# AN INTRODUCTION TO SATELLITE TECHNOLOGIES FOR TRACKING WILDLIFE

Written by

ZSL

Supported by

WILDLABS.NET

[ The conservation technology network ]

# An introduction to satellite technologies for tracking wildlife

---

*Kate Moses*[1], *Lydia Katsis*[2], *Phoebe Griffith*[1], *Rachael Kemp*[1], *Anthony Dancer*[1]

*1- Zoological Society of London, 2- University of Southampton*

*The authors are indebted to all of the people who kindly agreed to share their images and case studies with us. We also thank Stephanie O'Donnell and Talia Speaker for reviewing sections of the report.*

Cover Image: Satellite tagged green turtle ***(Chelonia mydas)***, (c) Miguel Varela

WILDLABS.NET
[ The conservation technology network ]

# Contents

# Contents

Suggested citation:

Moses, K., Katsis, L., Griffith, P., Kemp, R., and Dancer, A. (2022) An introduction to satellite technologies for tracking wildlife. London, U.K.: Zoological Society of London.

# FAQ

N.B. Throughout the document, when we refer to a satellite 'tag', we are referring to all types of attachments, including collars.

## What is a satellite tag?

Satellite tags are devices that periodically collect data on the location of the study animal to which they are attached, and generally use either GPS or ARGOS satellite technology to estimate the animal's position. In some cases, location data is also transmitted to the person conducting the research, via satellite. Tags can include additional sensors that capture data other than location, for example, speed of travel or height flown. Tag size, weight, and mode of attachment depend on the study species.

## Overview of tracking technologies

There are a variety of types of devices for tracking the location of individual animals, including, but not limited to, satellite tags (see Table 1). This guide focuses on technologies that use satellites for location acquisition (GPS or Argos) and can, but do not always, use satellites to relay positional data to the end user. Biologging refers to the general methodology of attaching data-recording devices to animals, including for location tracking.

| Method | Description | Data acquisition and download |
|---|---|---|
| **VHF or UHF tags** (Very High Frequency or Ultra High Frequency radio telemetry) | The tag emits a radio frequency pulse signal which can be detected using a receiver and a directional antenna. The location of the animal is calculated manually through triangulation of multiple bearings. This was the first real-time technique used to track individual animals from a distance.<br>Data captured: location of animal but it the requires the user to be in close proximity to the study species in order to obtain the data point.<br>Example uses: Tracking terrestrial mammals to determine home range and habitat use. | A directional antenna and receiver are used to locate and observe the animal from the radio pulse, emitted by the tracking device. The observer must be in relatively close proximity to the study animal to determine location. |
| **Acoustic tags** | Commonly used to track marine animals, typically fish or turtles. Each tag emits a unique sound, which is picked up by acoustic receivers (hydrophones) deployed in the ocean, along with additional information captured by the tag (depth, water temperature). As the animal moves through a network of receivers, their behaviour is captured and revealed through data analysis.<br>Data captured: location of animal and may provide additional information such as depth and water temperature.<br>Example uses: tracking marine animals that do not surface, for example, fish. | The data captured by the receivers is either transmitted via satellite, or downloaded remotely from the ocean surface, or the receiver is retrieved, and the data downloaded. |

# FAQ

| | | |
|---|---|---|
| **Geolocators** (also referred to as GLS [Global Location Sensor] tracking or light level loggers) | Small, lightweight archival devices typically used to study (although not limited to) bird migration, which use light levels to determine their location.<br>Data captured: location of animal.<br>Example uses: tracking large-scale migratory movements. | Some require recapture of the animal to retrieve the data whereas others can relay the data via radio or satellite. |
| **GSM** (Global System for Mobile communications) | Anything that uses GSM communicates via the phone network. GPS devices, for example, may acquire their location via the GPS satellite constellation and then transmit the location data back to the researcher via GSM (so long as the study animal is located within an area with phone network coverage).<br>Data captured: location of animal and may provide additional information such as speed travelled at, hours and type of activity.<br>Example uses: tracking animals in areas with mobile coverage. | In areas with GSM coverage, data is sent to the user via the phone network. |
| **GPS** (Global Positioning System) | Tags with GPS receivers connect to four or more Earth orbiting GPS satellites, allowing them to triangulate their location and elevation to an accuracy of ~10m. GPS tags acquire their location by receiving data from at least four (ideally more for improved accuracy) GPS satellites.<br>Data captured: location of animal and additional sensors may provide information such as speed travelled at and types of activity.<br>Example uses: tracking animals in equatorial regions or where finer detail is required | A number of methods can be used to retrieve data, including: via the satellite network; via the GSM network; in-person retrieval (recapture of the animal, drop-off mechanism used or VHF or UHF radio used to transmit data); Bluetooth or WiFi. |
| **ARGOS doppler** | This only requires the receiver within the tag to connect to one satellite within the ARGOS constellation. Location resolution is typically less fine (150m-1000m) than when using GPS. ARGOS tags send out a radio signal to a satellite to determine the tag location.<br>Data captured: location of animal and additional sensors may provide information such as speed travelled at, hours and type of activity.<br>Example uses: tracking marine mammals, or other species where rapid location acquisition is required | A number of methods can be used to retrieve data, including: via the satellite network; via the GSM network; in-person retrieval (recapture of the animal, drop-off mechanism used or VHF or UHF radio used to transmit data); Bluetooth or WiFi. |

*Table 1. Overview of tracking technology options*

## How much does satellite tracking technology cost?

Satellite tracking technology is a relatively expensive option within the realm of wildlife tracking. The hardware (tags or collars) is expensive, especially in comparison to VHF or UHF counterparts, and there is an ongoing cost (monthly or annual) associated with data retrieval. Cost varies greatly depending on the study context and is often driven by the volume and type of data needed. It is difficult to make realistic cost estimates due to a lack of publicly available information, but as a ballpark estimate you can expect to pay approximately US$2,000-8,000/unit for satellite tags, each of which have additional data transmission costs associated with them. Examples of data costs for studies conducted before 2009, from Thomas, Holland and Minot (2011), ranged from $5-55 per data point. Additional costs to be factored in include the costs of deployment and repairs or replacement parts.

## Why use satellite tracking technology?

Satellite tracking technology enables collection of unbiased, high resolution animal location data at much greater scales than was previously possible with radio tracking technology, allowing the collection of rich datasets from a wide range of species in terrestrial and aquatic habitats. The data collected have contributed to our understanding of animal movement and behaviour, including habitat selection, migrations, home ranges, human-wildlife conflict, and the impact of climate change on species. These data are often critical for effective conservation and have been used to inform the suitability of proposed protected area plans and to assess the success of mitigation measures, including translocations of problematic animals.

## What level of expertise is needed to use them?

Considerable expertise is needed to plan a satellite tracking study, deploy devices on animals, and analyse the data. Planning a study requires a clear understanding of research objectives, type of data required, and proposed analytical methods, and a detailed knowledge of the study species and study area. This impacts design decisions, such as number and type of tags to deploy, and the duty cycle of the tags. Capture and restraint of the study species and determining a suitable attachment method requires expertise in animal capture and welfare. Attaching a tag to a new species (i.e., not previously tagged before) requires the involvement of a vet and is a legal requirement for tagging of any animal in some countries. For attaching a tag to a previously tagged species, training by (or inclusion of, within the team) an experienced individual is critical.

## Do I need satellite tags or would a non-satellite biologger (see Glossary, pg.10 for definition) suffice?

Satellite technology is generally preferred when tracking animals in large, remote, and/or inaccessible locations. Non-satellite biologgers may be more appropriate in certain contexts, including:

- If the study species is easily located and recaptured for physical tag recovery.
- If field work is confined to a small area with easy accessibility.
- If the study species' physiology precludes the use of relatively heavy satellite tags (e.g. the species is too small, lightweight, or delicate).
- When few data points are needed and/or deployment duration is brief.
- If available budget is low.

Thomas, Holland and Minot (2011) provide a useful decision tree that will help to determine the technology best suited to your work.

# FAQ

## What data do they capture?

At their most simple, satellite tags capture time-stamped geographic location data points (e.g. geographic position A at date and time B) (Figure 1). Typically, GPS tags offer greater location accuracy than ARGOS tags, but they are also slower to acquire a location fix, as GPS tags need to connect to 4 satellites (vs. 1 satellite for ARGOS). ARGOS tags may be better suited to instances where a location fix needs to be rapidly acquired, for example, when tracking marine species which surface infrequently (although note that fast-acquisition GPS is under development, e.g. Fastloc, Baseband).

Through the inclusion of additional sensors within a tag, it is also possible to record supplementary data, including, for example, depth, salinity, temperature, heart rate, acceleration, oxygen levels, light levels, pH, or altitude. However, there are energetic costs associated with the capture and transmission of these ancillary data, necessitating either larger and heavier batteries, or trade-offs with quantity of location data.

## How do I retrieve the data?

There are several ways that the data may be retrieved (Figure 1):

- Recapture the animal, then manually remove the data from the tag.
- Pre-programme the tag to release from the animal at a certain time, retrieve the tag from the field, then manually remove the data from the tag.
- Remotely download data from the tag when in close proximity to the animal using a VHF or UHF radio receiver (i.e., by a researcher in the field).
- Remotely download the data using a WiFi or Bluetooth connection (often via a base station).
- Relay the data back to the user from the tag via the cellular GSM network.
- Transmit the data back to the user on a pre-set schedule via various satellite networks (e.g. Iridium, ARGOS, Globalstar).

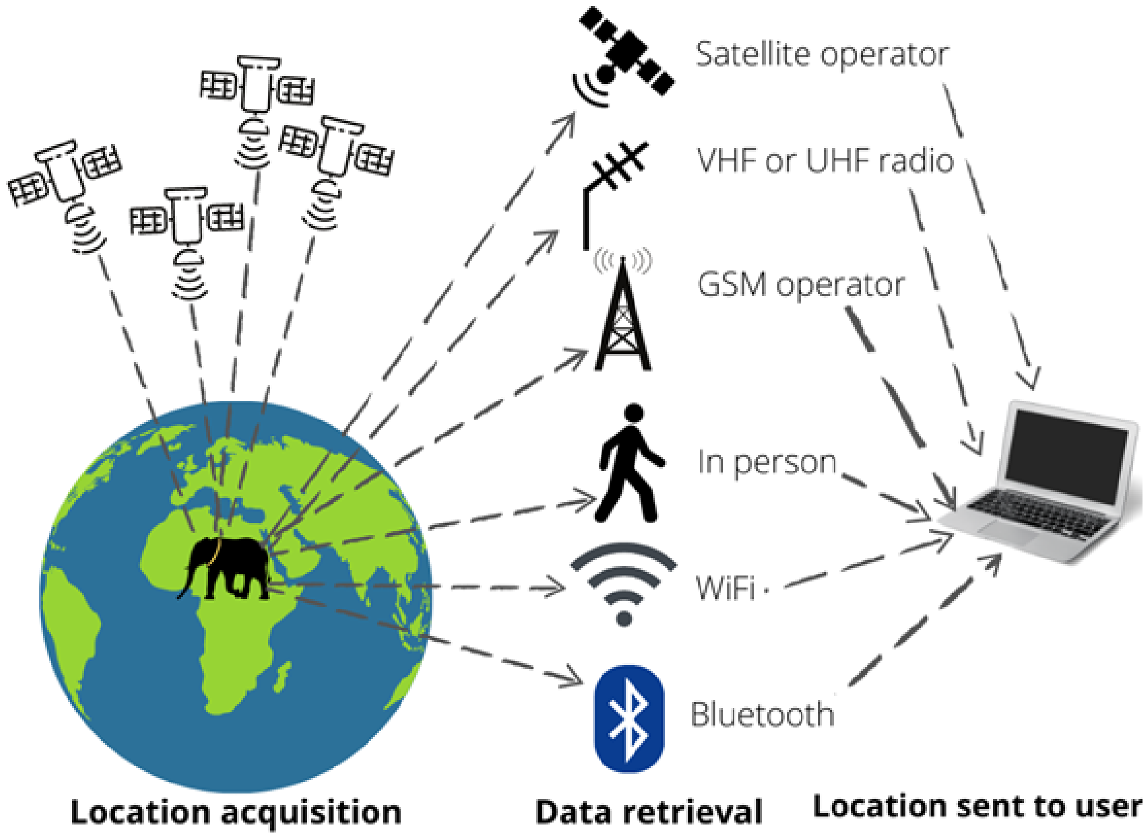


*Figure 1. A simplified overview of satellite location acquisition and data transmission methods.*

## Glossary of terms and abbreviations

**ARGOS**: Advanced Research and Global Observation Satellite network.

**Biologging:** The practice of attaching data-recording devices to animals. These devices can – but do not always – relay information back to the researcher. Technologies include satellite tags, video cameras, and accelerometers, amongst others.

