.D. T, Metts BS, Greene JL, Mills T, Leiden Y, Poppy S, Winne CT (2000) The Global decline of reptiles, Deja Vu Amphibians. Bioscience 50:653–666
- Wiggers EP, Beckerman, Scott F (1993) Use of Thermal Infrared Sensing to

Survey White-Tailed Deer Populations. *Wildlife Society Bulletin* (1973-2006), 21,3: 263-268

Williams TM, Davis RW, Fuiman LA, Francis J, Le Boeuf BJ, Horn- ing M, Calambokidis J, Croll DA (2000) Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* 288:133– 136. doi:10.1126/science.288.5463.133

Wilson B, Hammond PS, Thompson P. (1999) Estimating Size and Assessing Trends in a Coastal Bottlenose Dolphin Population. *Ecol Appl* 9:288–300

Witt MJ, Baert B, Broderick AC, Formia A, Fretey J, Gibudi A, MOUNGUENGUI GAM, Moussounda C, Ngouessono S, Parnell, Richard J. Roumet D, Sounguet G-P, Verhage B, Zogo A, Godley BJ (2009) Aerial surveying of the world's largest leatherback turtle rookery: A more effective methodology for large-scale monitoring. *Biol Conserv* 142:1719–1727

Witt MJ, Hardy T, Johnson L, McClellan CM, Pikesley SK, Ranger S, Richardson PB, Solandt JL, Speedie C, Williams R, Godley BJ (2012) Basking sharks in the northeast Atlantic: Spatio-temporal trends from sightings in UK waters. *Mar Ecol Prog Ser* 459:121–134

Witzeil, W. 1998. Messages in bottles. *Marine Turtle Newsletter*, 80, 1-3

Würsig B, Lynn SK, Jefferson T. A., Mullin KD (1998) Behaviour of cetaceans in the northern Gulf of Mexico relative to survey ships and aircraft. *Aquat Mamm* 24:41–50

Supplemental Material

Supplemental Table 1.

Description of the average discrepancy between perceived counts of seals and actual counts of seals from images when undertaking method proofing analysis of flipbook method.

Month	Date	Year	Perceived Count			Actual Count			N Difference (Seals)	N Difference (Photo)
			Photo ID Number	Time (24 hr)	Count	Photo ID Number	Time (24 hr)	Count		
January	5	2015	9300	09:40	125	9299	09:35	133	9	-1
February	9	2014	4024	17:04	4	4024	17:05	4	0	0
March	9	2015	286	07:36	51	285	07:30	54	3	-1
April	19	2014	3534	10:50	49	3536	11:00	54	5	2
May	14	2014	6072	08:21	17	6071	08:15	19	2	1
June	11	2015	1499	09:28	8	1499	09:30	8	0	0
July	7	2015	68	12:24	10	68	12:25	10	0	0
August	18	2014	6002	14:16	12	6002	14:15	12	0	0
September	17	2014	1966	08:10	29	1966	08:10	29	0	0
October	6	2014	5871	11:45	69	5871	11:45	69	0	0
November	26	2014	133	12:10	50	133	12:10	50	0	0
December	22	2014	6625	13:40	119	6625	13:40	119	0	0

Supplemental Table 2.

Supplemental table of survey effort and counts determined from time lapse cameras (July 2013-October 2015).

Day	Jul-13	Aug-13	Sep-13	Oct-13	Nov-13	Dec-13	Jan-14	Feb-14	Mar-14	Apr-14	May-14	Jun-14	Jul-14	Aug-14	Sep-14	Oct-14	Nov-14	Dec-14	Jan-15	Feb-15	Mar-15	Apr-15	May-15	Jun-15	Jul-15	Aug-15	Sep-15	Oct-15
1	0	26	38	3	30	81	62	2	84	106	44	0	0	0	52	64	56	92	58	NA	110	239	50	9	24	1	1	19
2	0	42	46	22	72	76	2	3	93	98	47	0	0	0	33	66	49	NA	24	NA	116	156	26	12	22	0	25	21
3	0	18	1	21	21	56	13	3	51	85	49	0	0	0	35	55	75	NA	83	NA	72	117	41	20	1	0	32	12
4	0	3	1	32	85	36	3	22	90	104	42	0	0	0	9	80	75	64	125	NA	104	NA	40	27	0	10	34	17
5	0	0	3	19	65	60	47	39	64	103	60	0	0	0	0	70	45	62	NA	NA	117	NA	48	22	0	39	NA	53
6	0	13	20	5	83	118	78	1	79	72	44	0	0	0	0	69	50	72	NA	NA	173	NA	39	16	10	42	NA	31
7	0	6	35	7	63	87	62	4	77	125	88	0	0	0	43	65	55	69	NA	NA	176	49	53	11	40	0	NA	84
8	0	0	24	10	66	100	6	22	149	171	49	0	0	0	29	61	53	49	NA	NA	115	81	43	6	34	0	3	48
9	0	0	53	53	38	65	30	39	154	197	79	0	0	0	19	50	98	135	NA	NA	142	69	29	3	2	39	1	41
10	0	0	69	54	45	80	30	4	67	156	23	0	0	0	5	82	84	62	NA	NA	188	101	57	8	17	20	26	62
11	0	0	74	54	60	44	29	8	84	84	19	0	0	0	0	44	100	17	NA	NA	NA	99	70	0	40	52	52	56
12	0	0	40	32	50	60	61	24	118	126	45	0	0	2	1	46	NA	101	NA	NA	NA	144	29	5	42	39	NA	45
13	0	4	38	49	45	34	20	12	156	84	45	0	0	0	0	43	NA	123	NA	NA	NA	117	35	4	51	73	NA	NA
14	0	0	36	33	50	21	82	88	97	51	17	1	0	0	2	62	NA	86	NA	NA	NA	NA	13	4	22	35	NA	NA
15	0	0	38	42	39	32	60	42	95	61	21	0	0	0	2	44	NA	120	NA	NA	NA	NA	51	0	22	6	NA	NA
16	15	0	51	51	22	99	23	48	101	61	12	0	0	0	5	76	NA	97	NA	NA	NA	68	44	0	31	1	NA	NA
17	NA	2	58	50	32	116	17	NA	NA	48	13	0	0	0	29	75	NA	71	NA	NA	NA	78	59	5	23	0	NA	NA
18	NA	28	16	64	44	13	57	NA	NA	57	7	0	0	12	45	71	NA	93	NA	NA	NA	59	33	19	14	1	NA	NA
19	NA	14	40	33	35	20	4	NA	NA	49	19	0	0	11	5	106	NA	91	NA	NA	NA	NA	47	2	3	0	NA	NA
20	NA	0	42	35	23	41	2	NA	NA	37	12	0	0	1	6	83	NA	97	NA	NA	NA	NA	65	5	11	1	NA	NA
21	NA	0	18	44	72	62	54	NA	NA	66	21	0	0	0	5	59	NA	79	NA	NA	NA	82	58	12	27	12	NA	NA
22	NA	0	3	52	75	18	67	NA	NA	121	18	0	0	7	23	83	NA	119	NA	NA	NA	66	34	23	15	13	NA	NA
23	NA	1	5	42	63	13	NA	NA	NA	50	29	0	0	9	11	81	NA	65	NA	NA	NA	54	21	0	14	58	NA	NA
24	NA	10	27	62	77	13	NA	NA	NA	83	33	0	0	0	24	60	NA	77	NA	NA	NA	NA	30	1	31	48	NA	NA
25	NA	37	25	54	82	39	NA	NA	NA	82	18	0	0	0	13	68	NA	81	NA	NA	NA	NA	44	5	10	59	19	NA
26	NA	49	35	3	72	64	NA	NA	NA	34	7	0	0	0	19	55	50	29	NA	NA	NA	NA	22	1	44	67	10	NA
27	NA	36	22	3	80	3	NA	NA	NA	25	0	0	0	21	7	75	91	25	NA	NA	NA	98	24	37	65	64	6	NA
28	NA	15	49	9	59	17	NA	NA	NA	86	16	0	0	33	22	54	55	NA	NA	NA	NA	115	23	32	89	58	12	NA
29	NA	12	28	93	44	87	NA	NA	NA	49	9	0	0	46	47	54	51	NA	NA	NA	NA	91	32	9	14	33	NA	NA
30	NA	16	10	4	NA	6	NA	NA	NA	36	5	0	0	67	40	51	78	NA	NA	NA	NA	76	11	NA	11	NA	NA	NA
31	NA	43	NA	4	NA	18	NA	NA	NA	NA	0	NA	0	58	NA	52	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Supplemental Figure 1.