**Duty cycle:** The cycle of operation for a device which operates intermittently (rather than continuously), i.e., the amount of time that the device is 'on' for.

**GPS**: Global Positioning System satellite network.

**GSM**: Global System for Mobile communications. If a device is GSM-enabled or compatible, it can transmit data via the cellular (phone) network.

**HWC**: Human-Wildlife Conflict.

**HWCx:** Human-Wildlife Coexistence.

**IoT**: Internet of Things. The interconnection (via the internet) of physical objects, enabling them to send and receive data. Devices that use IoT include fitness trackers, smart fridges, and smart home security systems.

**LoRa**: Abbreviation of 'Long Range'. A radio modulation technique used in Low-Power Wide-Area Networking (LPWAN). Enables wireless, long-range connectivity with battery-powered end devices.

**NB-IoT**: Narrowband Internet of Things. Another LPWAN radio technology standard developed for cellular devices.

**Sigfox:** The first service provider to use LPWAN to connect low-powered devices to the internet.

**Spatiotemporal**: 'Spatiotemporal data' refers to data that relate to both space and time, such as geographic locations with an associated timestamp. 'Spatiotemporal patterns' refer to phenomena inferred from the data collected, for example, how animal movements across a geographical area change over time.

**Telemetry**: The process of collecting and transmitting data from remote objects.

**UHF or VHF**: Ultra High Frequency or Very High Frequency. This refers to radio tags that were the precursor to satellite tracking and are still used in some instances today. The first real-time technique used to track animals from a distance.

# 1. Introduction

## 1.1 Who is this guide for?

There are a wealth of studies and reviews that document the ways in which satellite tracking is advancing our collective understanding of the wildlife with which we share our planet. However, these articles often assume some level of existing knowledge or focus on use of the technology to investigate specific research questions.

This guide aims to fill this gap and provide an introductory overview of satellite tracking technologies for users with minimal experience or understanding. It will enable readers to develop an understanding of the fundamental concepts in satellite tracking technology, prior to going on to do their own further context- and species-specific study.

## 1.2 What does this guide cover?

This guide provides an overview of the various satellite technologies available for tracking wildlife (Section 2) and how they work (Section 3), the different habitats they can be used in (Section 4), and research questions that they have been used to answer (Section 5). It also details some limitations of the technology (Section 6), things to consider ahead of beginning your own research (section 7) alongside a potted history of the technology's development (section 8).

## 1.3 What it does not cover

This guide is not intended to be an exhaustive review of the satellite tracking technology ecosystem. It is intended to provide an overview of the satellite tracking space and typical options available to users, and to familiarise the reader with the language, concepts, and considerations, which will enable them to do further individual reading and investigation, ahead of beginning any satellite tracking work.

Moreover, given the rapid pace of change, this guide does not reference nor recommend specific makes or models of tags, beyond providing a list of common tag providers in Appendix 1.

This guide also does not provide a detailed 'how to' for satellite tracking, in recognition of the fact that a) the underlying technology is rapidly evolving, and b) the use of said technology has to be carefully tailored to each species and context, with significant ethical and welfare considerations.

# 2. What is a Satellite Tag?

At their most basic, satellite tags collect data on the geographic location of study animals, along with a time and date stamp for each location point. Tags are attached to study animals to collect location data and, depending on their design, may relay this information remotely back to the user.

For clarity, when we use the umbrella term 'satellite tags' throughout this guide, we are referring to any of the following:

- Tags that collect positional information using satellites and then transmit that information to the researcher, also using satellites (e.g. ARGOS).
- Tags that collect positional information using satellites and then transmit it through non-satellite means, e.g. via another wireless connection, or through device retrieval. For example, some GPS satellite tags use cellular networks to transmit data.
- Tags that collect positional information (and other data) using a method other than satellites, and then transmit it using satellites (e.g. PSATs).

Satellite tags generally consist of three main components (Figure 2):

- **The payload**: The payload is the electronic element of the tag, responsible for collection, storage, and in some cases transmission of location data. Can also record movement and health information, amongst other data, by using 3-axis accelerometers, temperature sensors, heartbeat sensors, and even cameras.
- **The antenna:** Antennas on satellite trackers are used to send and/or receive radio or satellite signals. The choice of antenna will vary based on the study species and can be a PCB (Printed Circuit Board) antenna, or a chip or whip antenna.
- **An attachment mechanism:** To fit the device to the animal, whether via a collar, backpack, gluing the device directly on to the animal, or some other method. This will vary depending upon the species and the environment in which it lives, with different methods being used across terrestrial and marine environments.

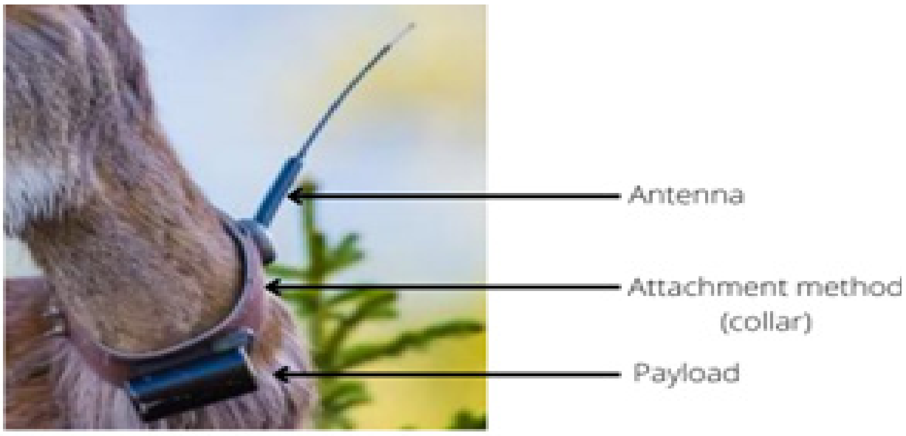


*Figure 2. The three main components of a satellite tag. In this instance a GPS collar on a deer species.*

## 2.1 Payloads

Payloads are the most important part of any tracking device. The payload generally consists of an enclosure containing tracking circuitry and a battery pack.

Enclosures are made of robust materials, such as polycarbonate or aluminium, or potting compounds like polyurethane. Some enclosures are designed to be opened to extract the tracking circuitry or to charge batteries, while others are hermetically sealed and use wireless communications and magnetic switches to control the electronics. The size and shape of the payload and the type of enclosure material will depend on the tracking technology being used, as this will affect circuitry and battery size. The design of the enclosure will vary substantially depending on the likely conditions after deployment, e.g. for aquatic species that dive to depth. Enclosure design will also consider how to minimise impacts on animal fitness, welfare, and behaviour, e.g. to minimise drag for aquatic or aerial species.

For location monitoring, a wide variety of technologies are available that provide a range of spatial and temporal resolutions. Some tracking devices can record location data accurately to within 10 m and provide hundreds of position fixes a day, while others may provide a location to within 1 km with just 1 fix a day. Choice of tracking device and frequency of position fixes will depend on the study species, the research question being answered, and the budget available.

Generally speaking, the higher the spatial and temporal resolution of the tracking device the greater the power consumption, and so the larger the battery that will be required. Researchers must thus strike a balance between spatiotemporal resolution, deployment longevity, and payload size and weight, while minimising negative effects on the animal. Weight is a critical consideration in terms of impacts, particularly for small animals and birds. A review of bird tracking studies found that more negative impacts were reported for heavier tags, and so recommended that device weight should be as low as practicable, and that researchers should rigorously assess the impact of tags on their study species (Geen et al., 2019). When considering the use of satellite tracking,  the weight and size of a tag are constrained by what is judged to be suitable for the animal to live with, whilst minimising any negative effects - this must be judged on a case-by-case ethical review (see ethics overview, pg. 47)

The simplest tracking devices – and therefore the cheapest – only store location data, rather than transmit it. This offers a number of advantages, in addition to lower cost, including smaller sizes and weights, and maximised battery life (as data transmission can be energy intensive). However, there are also drawbacks. To recover tracking data, the device must be physically retrieved and plugged into a computer for manual download. To retrieve the device, the animal must be found and recaptured (thus enduring further stress) and the device removed by the researcher, or a 'drop-off' mechanism deployed where the device comes off the animal and is recovered from the environment (Moen et al., 1996). Deploying a drop-off mechanism is ideal, where possible, as it saves an animal from the additional stress of recapture and further handling, but there is no guarantee that the data or device is retrievable. Devices may come off in inaccessible locations, such as down a small rocky crevasse which your study animal can easily traverse but you cannot, or the mechanism may fail, meaning you still need to capture your animal to retrieve your data. Users must also wait until the tag has been retrieved to know if data collection has been successful, and tag settings cannot be changed or updated after deployment.

Payloads may also contain communication technology to transmit recorded data without having to recover the device. This functionality has resulted in significant benefits within the field of wildlife tracking, including enabling (a) reduced data loss, (b) for data to be viewed and responded to in near real time (which is useful, for example, in human-wildlife conflict mitigation), and (c) 2-way configuration of tags once deployed in the field, (d) study animals to be located. Data transmission is achieved through a range of technologies, including radio telemetry, and cellular and satellite communications, which are covered in more detail below.

## 2.2 Antennas

An antenna is a metallic structure that transmits and/or captures electromagnetic radio waves. In transmission, they convert electric current within the antenna and radiate it out as electromagnetic radio waves. In reception mode, they intercept waves propagating through space and convert this into an electric current, which is then amplified by a receiver.

An antenna will also have a ground plane, which is a flat horizontal conducting surface that reflects radio waves from other antenna elements, and the shape, size, and orientation of this is important for antenna effectiveness.

Antennas come in a huge variety of shapes and sizes, and choice of antenna will depend on how they are to be used. Suppliers of tracking technology will advise on which antenna choice is most suitable for specific tracking needs, or on species -specific consideration (e.g. a whip antenna is generally inappropriate for species that live in complex vegetated environments, like swamps, as they may become entangled). Transmission antennas transmit locations from a deployed device to a satellite, or to a GSM, radio, VHF or UHF receiver. Receiver antennas receive this signal. Antennas can be omnidirectional or directional. Direction and efficiency depend on antenna dimension. High levels of direction and efficiency are hard to achieve with antennas that are smaller than half a wavelength.

A whip antenna is omnidirectional and radiates energy equally in all horizontal directions. These are often used for wildlife tags and collars to transmit locations to a receiver. Directional antennas used in radio tracking are typically Yagi-type (similar to a rooftop antenna used for television reception) and receive a signal from a device.

For VHF, devices are fitted with a whip or loop antenna that give off unique electromagnetic short-range radio signals, which can be decoded using a custom receiver and allow the animal to be located. The operator uses an antenna, attached to a receiver, which is programmed to the transmitter's frequency, to pick up the electromagnetic signals given off by the transmitter affixed to the target animal.

Receiver antennas may be hand-held, mounted on an object, or affixed to towers to avoid interference from buildings and trees. They may also be fixed to a vehicle, boat, or aircraft to allow the operator to exploit larger areas. They are available in a variety of forms and functions and produce a tone that increases in loudness or has a visual signal strength indicator that pulses as the operator approaches the transmitter (Ministry of Environment, 1998). Omnidirectional antennas have only one element and are used to determine the presence or absence of a signal, not its exact location. Elements are added segments of an antenna which increase the range of detectability of the receiver. Adcock antennas consist of two elements and are used to locate the direction of the signal. Loop antennas are small and useful for locating low frequency transmitters. The Yagi antenna contains 3 or 4 elements and is a strong, directional antenna commonly used to determine the location of a transmitter.