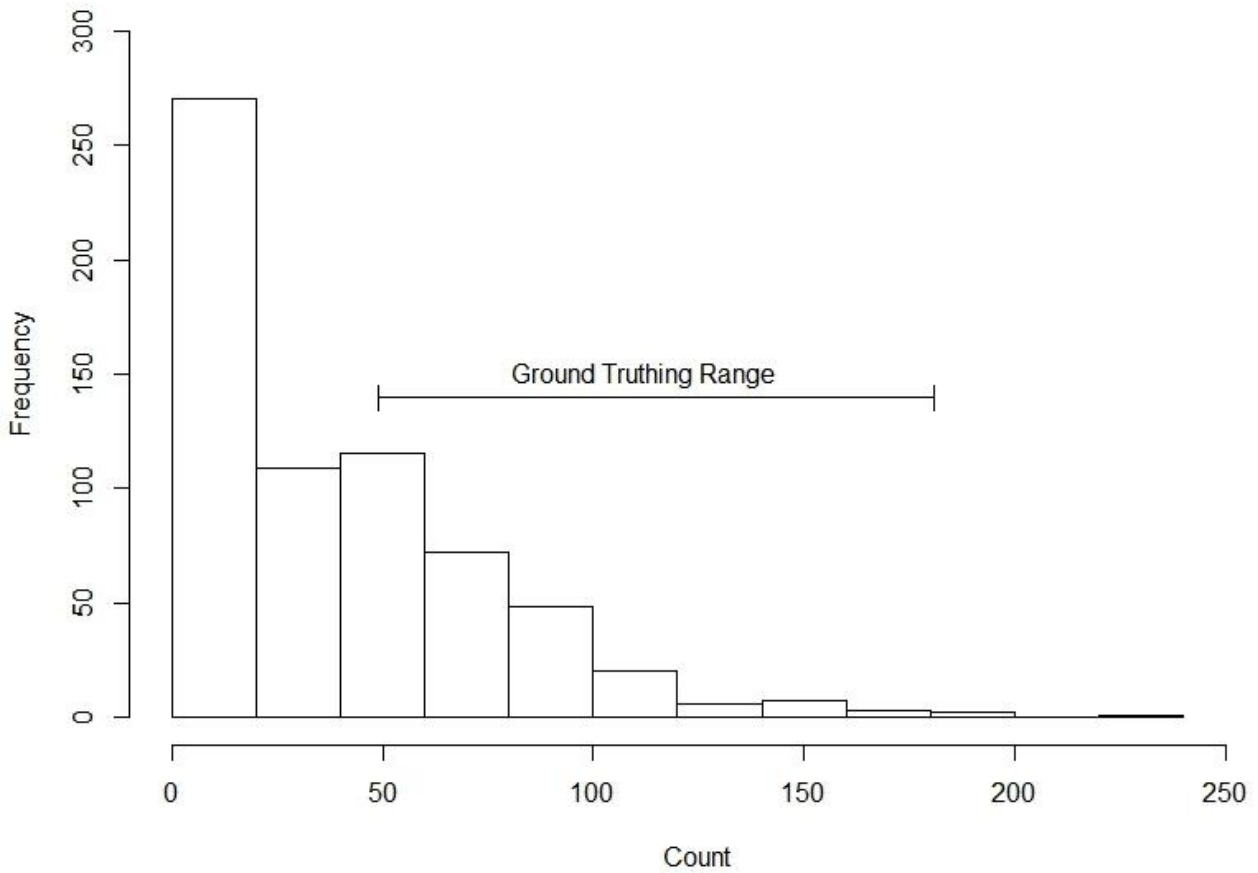


Figure 1. Frequency histogram of counts between July 2013-October 2015 determined from time-lapse cameras. Ground truthing range specified on figure, 30% of all counts fell between the ground truthing range. Ground truthing analysis was undertaken on the 21st November 2017.