## 2.3 Attaching satellite tags

Before attaching a satellite tag, it is necessary (with a few exceptions) to capture the study animal, which will cause the animal distress. This is briefly discussed in section 7, 'Ethics overview' (pg. 47). To minimise negative effects on the study animal, it is essential to ensure that the expertise and equipment required for safe and ethical capture is in place.

There are a range of attachment options that are typically used. The most appropriate option will be determined by the physiology and behaviour of the species being tracked, and characteristics of the habitat in which the technology is deployed. See Table 2 and Figure 3 for example attachment options for a variety of taxa.

Great care must be taken to ensure that satellite tags are fitted safely to the study animal and to minimise any negative effects. Attachments can cause mild irritation, severe tissue damage, reduced fitness, behavioural changes, and even death.

There are multiple recorded instances of tracking devices negatively affecting study species (e.g. in terms of movement, reproduction, and behaviour) (Burnside et al., 2019). Consequently, it is critically important to follow best practice, including (a) reviewing the literature for suitable attachment techniques, (b) seeking guidance from technology manufacturers or retailers and from experienced users who have tagged the same species, in order to understand common pitfalls and strategies to minimise any negative effects, and (c) requesting approval for your study from an appropriate ethical review committee.

There are potential trade-offs between safe attachment method and optimal data gathering to be considered, which vary by species and context. For example, a harness may be the most suitable method for a bird that spends the majority of its time in open environments, but may cause unacceptable risk, for example, in crocodilians who spend their time in complex, vegetated habitats where they may become caught.

| Attachment type | Description | Example species |
|---|---|---|
| Collars | Designed with attachment in mind and so are generally easier to deploy. | Large carnivores; ungulates |
| Harnesses or backpacks | A small harness, whereby the tracker is fitted snugly to the animal and secured. | Large birds, e.g. skuas and bustards |
| **Direct attachment to animal** | | |
| Epoxy resin | Glues the base plate of the tag directly to the skin | Hard-shelled turtles; head of a pinniped |
| Piercing through carapace | The tag is attached by looping a line of stainless steel or monofilament through the ridge on the carapace | Soft-shelled turtles, e.g. leatherback |
| Piercing through dorsal fin | Attach the tag through a small hole in the dorsal fin. | Small cetaceans |
| GPS mounted tail logger | Loggers are taped or glued to the base of the central pair of flight feathers | Penguins; gulls; red-footed boobys |

*Table 2. Examples of tag attachment options and species on which they may be used*

## 2.4 Sourcing satellite tags

See Appendix 1 for a non-exhaustive list of common providers of satellite tags (in 2023). Note that these are not recommendations, and the solutions may not be suitable for your needs.

*Figure 3. Various attachment options: 1. Lioness with satellite tracking collar; 2. Tail Mounted GPS logger on a red footed booby (Image courtesy of Dr Malcolm Nicoll); 3. Satellite tracking equipment attached to the back of a Beluga whale using suction cups; 4. Green turtle with satellite tag attached using epoxy resin (Image courtesy of Dr Rita Patricio)*

# 3. How do satellite tags work?

Present-day wildlife tracking generally involves using technology to remotely observe the location and movement of free-ranging animals. Satellite tagging specifically typically involves attaching a device to a study animal to enable the location of the individual at a given time to be estimated, and then returning that spatiotemporal data to the researcher, either through physical collection or by some form of remote transmission. The 'satellite' element can be used to either acquire a location fix or to relay the data (or both). There are several other methods available to acquire location fixes or relay data that do not use satellites, which will also be described here. These can be used in various combinations, depending on the study species and the environment. Common combinations are described in Table 3.

| Method (location acquisition/data retrieval) | Description |
|---|---|
| Argos (satellite)/Argos (satellite) | Argos doppler is used to determine the location of the tag. Information is relayed to the user via the Argos network. |
| GPS (satellite)/Iridium (satellite) | GPS is used to acquire location and the Iridium satellite network is used to transmit data to the user. |
| GPS (satellite)/Globalstar (satellite) | GPS is used to acquire location and the Globalstar satellite network is used to transmit data to the user. |
| GPS (satellite)/Geostationary (satellite) | GPS is used to acquire location and a geostationary satellite system, for example Inmarsat, is used to transmit data to the user. |
| GPS (satellite)/GSM (non-satellite) | GPS is used to acquire location and the cellular GSM network is used to transmit data to the user. |
| GPS (satellite)/VHF or UHF (non-satellite) | GPS is used to acquire location and VHF or UHF is used to retrieve data when in close proximity to the study animal in the field. |
| GPS (satellite)/drop-off (non-satellite) | GPS is used to acquire location and stored on the tag. The tag is pre-programmed to release and then manually retrieved, after which the data download occurs. |
| GPS (satellite)/recapture (non-satellite) | GPS is used to acquire location and stored on the tag. The study animal is recaptured, the tag removed, and data downloaded. |
| Geolocation (non-satellite)/ Argos (satellite) | PSATs use geolocation to determine location (either light-based or a combination of ambient light and the Earth's magnetic field) and store data on the tag. The tag releases from the study animal based on a pre-determined schedule and floats to the surface, where it transmits data via the Argos network. |
| Passive Acoustic Monitoring (non-satellite)/Iridium (satellite) | Hydrophones capture data when tagged fish swim in close proximity. Information is relayed to a communication device that floats on the water's surface, and then to the user via the Iridium network. |

*Table 3. Common wildlife tracking methods that use satellite technologies for location acquisition and/or data transmission.*

## 3.1 Technologies used to collect location data

### 3.1.1 Non-satellite location acquisition

It is possible to determine tagged animal location without the use of satellite technology. The first three options discussed below both acquire their location and transmit their data via non-satellite methods, whereas the last two methods use satellites to transmit data.

The simplest location tracking devices use radio transmitters that continually send out a pulsed radio signal that can be picked up by a receiver tuned to that frequency. These repeated 'beeps' or 'pings' can be tracked by researchers using a directional antenna, which can locate an animal within a range of tens of metres. The radio channels used are Very-High Frequency (VHF, 30 MHz to 300 MHz) or Ultra-High Frequency (UHF, 300 MHz to 3 GHz). The main cost of these tracking devices will be researcher time to locate and record the animal's location (Palmintieri, 2017).

The next level up from this use radio triangulation, where a radio transmitting collar simultaneously contacts at least three fixed receivers to achieve a positional fix. Location information can then be sent to one of the receivers. Cellular tracking devices can also be used in this way to get a location and then transmit the location.

Low power radio protocols in development as part of the Internet of Things (IoT) revolution are increasing the options available for these types of radio devices, and there are now tags using a variety of protocols, including LoRa, Sigfox and NB-IoT (e.g. Maroto-Molina et al., 2019). (NB: IoT allows devices on closed private internet connections to communicate with others, e.g. smart fridges, smart watches, fitness trackers, etc.)

These non-satellite methods for collecting location data are lower power than satellite devices, and so can be smaller and lighter, provide more fixes per day, and/or remain active for longer, and can track animals over a range of hundreds to thousands of metres, depending on terrain. As more areas are covered with cellular reception and IoT infrastructure it is likely these devices will become more widely used.

Acoustic telemetry is one of the main methods used to track the movements of aquatic animals. It uses trackers that are internally or externally attached to an animal. The trackers emit a unique ping (or acoustic signal) that is detected by stationary or mobile passive acoustic receivers – small, data-logging computers, that 'listen' for tagged animals. Location data from multiple receivers can be combined to provide an approximate route of travel. There are networks of receivers deployed across large areas of the world within aquatic habitats, and collaborative groups and monitoring systems support regional and global tracking efforts.

Geolocation tags collect measurements of light levels that are used to estimate sunrise and sunset times, which can then be used to estimate animal movements. The tags are generally small and inexpensive and offer a solution for small animals or aquatic species, where satellite tracking cannot be used. However, the location estimates created from the data can have large errors, depending on animal location and time of year.

### 3.1.2 Satellite location acquisition

Tracking devices generally use one of two different satellite technologiesfor location acquisition: GPS or ARGOS doppler.

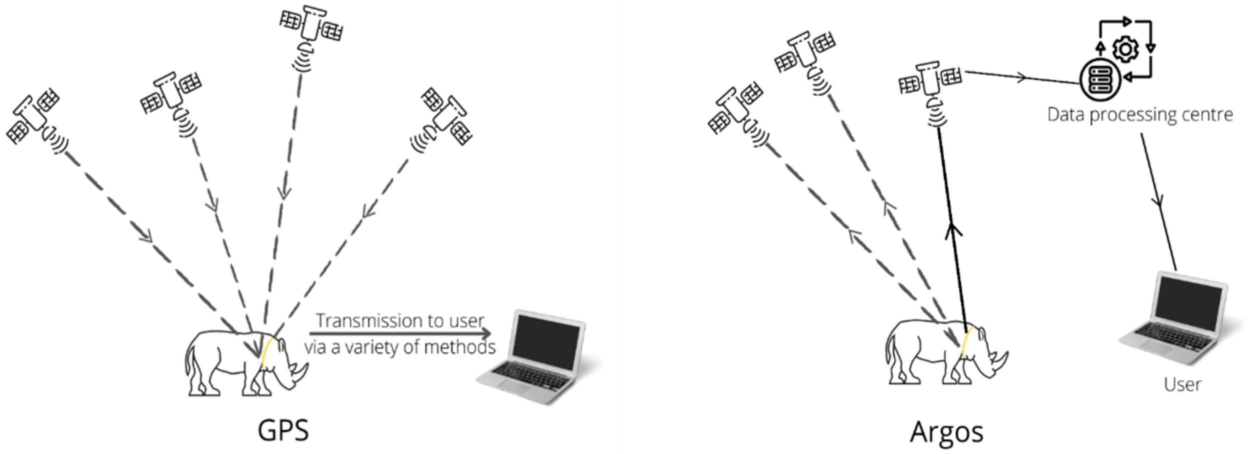


*Figure 4. GPS tags (left) triangulate their location by connecting to and acquiring the position of four, ideally more GPS satellites. Data is then transmitted to the researcher via multiple methods. Argos tags (right) emit a pulsed signal that is received by the Argos satellite network. Only one satellite is needed but more can increase accuracy. The information sent to the satellite is transmitted to a data processing centre where the location of the tag is estimated via the Doppler effect, and then shared with the user.*

### Global Positioning System (GPS) fixes

The Global Positioning System uses a constellation of earth-orbiting satellites that continuously transmit information about their position and course to the earth's surface. By connecting to four or more of these satellites, a tracking tag with a GPS receiver can triangulate its location and elevation to an accuracy of 10 m. The more spread out the satellites, the more precisely the location can be estimated. The tracking device can archive the received GPS signal information for later processing to estimate location after the data have been retrieved, or location can be processed on the tracking device itself. Various GPS parsing software is provided by different tracking device manufacturers to decode the raw data into locations..

### Advanced Research and Global Observation Satellite (ARGOS) Doppler

ARGOS is both a location estimation system and a data transmission system (ARGOS, 2020). ARGOS satellite tracking is similar to VHF radio tracking, in that a small electronic tag fitted to an animal sends out an electromagnetic radio signal, except that in this case the signal is sent to a network of satellites instead of to a radio receiver on earth. The tags are also known as Platform Transmitter Terminals (PTTs).

The researcher programs the tag to send information—such as the time, date, latitude, longitude, animal's ID, and quality of the transmission (to estimate position accuracy)—to the satellite network. The ARGOS system has seven polar-orbiting, sun-synchronous satellites, with three generations of the system coexisting today: ARGOS 2, ARGOS 3 and ARGOS 4. There are also a number of ARGOS ground stations to which ARGOS satellites transmit information.

By calculating the Doppler shift of the radio frequency received during the passing of one of the satellites the location of the tag can be estimated, as the signal frequency varies as the satellites approach or move away. This information is then sent to the user via a ground station. ARGOS requires four or more transmissions to calculate the location estimate. Depending on the quality and number of transmitted signals, there are seven different accuracy classes; the most precise of which gives a positional error of less than 150m (Miller et al., 2005) but a good resolution can be up to 1000m, and at times it may exceed this. Due to the polar orbits of the satellites, tracking tags at high latitude locations typically have better coverage than those near the equator, which is an issue for species that live in equatorial regions.

## GPS versus ARGOS Doppler

Whether to use GPS or ARGOS Doppler is generally a choice between spatial resolution, reliability of fixes, payload size and weight, antenna size and weight, and, ultimately, cost (see Table 4).

ARGOS Doppler can only achieve a location resolution of 150-1,000 m compared to 10 m or less with GPS. Moreover, as ARGOS satellites are polar orbiting, coverage tends to be substandard near to the equator.

On the other hand, ARGOS Doppler is more likely to achieve location fixes reliably than GPS. ARGOS Doppler only needs one satellite to acquire location, compared to GPS where four or more are needed (Figure 4). Connecting to multiple GPS satellites takes time (and power). Standard GPS receivers download both almanac (status and low-resolution orbital information for every satellite) and ephemeris (precise orbital information for the transmitting satellite) data to enable them to determine their location (Witt, 2010), which is a relatively slow process, sometimes taking from 30 seconds to several minutes (Ryan et al., 2004). In situations where a GPS antenna's view of the sky is impeded (e.g. because of dense vegetation), or infrequent and ephemeral (e.g. tracking of air-breathing aquatic species, which spend a short period of time at the water's surface), this can affect location accuracy, or even the ability to get a location at all. ARGOS Doppler is therefore primarily used when there is insufficient time or power to get GPS fixes. ARGOS antennas are also smaller than GPS antennas, which allows for tracking smaller animals.

Recent advances in GPS may provide a route to faster and more accurate GPS location acquisition (e.g. trademarked Fastloc technology). Fastloc receivers can record the presence of signals transmitted by GPS satellites within milliseconds. However, using Fastloc involves a large licensing fee (approximately $1,250 per tracking device).

| | Argos doppler | GPS |
|---|---|---|
| Location resolution | Up to 1500 m with an error class, or over 1500 m with no error estimation. | Typically <10m |
| Time to fix | < 1 second. | Typically, 30 s to several minutes, as requires almanac and ephemeris data to be downloaded. |
| Power requirement | Relatively low, as the tag only needs to transmit to one satellite. | Higher power usage, as the tag needs to connect with at least four satellites and download and store data. |
| Coverage | Satellites in the constellation are polar orbiting, resulting in sub-standard coverage at the equator. | The constellation is arranged in six equally spaced orbital planes to enable global coverage. |
| Better suited to | Situations where battery power or acquisition time is relatively limited (e.g. marine mammals). | Situations where high positional accuracy is required, or if the study animal lives within equatorial regions. |

*Table 4. Provides a comparison of the two satellite based location acquisition options*

## 3.2 Technologies used to transmit location data

### 3.2.1 Non-satellite location transmission

When GPS wildlife tracking technology was first introduced location data were collected by manually retrieving devices from study animals. Although still in use, manual retrieval can be challenging or even impossible in some contexts (e.g. from certain aquatic species), so alternative methods have been developed that overcome the need for device recovery.

These include non-satellite devices which can transmit recorded location data wirelessly to a base station or to a handheld unit via a local network, including via UHF, VHF, Wi-Fi, Bluetooth, or other IoT technologies. However, a key limitation with these devices is that the vast majority of the Earth's surface does not yet have the requisite connectivity.

GPS location data can also be transmitted via the GSM phone network using SMS messages over 2G and 3G networks or internet protocols. A GSM module will be added to the tracking device deployed on the animal allowing longitude and latitude data to be received to a registered mobile device. Data is typically sold according to the total volume of data transferred during the billing cycle. GSM coverage is generally high in human-populated locations, but lower or non-existent in remote terrestrial and marine areas.

### 3.2.2 Satellite location transmission

The paucity of local network or GSM coverage in remote areas led to the development of tracking devices that can transmit recorded location data wirelessly via satellite networks, which potentially provide coverage across the entire surface of the planet. There are a range of satellite communication providers available within the wildlife tracking space, offering different levels of coverage and data plans. The three most commonly used are Iridium, ARGOS, and Globalstar (covered below). The rise of nanosats and Cubesats may also offer opportunities to significantly reduce costs. An increasing number of providers are emerging, with differing pros, cons, and price points. These providers are discussed in Appendix 1.

Most satellite tags connect to satellites whilst still in place on the animal, but Pop-up Satellite Archival Tags (also known as a PSATs or PATs), used primarily on large, migratory marine animals, use an alternative method. They collect location data using non-satellite methods and release from the animal on a predetermined schedule. Once at the water's surface, the data collected is relayed to the researcher via a satellite network. Many PSATs have radio pingers to enable their location to be determined, and for the device to be retrieved.

### Argos [1]

The Argos system was created in 1978 by the French Space Agency (CNES), the National Aeronautics and Space Administration (NASA), and the National Oceanic and Atmospheric Administration (NOAA); originally as a scientific tool for collecting and relaying meteorological and oceanographic data around the world. CNES created a subsidiary, CLS, to operate, maintain and commercialise the system. CLS are now the exclusive provider of Argos satellite telemetry services for scientific and environmental applications. The current service is provided by seven of the original orbiting ARGOS satellites. Kineis is a subsidiary of CLS which will plans to take over operation of the ARGOS system (CLS, 2020), and launch a constellation of 25 nanosatellites to improve global coverage.
ARGOS tracking devices may either collect location data using ARGOS doppler, or via a GPS receiver, whose data is then sent using the ARGOS satellite system.

### Iridium [2]

Iridium provides global coverage and fast transmission of data to the user (typically <20 s, compared with ARGOS, which can take up to two hours), enabling researchers to locate and track study animals in near real-time. In situations where larger volumes of data need to be sent, many people use Iridium over the other options available (particularly in the ocean) because they can fulfil this need. Tracking devices are equipped with a GPS antenna for location acquisition, and then use the data-relay capabilities of the Iridium satellite constellation. Iridium transmitters require a hardware handshaking process with the satellite in order to send data, which leads to a relatively large transmitter being required, when compared to ARGOS.

### Globalstar [3]

Globalstar Inc. is an American satellite communications company, launched in 1991, who operate a Low Earth Orbit (LEO) satellite constellation for satellite phone and low-speed data communications. Data received by the satellite is relayed to a ground station and is made available to the user, usually within minutes. Signals are picked up by terrestrial gateways and routed through local networks, in theory resulting in short latency times and affordable message relay to customers. Coverage is not worldwide because of the service's reliance on ground stations. The first-generation system launch of 52 satellites (48 satellites and four in-orbit spares) occurred in 1998, with an additional eight spare satellites launched in 2007 to help compensate for premature failure of in-orbit satellites. The second-generation constellation consists of 24 LEO satellites, launched between 2010 and 2013. Tracking devices collect GPS positions and transfer the data to the user through the Globalstar satellite system.

1. https://www.argos-system.org/
2. https://www.iridium.com/
3. https://www.globalstar.com/en-gb/

### Icarus [4]

(International Cooperation for Animal Research Using Space) is a Max Planck led initiative. Icarus transmitters collected GPS positions and transferred the data to a receiver station on board the Inter-national Space Station (ISS) which offers a two-way data link, allowing tracking collars to be updated as necessary. The ICARUS on-board system sat on the Russian Segment of the ISS. Previously, the ISS stored the data and transmitted it at the next radio contact with the ground station to a Russian con-trol centre in Moscow, which forwarded the data to a user data centre where it was processed and made available to users within the Movebank database [5]. More than 24 hours passed between meas-urement and publication in Movebank. In future, Icarus aims to develop tiny transmitters that will make it possible to satellite track much smaller species than is currently possible.

Although Icarus have (up until March 2022) been able to prove their principle, successfully tracking 15 species, data transmission has stopped. The Russian space agency have ended their cooperation with Icarus, so Icarus are currently looking for alternative options, and have paused the work until a new partner is found.

---

4. https://www.icarus.mpg.de/en
5. www.eoportal.org/other-space-activities/iss-icarus#iss-utilization-icarus-international-cooperation-for-animal-research-using-space

# 4. Satellite tracking across habitats

Although tracking technology has helped to greatly improve our understanding of the natural world, environmental and behavioural factors constrain its utility in different habitats. This section examines these considerations and highlights common technologies employed across habitats.

## 4.1 Marine

Radio waves do not propagate in water, so animal tracking in the marine environment is generally undertaken using either acoustic telemetry (Donaldson et al., 2014) or satellite telemetry (Hazen et al., 2012).

Acoustic telemetry allows for tracking of individuals below the water's surface. Transmitters are attached internally or externally to animals and transmit encoded acoustic signals, unique to each individual, which are detected by stationary or mobile receivers (e.g. on a pursuit vessel), revealing the presence and location of animals (Matley, 2022). Some tags also provide data on environmental characteristics (e.g. depth, temperature) and acceleration. Hydrophone receivers convert these signals into data which can be downloaded via satellite link, remotely from the ocean surface via a modem, or by physically collecting the receivers from the ocean floor (Census of Marine Life, 2009). Sound waves propagate four times faster in water than in air, enabling almost real-time tracking, and making acoustics an attractive method for collecting data on marine fauna.

There are two primary types of satellite telemetry used in marine environments: Pop-up Satellite Archival Tags (PSATs) and real-time satellite tags. PSATs can record data on ambient light levels, swimming depth, speed, and/or internal/external temperature, and are then released from the animal and float to the surface to transmit data to land-based receivers via orbiting satellites. Real-time satellite tags, include SATellite tags (SATs) and Smart Positioning Or Temperature-transmitting tags (SPOTs). SATs transmit locations and logged dive behaviour of animals each time they surface (Hussey et al., 2015). SATs are generally limited to larger individuals, as they are bigger than acoustic tags, but can provide fine-scale series data on depth, temperature, and location of animals, travelling over thousands of kilometres (Hussey et al., 2015). SPOTs use ARGOS doppler to calculate locations with accuracies up to 250 m. They can also record a variety of measurements, such as temperature, salinity and depth, which they transfer to ARGOS when contact is made with satellites (Cyr & Nebel, 2013). SAT and SPOT tags are primarily designed for animals that surface regularly, such as dolphins, penguins, turtles, and seals. To conserve battery power, they are often fitted with a salt-water switch, which indicates whether the device is under or above the water and thus whether data transmission should be attempted.

## 4.2 Terrestrial

As with marine tags, terrestrial tags often have built in accelerometers, heart rate monitors, electroencephalographic (EEG) sensors, internal temperature sensors, cameras, etc. They are usually attached to the animal using a backpack, tape, or glue to the back, or using a weighted collar or bracelet. Trackers deployed on terrestrial species stand a greater chance of having a clear view of the sky to collect position data and transmit it via satellite networks than marine tags. However, various factors might influence success, for example, if the species lives in a burrow or or dense forest, or if it lives in equatorial regions, where satellite coverage is less consistent. A huge variety of choice exists amongst the different technologies and attachment methods available, that need to be selected carefully according to each use case.

GPS tags with remote data download have dropped in size from 250 g to 20 g in the last decade, (Kays et al., 2015), allowing tracking to be an option for most medium- or large-sized vertebrates. However, it is estimated that approximately 70% of birds and 65% of mammals cannot be tracked in real time due to the size of devices with remote download functionality, so miniaturisation of devices remains a priority (Kays et al., 2015). Remote data download via satellite involves tags collecting location data via the GPS or ARGOS doppler system and then transmitting it via satellite back to the user. This can be done over a variety of satellite networks (see Satellite Communication Providers, pg.s 23& 24, and Appendix 2). This requires a satellite module on the deployed tracking device which will vary in size depending on the communications provider. Some antenna sizes render tags too large to be deployed on anything but the largest terrestrial mammals. Data is usually transmitted to a data portal and can be viewed on a smartphone, tablet or laptop.

## 4.3 Freshwater

Radio telemetry has historically been the most commonly used technology in freshwater systems, but Passive Integrated Transponder (PIT) technology, acoustic telemetry, and biologgers are becoming more popular (Cooke et al., 2013). Satellite tags on freshwater species share some of the same limitations as marine systems, as satellite position cannot be obtained underwater. As in marine systems, freshwater species can use satellite tags that remain on the animal, or PSATs. Studies on semi-aquatic, amphibious or air-breathing species (e.g. reptiles, like turtles or crocodilians) can use satellite tags, as these taxa spend time at the surface or on land (Franklin et al., 2009). For freshwater fishes, PSATs have occasionally been used; however, the traditional galvanic corrosion methods for tag release require sea water, so alternative tag-release procedures are necessary. PSATs have been used in freshwater fishes, such as sturgeon (Kough et al., 2017), and can collect and transmit non-location data, such as depth, temperature, and acceleration, but do not obtain position fixes, they collect location information from which large-scale movements can be determined.

Unlike many marine and terrestrial ecosystems, rivers are linear by nature, and lakes are limited in area (as opposed to the unconstrained shape of most marine areas). Telemetry applications can, therefore, capitalize on the physical structure of freshwater ecosystems in capturing movement processes (e.g. by tracking stretches of river using the relatively limited range of acoustic or radio receivers placed along the riverbank (Cooke et al., 2013)). Miniaturisation is allowing for tracking of small-size life stages and species, and fixed stations can enable tracking over large distances. Inexpensive PIT systems can also enable population- and community-level sample sizes (Cooke et al., 2013).

## 4.4 A note on avian tags

The key consideration with avian tracking is, of course, device size, to ensure that flight ability is not impacted. The advantage of avian tracking, particularly of seabirds, is that there is usually a clearer view to sky, allowing devices to obtain accurate locations more easily, which is also an ideal scenario for the use of solar powered devices. Accuracy will vary for bird species living in certain environments (e.g. forests). As satellite tracking technology becomes increasingly light, efficient, and cheap, and new low-power satellite data communication systems and battery technologies are developed, the technology will become an option for an increasing array of smaller avian species. New sensor integrations, such as the incorporation of cameras, accelerometers, and gyroscopes, increase behavioural insights, and radar sensors can enable tracking of interactions with fishing vessels, turning seabirds into unofficial monitors of fishing patterns, including illegal fishing.

# Case study 1


Tagged pygmy sloth
(c) Hidalgo Taylor

## Estimating home ranges of pygmy sloths in Panama

**Researcher:** Dr. Diorene J. Smith C., EDGE of Existence [6] alumna

**Species being collared:** Pygmy three-toed sloth (Bradypus pygmaeus)
– a Critically Endangered EDGE species

### What research question are the satellite collars being used to answer?

*The satellite collars have been used to obtain ecological information and improve the understanding of the species. Particularly, the habitat use of the pygmy sloth across Escudo de Veraguas Island, estimation of its home range size, proportion of time spent moving in different habitat and whether it is subject to seasonal conditions.*

### What are the challenges of tagging your species?

*During the collaring process, one of the challenges was the accessibility of the field site. There are limited times throughout the seasons that it is possible to visit Escudo de Veraguas Island. Additionally, the study animals were 10 adult pygmy sloths, the maximum number possible for the study, it was often challenging to access them or find them, as many were located in trees that were over 5 metres high, within dense forest.*

---

[6] https://www.edgeofexistence.org/

## Case study 1

**What tags did you use & why did you choose them? What considerations and tradeoffs did you make?**

*We used Litetrack 30 collars, from Lotek.*

*The most important considerations were:*

- *that the collars weighed no more than 75g (a similar weight to the previous collars used)*
- *they were tailor made for the animals (the pygmy sloth neck has a circumference of approximately 14 cm)*
- *they included an automatic drop-off mechanism to ensure the animal safety after the year of study*

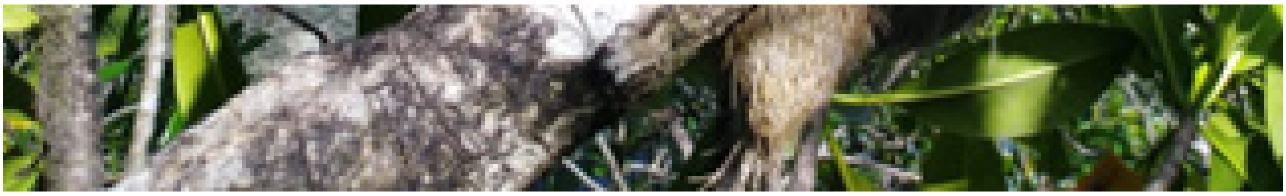
*We programmed each satellite collar to record its position four times per day and to trigger the drop-off mechanism one year after the collar is attached to the animal. The collars were equipped with VHF transmitters that allowed us to locate the sloths. The data were downloaded remotely over VHF.*

**What have you learned from your work?**

*The use of this technology has allowed us to get the first ever-scientific estimate of the home range of the pygmy sloth. In general terms, the ecological monitoring of the pygmy sloth population has helped to identify core habitats for the protection of the species across the Island. The ability to download the data from the collars remotely and the drop-off mechanism that allows for collars to be safely retrieved without adverse effects on the sloth have meant that this method has become a choice for future studies.*

**How has what you've learnt about the species and tech been translated to conservation action?**

*The information from our recent studies in conjunction with home range data provide an important scientific basis to generate a conservation action plan of the pygmy sloth and increase the conservation of the island's habitat and the appropriate zoning of the area for a sustainable management plan.*



# 5. What satellite tags can be used for

**“Every time a new study comes out with tracking data, it’s upending preconceived notions of how animals use space”**

*Ruth Oliver, (Rahim, 2021)*

Traditional tracking methods, such as VHF or UHF, require the researcher to be in relatively close proximity to the study animal. Satellite tracking technology has enabled the gathering of higher resolution location and movement data and ever more sophisticated analyses and insights, from remote locations where wildlife tracking was not previously possible, and at much greater scales (Figure 5). Multi-sensor satellite tags, which collect supplementary non-location data, such as altitude, depth, temperature, oxygen levels, and acceleration, have further enriched our understanding of animal physiology and how a species interacts with its environment (Hammerschlag, 2011).

These data have enabled ever more sophisticated analyses and insights and have contributed to our understanding of animal movement and behaviour in new ways. In this section, we highlight some common research and conservation applications of satellite tracking technology, including (following Hebblewhite and Haydon (2010)) studies of:

- Resource selection and movement corridors
- Behaviour
- Migration
- Home range
- Demography
- Movement ecology
- Human wildlife conflict
- Climate change impacts

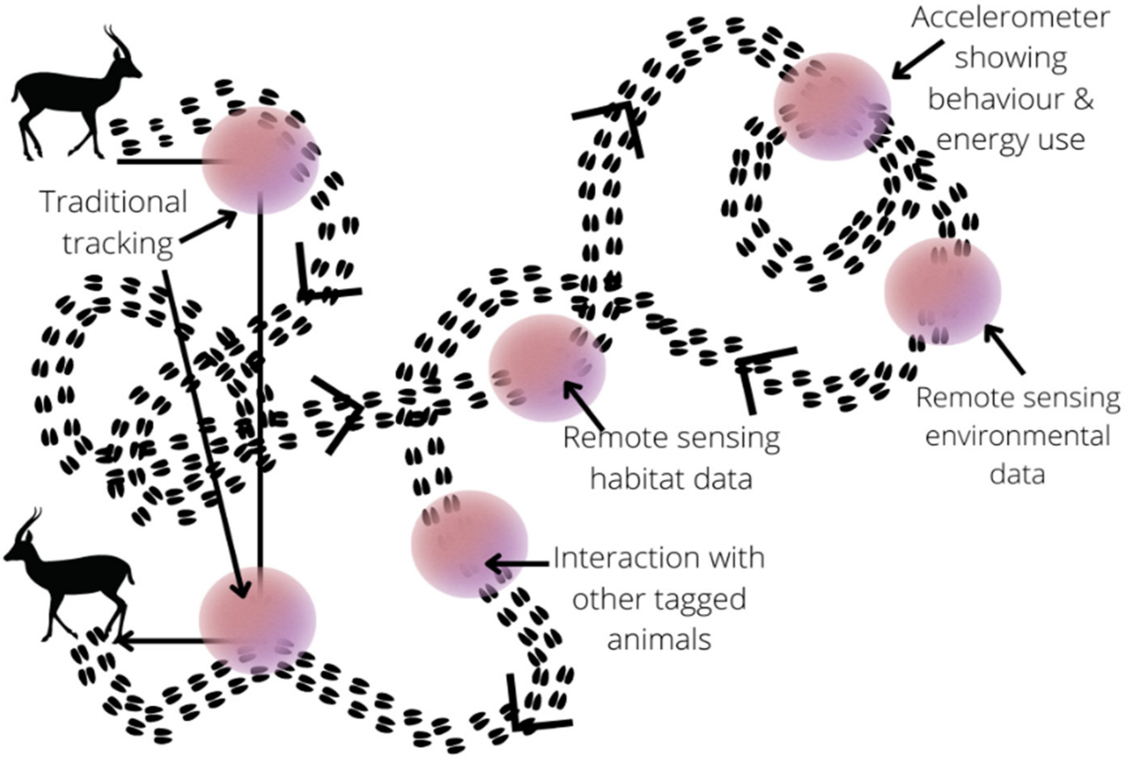


*Figure 5. Traditional tracking methods, such as VHF or UHF, require the researcher to be in close proximity to the study animal to obtain data. Satellite tracking technology enable tracking of species on the other side of the world and has generated a wealth of location and movement data. Multi-sensor satellite tags provide supplementary data that can provide insights into more complex research questions (Recreated from Kays et al., 2015).*

## 1. Resource selection and movement corridors

Resource Selection Functions (RSF) are a popular tool for identifying critical resources for animal populations. When estimating RSFs, location observations derived from satellite tracking technology are the primary means of quantifying whether a resource, such as specific habitat, water or food, has been selected. There are many practical motivations to study resource selection, such as quantifying anthropogenic impacts, analysing interspecific competition, and delineating conservation corridors. The creation and protection of movement corridors is a popular strategy to maintain population connectivity between fragmented habitats or protected areas. Connectivity models, informed by tracking data, help navigate land-use planning in increasingly complex multiuse landscapes.

### *Case study: Habitat selection of mule deer before and during gas field development*

Sawyer et al. (2006) investigated the impact of the development of a natural gas field on habitat selection of mule deer in Wyoming in the United States. Using telemetry data from tagged deer, they modelled habitat selection of adult female deer before and during the development, and found an almost immediate response, including avoidance of areas near gas wells, and shifts to less preferred – and presumably less suitable – habitats.

### *Case study: Prioritizing corridors and core areas for lion conservation in southern Africa*

Cushman et al. (2018) used an extensive dataset from satellite-tagged lions to map key areas for lion dispersal outside National Parks across southern Africa, corridors between these key areas, and areas of highest human-lion conflict risk. Results were used to guide spatial prioritization of conservation areas in the Kavango-Zambezi Trans frontier Conservation Area.

### *Case study: Shark habitat selection*

Until recently, it was thought that whale sharks predominantly used the shallow, surface waters of the oceans, but data from satellite tags showed that they dive to at least 980 m, (the maximum depth that could be recorded by the sensors) and helped create a fuller picture of how individuals use the ocean and interact with each other (Hammerschlag et al., 2011). They were previously thought to spend all of their time in the shallow, surface waters, whereas satellite data suggest the proportion of time is closer to 50% (Rowat et al., 2007). Satellite tagging of basking sharks also helped dispel the myth that they hibernate – a belief that had been held for 50 years – and revealed that they migrate seasonally to warmer waters (Skomal et al., 2009).

## 2. Behaviour

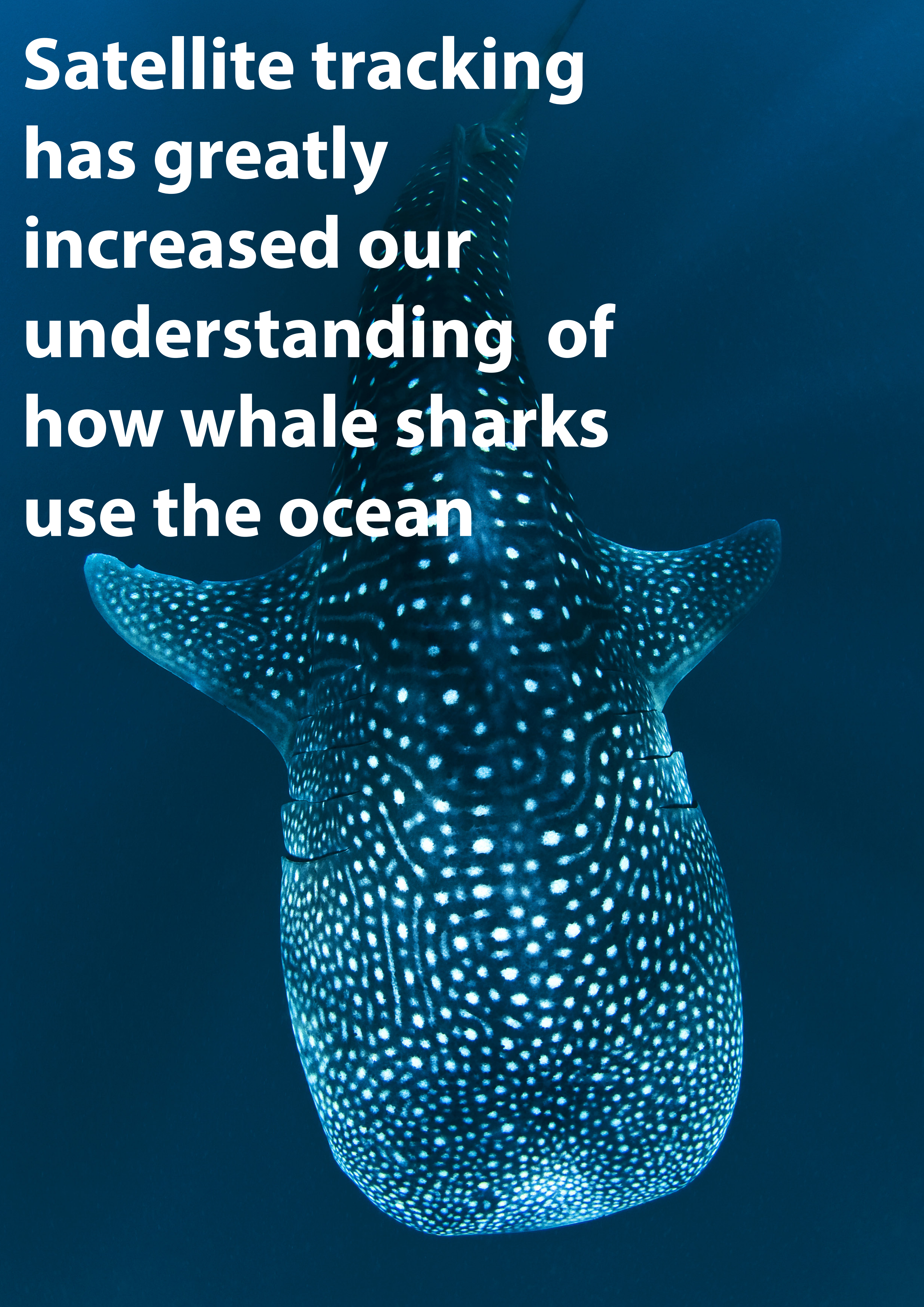
Satellite tracking has provided insights into the behaviour of a variety of wide-ranging species, who cannot be studied using traditional techniques, and to inform behaviour-dependent conservation interventions, such as species reintroductions or relocations. Satellite tracking has been particularly integral for studying the behaviour of marine species, due to the visually obscure nature of the ocean. Prior to the introduction of the technology, animal tracking was frequently based on direct observation, or inferred from industrial data, such as from fisheries and whaling records. Satellite trackers have also enabled measurement of subtle changes in the behaviour of ocean-dwelling species, such as swimming speed, frequency of tail beats, acceleration, and muscle contraction (Hammerschlag et al., 2012).

### *Case study: Megamouth sharks*

Satellite tags have helped improve understanding of the behaviour of an obscure species – the megamouth shark, which was first discovered in Hawai'i in 1976 (Heathcote, 2017). Tag data revealed that megamouth sharks are explorers, travelling the temperate oceans of the world, but with fidelity to Taiwanese waters. As a result, the Taiwanese government has banned fishing of the species (Rahim, 2021). These data also indicated that megamouths are diurnal, and regularly alternate between deep and shallow waters, potentially following plankton and other organisms that spend their time at the bottom of the ocean during the day and migrate up to the surface at night (Heathcote, 2017).

### *Case study: Sea turtle life history*

Commonly referred to as 'the lost years' within the field of sea turtle research, little is known about what happens between sea turtles hatching and when they return to shore to nest years later. After hatching, they enter the sea and disappear from sight. However, a satellite tracking study by Putman & Mansfield (2015) demonstrated that turtle hatchlings do not passively migrate along ocean currents, as was previously thought, but swim with intention to specific locations.



Satellite tracking has greatly increased our understanding of how whale sharks use the ocean

*Figure 6. Loggerhead turtle (Caretta caretta) hatchling journeying from nest to sea (c) Kate Moses*

### Case study: Oilbird roosting behaviour

Cheshire & Uberti (2016) highlight an interesting example of satellite telemetry being used to dispel preconceived notions of the behaviour of oilbirds in Venezuela. These nocturnal birds were thought to be cave dwellers, who ventured into the forest only at night to forage. However, data retrieved from GPS trackers revealed that they roost in the forest for three days at a time, only then returning to the caves. As a result, they spend far more time in the forest than was previously assumed and may play a major role in seed dispersal.

### Case study: Behaviour of hand-reared vs. naturally reared albatross chicks

Satellite tags were used to monitor the behavioural response of albatross chicks to translocation and hand rearing, in comparison to naturally reared individuals (Deguchi et al., (2014).

## 3. Migration

Satellite tags deployed on a wide range of migratory species have provided important insights into migration dynamics, including routes and distances, durations, final destinations, and location and frequency of pit stops and feeding areas (Miller et al., 2005; Dodd et al., 2007).

Mass migrations are one of nature's great phenomena, however, although a few mass migrations are well known, such as the approximately 1.3 million wildebeest who move through the Serengeti-Mara Ecosystem (Thirgood et al., 2004), most of them are poorly studied. While our knowledge is poor (Berger, 2004), anthropogenic effects on migrations are high (Pimm et al., 2001), meaning that implementing successful conservation measures can be challenging (Berger, 2004). Migrations are also often transboundary and require international cooperation. Satellite technology has played a significant role in increasing our knowledge of mass migrations and informed the development of conservation solutions, while fostering cross boundary cooperation (Harris, 2009).

### Case study: Discovery of Burchell's zebra migration route

The use of satellite tags has uncovered migrations in species that were not widely known to migrate, such as the 500 km round trip from Namibia to Botswana made by Burchell's zebra (Naidoo et al., 2017). At the time of the analysis, their migration was thought to be the longest of all large mammal migrations in Africa, although this has since been disputed (Schapira et al., 2016).

*Figure 7. Burchell's zebra*

### Case study: White eared kob migration

Another migration that was recently rediscovered as a result of the use of satellite tracking devices is that of the white eared kob, which migrate through the South Sudan and Ethiopia landscape (Schapira et al., 2016; Naidoo et al., 2017). Their migration is comparable in size to that of the great wildebeest migration (approximately 825 km) and may be the longest mammal migration in Africa, yet remains poorly understood (Schapira et al., 2016). This is likely to remain the case in the near future due to ongoing security and logistical challenges posed by armed conflict within the study area, yet satellite technology has enabled researchers who are unable to cross borders or spend time on the ground to continue studying the migration.

### Case study: Flight capacity of migrating birds

Data generated by satellite tracking technology has also improved our understanding of the flight capacity of migratory birds. For example, Gill et al. (2008) demonstrated that bar-tailed godwits flew across the central Pacific Ocean in one, non-stop flight (11,860 km), thus surpassing what had previously been considered possible (Perras & Nebel, 2012).

### Case study: Knowledge of migratory routes over generations

A study of plains zebra in Botswana captured behaviour suggesting that knowledge of migratory routes can persist through multiple generations of animals, even in the absence of migration (Bartlam-Brooks et al., 2013). Upon removal of a wildlife control fence in the Okavango Delta, which had been in place for 36 years, 11 individuals migrated >250 km to the Makgadikgadi grasslands, despite the average lifespan of a zebra being only 12 years.

## 4. Home range

A species' home range is a fundamental metric in the field of ecology (Viana et al., 2018), and this knowledge is often critical for conservation, including population management, species reintroductions, and protected area planning. Satellite technology has improved understanding of species' home ranges, enabling tracking at finer spatiotemporal scales and with greater accuracy.

### Case study: Grevy's zebra home range in relation to protected areas

In the case of Grevy's zebra in Kenya, data collected using satellite tracking showed that key foraging areas fell outside of protected areas (Levikov, 2014).

### Case study: Olive Ridley Sea turtle home range

Maxwell et al., (2011) used satellite tracking data to estimate the home ranges of 18 olive ridley sea turtles, which provided scientific support for a proposed transboundary marine protected area between Gabon and the Republic of Congo that would cover 98% of the turtles' home range.

## 5. Demography

Satellite tracking data have been used to inform estimation of key demographic rates, such as survival and reproduction, which are often critical for informing conservation, e.g. extinction risk assessments and harvesting quotas.

### Case study: Apparent survival rates of adult lesser spotted eagle

Väli et al. (2017) used a combination of satellite tags, wing tags, and plastic leg rings to conduct a mark-recapture study of the migratory lesser spotted eagle. Annual returns to nest sites after the spring migration were used to calculate apparent survival of adults.

### Case study: Survival and breeding of polar bears in relation to sea ice

Regehr et al. (2010) used satellite telemetry to model the movement of polar bears, leading to the first plausible estimates of polar bear survival and abundance, which were integral to the development of subsequent harvest quotas (Regehr et al., 2016).

## 6. Movement ecology

High-resolution satellite tracking data has enabled sophisticated analysis of the movement of individuals and populations of wildlife, and improved our understanding of the role of movement in ecological processes.

### Case study: Influence of sea ice phenology on the movement of ringed seals

Yurkowski et al. (2016) investigated the influence of sea ice dynamics on the movement of ringed seals and found that adult and subadults spend most of the ice-free season in a resident (i.e. not travelling) state. In lower latitude populations, where the ice-free season is longer, seals spent longer periods in a resident movement state.

### Case study: Environmental drivers of variability in the movement of turkey vultures

Dodge et al. (2014) used satellite telemetry data to evaluate the effects of environmental conditions on the movement of turkey vultures. A large dataset, collected over 10 years from 24 individuals, suggested that the species is likely to adapt well during periods of climate change.

## 7. Human-Wildlife Conflict

Developing solutions to Human-Wildlife Conflict (HWC) requires in-depth knowledge of where and when such conflict is likely to occur. Satellite tracking has contributed greatly to this understanding, including enabling mapping of conflict hotspot areas (Cushman et al., 2018), and evaluation of the effectiveness of response measures (Power et al., 2021; Read et al.,2007). Moreover, satellite tags that provide location data in near real-time have proven to be an effective tool for protecting species at risk of hunting and mitigating conflict risk (Wall et al., 2014).

### Case study: Mapping HWC with cheetahs

Satellite collaring of 300 cheetahs in Namibia enabled researchers to build a detailed picture of the animals' movements. This information was used to inform changes to livestock grazing, which reduced livestock losses for local farmers by 86% (Khan, 2022).

### Case study: Success of problem leopard relocation

Power et al. (2021) found limited success for translocation of problem leopards as a HWC mitigation measure, using satellite collars data from 16 relocated and translocated animals.

### Case study: Success of saltwater crocodile translocation

Satellite tracking of three adult saltwater crocodiles, which had been translocated as they posed a threat to humans, revealed that all three returned to their capture locations, including one that travelled 400 km in 20 days, illustrating that (a) large male estuarine crocodiles have exceptional navigation ability and exhibit high site fidelity, and (b) translocation of large saltwater crocodiles that pose a threat to humans may not be an effective mitigation strategy (Read et al., 2007).

### Case study: Effectiveness of railway underpasses for elephants

In 2016, ten elephants in Tsavo National Park, Kenya were collared to determine how they were adapting to a new railway line that bisected their habitat. Researchers were able to ascertain that within 30 days half of the elephants had used underpasses constructed to mitigate the impact of the railway line (Cheshire & Uberti, 2016).

### Case study: Reducing elk traffic collisions

Data generated by satellite collars deployed on Rocky Mountain elk were used to develop mitigation methods, including fencing and re-routing strategies, as a means to decrease the number of elk killed in traffic collisions on busy roads (Dodd et al., 2007).

## 8. Real-time monitoring

Satellite tags that provide location data in close to real time can also be an effective tool for protecting at-risk individuals and mitigating HWC (Wall et al., 2014). Automated analysis of near real-time animal location data can detect changes in behaviour that may be indicative of an injury or poaching attempts (e.g. slower than normal movement or an abnormal track), enabling rapid response by conservation managers. For species at risk of conflict with people, real-time data can be used to alert local communities if tagged individuals breach important 'geofenced' areas (e.g. settlements, water sources, or crops).

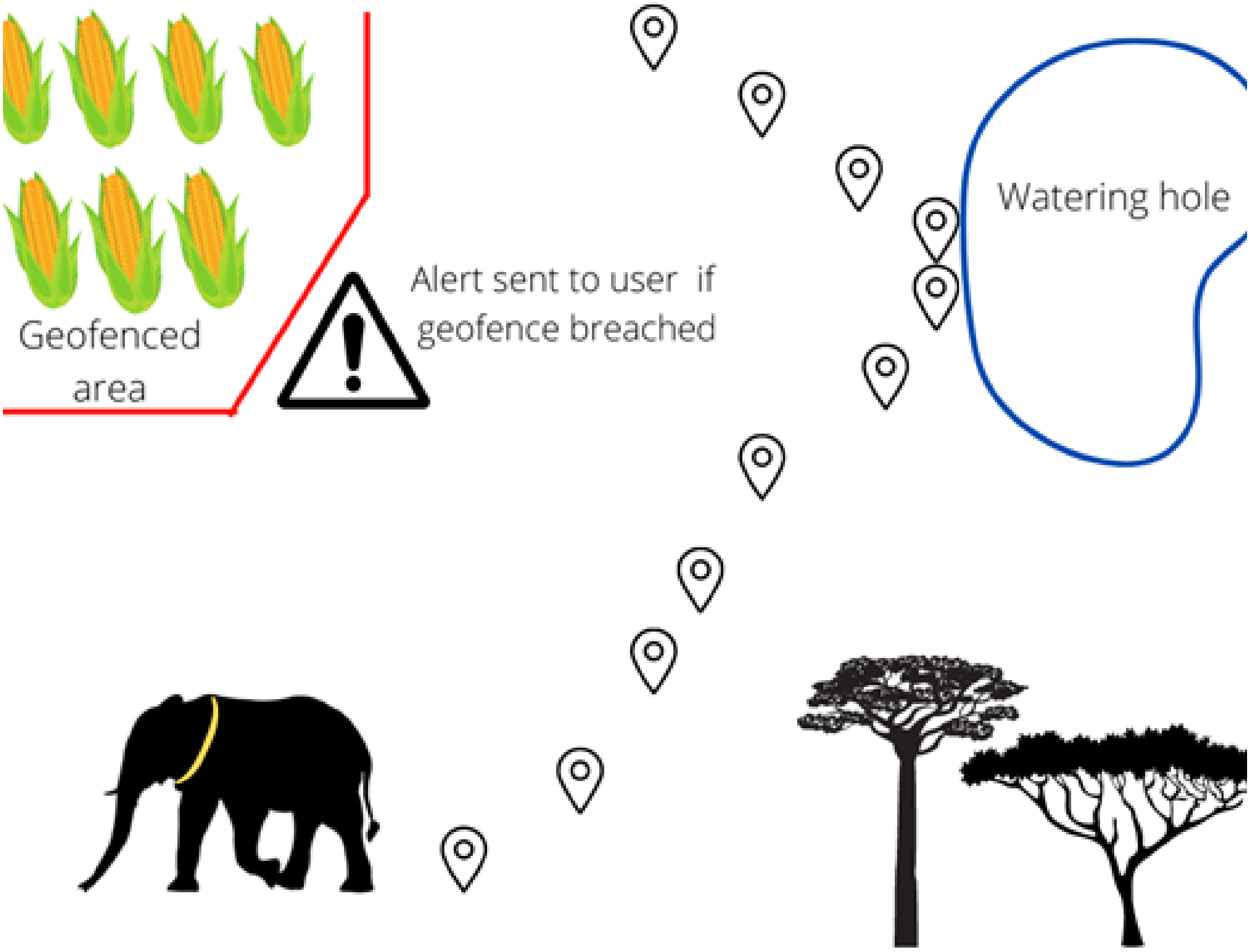


*Figure 8. Satellite tracking can provide near real-time monitoring of tagged animal within the landscape, and trigger proximity alerts to help mitigate human-wildlife conflict.*

## 9. Climate change impacts

Satellite tags have provided valuable insights into the effects of climate change on wildlife.

### Case study: Impact of climate change on American robin migration

Long-term satellite tracking suggested that American robins were starting their migrations approximately 5 days earlier per decade in response to climate change (Oliver, 2020).

### Case study: Temperature-dependent behavioural responses of African wild dogs

Rabaiotti & Woodroffe (2019) used GPS collars to assess the potential of African wild dogs to adapt to climate change. They found that wild dogs in Kenya increased their nocturnal hunting behaviour to cope with high daytime temperatures, but these changes were insufficient to balance decreases in daytime activity, particularly when the dogs were raising pups, suggesting that the species may not have sufficient behavioural plasticity to adapt to increasing temperatures.

# Case study 2

Tagged Silky shark (c) Dr David Curnick

## Silky shark research in the Chagos Archipelago

**Researcher:** Dr David Curnick, Head of Marine Predator Lab at ZSL's Institute of Zoology

**Species being collared:** Silky sharks *(Carcharhinus falciformis)*

---

**What research question are the satellite collars being used to answer?**
*Our primary aim was to understand the horizontal movement patterns, habitat use and site fidelity of silky sharks around the Chagos Archipelago. This was in the context of the large Marine Protected Area that surrounds the archipelago and how they are connected to the wider Indian Ocean. Additionally, we sought to quantify the vertical habitat use by silky sharks in the area.*

**What are the challenges of tagging your species?**
*Finding the animals was the biggest challenge. The Chagos Archipelago is very remote and difficult to access, so, we are only able to visit for a few weeks each year. Each expedition is multi-purpose and often reef focused, meaning we have very little time available to specifically look for silky sharks that tend to hang out in deeper water and around offshore features, like seamounts. When we did manage to spend time around the seamounts, silky shark presence was, at the time, seemingly unpredictable and fleeting, and we were often mobbed by hungry groups of silvertip sharks.*

*Costs are also a major hurdle. Each satellite tag costs more than $4,000 to buy, not including the boat and staff time and equipment needed to find and handle these animals safely. More affordable electronic tags would not only facilitate greater sample sizes, but also improve accessibility and equity in data-poor regions.*

## Case study 2

**What tags did you use & why did you choose them? What considerations and tradeoffs did you make?**

*We used MiniPAT tags from Wildlife Computers. The MiniPATs were programmed to track large-scale horizontal movements and fine-scale use of the vertical water column. MiniPATs give a horizontal location estimate every day via geolocation. This is good for large scale movements, but the error associated with these positional estimates is sometimes >1km, limiting their effectiveness to understand finer-scale horizontal movements. Each animal was therefore double tagged with an internal VEMCO/Innovasea acoustic tag. These tags emitted a 'ping' every minute or so and were detected if the individual carrying it swam within approximately 500 m of one of the receivers we were strategically deployed across two seamounts in the south of the archipelago. By combining these tagging technologies, we were able to assess residency behaviours associated with the seamount features.*

**What have you learned from your work?**

*We observed high fidelity to the Chagos Archipelago, and a sustained diurnal association with the seamounts, with individuals moving off at night and returning at sunrise. This fidelity bodes well for the effectiveness of the MPA, as animals are protected from the pressures of industrial fishing whilst within its boundaries. Yet, a couple of individuals undertook large-scale migrations outside of the MPA boundary and across the Indian Ocean. This included the furthest recorded displacement distance for a satellite tagged silky shark, with one traveling to the Kenyan coast – nearly 5,000km. Tagged individuals spent > 99% of their time in the top 100 m of the water column but made regular dives to depths of greater than 300 m, most likely foraging. This unfortunately overlapped directly with typical deployments of purse seine and longline sets in the Indian Ocean, likely contributing to the high by-catch rate of this species. Interestingly, one individual was recorded to a depth of 1,112 m, the deepest recorded silky shark dive to date.*

**Given the logistical challenges and high unit costs of tagging sharks, what is your sample size and are you able to infer population level conclusions from it?**

*Given all the above limitations, our sample size was very small, with only six individuals tagged with MiniPATs. Furthermore, of the six tags that were deployed, two failed to report their data, meaning our effective sample size was just four. This severely limits the questions we can answer, such as how does movement behaviour differ between life stages? How typical are the movements we observed of the wider population? Or how does movement vary between seasons and years?*

# 6. Limitations of satellite tracking technology use

Although satellite tracking has revolutionised our understanding of how wildlife uses the natural world, there are limitations associated with the technology, including variable satellite coverage and fix accuracy, and tag battery life. In this section, we describe these constraints; not to deter you from considering satellite tracking as an option for your study, but to give you a broader understanding of the main limitations that you may face if you do choose to use the approach.

Importantly, relatively little information exists on the effectiveness and limitations of different tracking technologies, so this analysis may be incomplete. Few studies have evaluated the technologies across habitats and species, so understanding of how reliability varies with context is limited (Hofman et al., 2019; Matthews, 2013). Satellite tracking is also a rapidly evolving field, so the information provided will quickly become outdated.

## 6.1 Satellite coverage

In theory, satellites can provide near global coverage, yet several factors may mean that achieving optimal coverage is not always a possibility, which, in turn, will influence the likelihood of obtaining a location fix, or the spatial accuracy of the fix obtained. Suboptimal coverage can also result in data loss or delays during data transmission.

For transmission of data, Argos, Iridium, Globalstar and Inmarsat all claim global or near global coverage. In practice, Globalstar and Inmarsat do not cover polar regions (Hofman et al., 2019). Argos and Iridium do cover polar regions but, due to the polar orbits of their satellites, tracking tags at high latitude locations typically have better coverage than those near the equator.

For location acquisition, ARGOS doppler is generally quicker to obtain a location fix as it only needs to connect to one satellite, whereas GPS needs to connect to four satellites.

Signal paths between tags and satellites can be blocked, e.g. by dense canopy cover or terrain. This means that the technology may be less suited to particular habitats and to certain species, e.g. burrowing species. Satellite tags are also unable to transmit or receive signals underwater (Wilson et al., 2002; Tomkiewicz et al., 2010). There can also be issues with the communication of collected data to the user.

ARGOS doppler is more likely to obtain a fix as it only needs to connect to one satellite whereas GPS need to connect to four satellites in order to determine the location.

In addition to the challenges associated with obtaining a location fix if coverage isn't optimal, there can also be issues with the communication of collected data to the user. This can result in data loss or delay in receiving it, until the tag is retrieved.

In analysis by Hofman et al. (2019) average GPS fix acquisition success rate was 85% (although variability was high), they suggest that in order to counter this expected data loss, a good strategy is to either increase the number of tags used in the study or to increase the fix attempt frequency per tag, in order to counterbalance the data that you expect to lose. Since the ability to get fixes from satellites is non-random e.g. it can be affected by terrain, or when species are underwater or underground, this can lead to bias in data if not accounted for. However, the issues that influence satellite fixes (such as terrain) may be easier to address at study design and analysis stage than for studies using other technologies such as VHF (Frair et al., 2010).

In situations where it takes a device a long time to obtain and/or transmit fixes, loss of battery capacity can become an issue, and affect the overall operating life of the device. In order to mitigate for this, devices can be programmed to only switch on at certain times of day/year, when fix acquisition is more likely, and fix acquisition 'time-outs' can be used to prevent the device draining battery unnecessarily.

## 6.2 Spatial accuracy

The ability of devices to acquire an accurate location fix varies by technology (e.g. GPS tags typically offer the highest level of accuracy, see table 4), and can be influenced by several factors, such as the size and behaviour of the animal (& therefore, size of the tag and antenna), the age of the device, the amount of vegetation present, the maximum time that the device allows to obtain a fix, and how recently the device last connected to a satellite. Consequently, thorough testing of tags is recommended prior to deployment (Villepique et al., 2008; Clements et al., 2022).

GPS position accuracy (as well as the length of time taken to obtain a fix) is dependent upon the length of time since the device was last in contact with the satellites. When a receiver has obtained a fix within the last 2 hours, the almanac, time, location, and ephemeris data on the device is up-to-date. The time to first fix and the accuracy of that fix is improved when the device is operating from this 'hot start' mode. When devices are inactive for 2-4 hours, they need to acquire new ephemeris data and the time to first fix can be longer and accuracy is reduced (referred to as a 'warm start'). If devices are inactive for >6 hours from the previous fix, they need to acquire new almanac, time, location and ephemeris data, meaning that acquisition times and position accuracy are reduced further (referred to as a 'cold start') (Tomkiewicz et al., 2010). Some providers of devices discard a set number of 'first' fixes and store the third or later fix as final position to reduce inaccuracies (Matthew et al., 2013).

One of the main contributing factors to GPS accuracy is the geometric configuration of satellites used to obtain a fix. Satellites that are closer together will produce a larger position error, and vice versa. The best position fix is given when a satellite is directly overhead and another three are equally spaced around the horizon. Figure 9 shows that when satellites are widely separated as on the left, there is a smaller position error, while satellites that are closer together as on the right will produce a larger position error (areas in red in the diagram). An Horizontal Dilution Of Precision (HDOP) value of 1 or below would give an accuracy of about 2.5m.

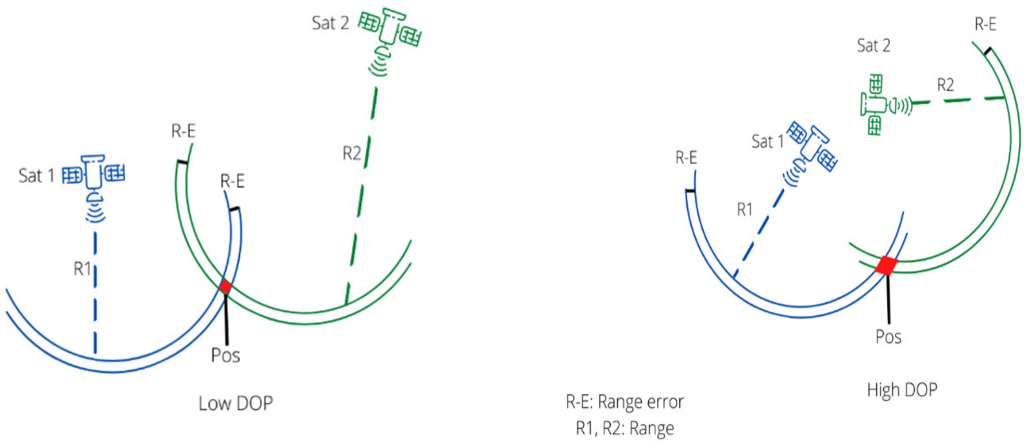


*Figure 9. Satellite precision error - recreated from*[7] *. When both satellites are widely separated (left figure) the position error (area in red) is smaller, giving a low Dilution of Precision (DOP). If the satellites are close to one another (right figure), then the area of error is more spread out, giving a high DOP.*

In mountainous areas, forests, and urban cities, some of the available satellites will be obstructed and those used to collect the GPS position will be closer together, resulting in larger errors (Figure 10). Researchers usually calculate accuracy thresholds in line with the study objectives and the level of movement resolution required.

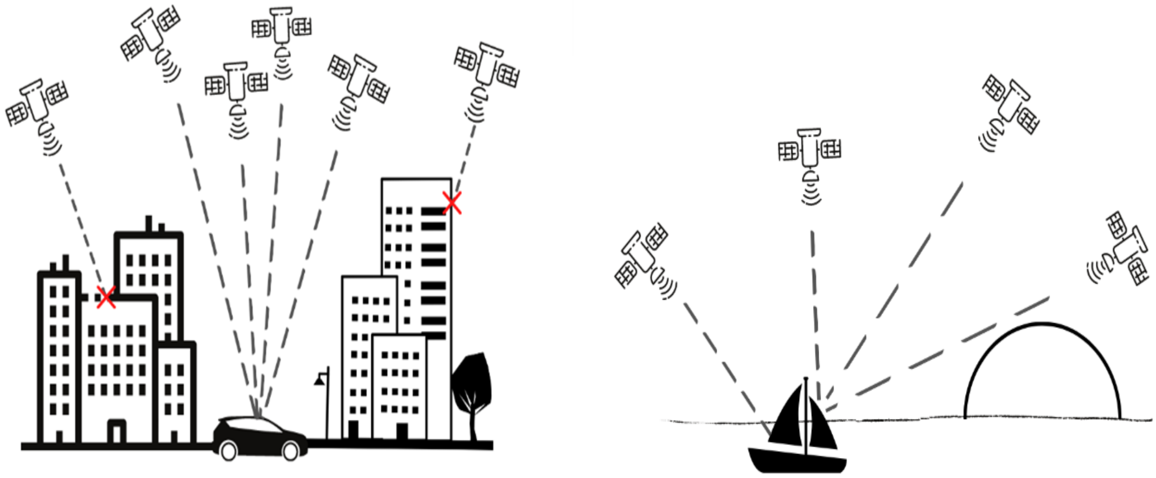


*Figure 10. Low GPS accuracy is common in cities, canyons, and forests, where devices' view of the sky is often obstructed so satellites used to gather a GPS position are close together (left). Higher accuracy will be obtained in an open environment, e.g. open water (right). Recreated from*[8]

[7] https://ozzmaker.com/gps-position-accuracy-and-how-to-tell-if-you-have-a-good-fix/
[8] https://ozzmaker.com/gps-position-accuracy-and-how-to-tell-if-you-have-a-good-fix/

## 6.3 Fix acquisition and data transmission success rates

Data transfer success rates are the lowest for satellite tracking technologies when compared with store-on-board, VHF/UHF, and GSM units, and they have the most variability in terms of success (Hofman et al., 2019).

There are, however, instances in which satellite is preferable to UHF/VHF and GSM despite these issues, for example, when species disperse over very large areas or inhabit really remote, inaccessible areas.

Overall fix success rate (fixes both collected and transferred to the user) was found to be 78% in one satellite telemetry study, with failures generally due to fix acquisition and unit failure, although data transfer was more important in certain situations e.g., where the animal lived in dense forest (Hofman et al., 2019). The limited bandwidth of satellite systems (e.g., Argos at 256 bits every 15s) also limits data transfer volumes so things like extended video or detailed accelerometry data cannot be transferred. It is easier for researchers to predict and control the chances of data transfer via UHF/VHF and GSM based on species behaviour and locations of receivers and sending towers than it is to predict transfer over satellite systems (Hofman et al., 2019). This is due to receivers being in closer proximity within the environment with less unknown variables.

## 6.4 Batteries

Transmission of information from a tag to a satellite in orbit is energetically costly, meaning that battery life, in comparison to non-satellite tracking, is typically shorter. This can result in a trade-off between an increase in battery size or the collection of fewer data points. Any increase in battery size must be balanced with the welfare of the study animal.

Battery life can be maximised in two main ways:

1. Tag settings: There are a couple of ways that the settings can be adjusted to enhance battery life:

a) Duty cycle: using a pre-programmed schedule that, for example, only transmits locations overnight, if your study species is nocturnal, and the tags turn off during periods when not scheduled to obtain fixes or transmit data.

b) Reduce maximum search time: Reduce the maximum time of the tag when searching to gain a fix. However, it is important to note that this can result in trade-offs with regard to accuracy and fix rate. We recommend speaking with the supplier to understand this in relation to the specific hardware that you will use. It is also worth noting that the optimal search time varies dependent on habitat and species, as well as other factors.

Selection of the right settings can require prior knowledge to set settings and expectations. In an absence of this data, tags with two-way communication can be key so that settings can be altered after deployment.

2. Solar power: It is increasingly common for tags to be integrated with a small solar panel that provides ongoing power. This has resulted in the ability to study species throughout their entire lifetime, providing a wealth of valuable information. However, this adaptation is not suited to the tracking of all species; for example, when tracking species that are nocturnal, or use burrows or caves, they will be of limited use. There have also been examples of siltation when used in freshwater habitats, that can render panels non-functioning (Pers. Comms, P Griffith, 2022).

Thomas, Holland & Minot (2011) provide a useful 'Technology choice decision guide for solar or non-rechargeable battery', which can help to determine if solar/rechargeable batteries are a feasible option for your work.

Note on battery weight: The relatively high weight of batteries currently needed for satellite tags (due to higher energy requirements) preclude them from use on many bird and mammal species (Kays et al., 2015). Additionally, device weight has welfare implications; see Ethics overview, pg 47.

# 7. Considerations when planning a satellite tracking study

This section details broader factors that should be considered ahead of beginning your tracking study, including ethics and welfare, costs, species specific constraints and legal considerations. This is not meant to be exhaustive, but it is hoped that it will help to stimulate thought and discussion ahead of an in-depth literature review of satellite telemetry studies focused on your study species that will help to inform your work. We also recommend checking the six ecological/ conservation focused questions in Latham et al.'s (2014) GPS focused paper which can be applied to satellite telemetry research as a whole. They will help to determine if satellite telemetry is a suitable methodology for your study and will provide you with broad considerations.

## 7.1 Ethics and welfare

Biologging, in its various forms, has undoubtedly resulted in significant advances within the field of conservation (Bodey et al., 2017). However, the use of biologgers of any kind presents a trade-off between the knowledge to be gained from the study and the potential negative effects on the study animal (Bodey et al., 2017). Negative effects on study species' welfare, health and behaviour are well documented (Paci et al., 2019; Bodey et al., 2017).

There are two ways in which the use of tags can be detrimental to the wellbeing of an animal (Wilson et al., 2002): firstly, the effect of the capture and restraint process; and secondly, the effects of the tag itself. The latter can manifest in several ways, including changes to behavior, increased energetic costs, physical injuries (Vandenabeele et al., 2012), irritation, and even death. For example, a comprehensive meta-analysis of the effects of tracking devices on birds spanning 214 studies found that the use of tracking devices had a small but significant negative effect on survival, reproductive success, parental care, and foraging trip length (Bodey et al., 2017).

Consequently, tracking devices should only be used when no suitable alternative method is available, and it is critical to carefully consider the ethical and welfare implications of attaching a tracking device to an animal before commencing your research, centered around a cost/benefit analysis for each individual study of the potential value of the information vs. any negative effects.

Before commencing your study, it is also essential to:
(a) Thoroughly research the literature for suitable attachment techniques;
(b) discuss attachment options with the supplier of your tags and experts who have previously tagged your species, and;
(c) submit your plans to an appropriate ethical review body.

New research is continually emerging on the effects of tag weight, shape and size on study species, although there are significant gaps in knowledge. For example, a commonly used practice is that tags must not exceed 3-5% of a study animals' body weight. However, there is little evidence to support this (Paci et al., 2019) and whether the threshold is generalisable to all species is unknown (Bodey et al., 2017). Notably, a review of tracking in birds found no threshold below which effects were not observed, although fewer negative effects were reported in smaller tags (Geen et al., 2019). Consequently, device mass should be as low as possible, and do not assume that a relatively small or light device will have no negative effects.

In general, we advise checking the most recent literature, and speaking with the collar/tag supplier, experts who have tagged your intended species, and your ethical review body to determine whether tagging is appropriate and which device will minimize the chance of harmful effects. Finally, when conducting your study, great care must be taken to ensure that satellite tags are fitted safely to the study animal and to minimise any negative effects.

## 7.2 Costs

Cost is a major consideration for satellite tracking, which limits who can access the technology and the scale at which it can be deployed. Satellite tracking is expensive because the technology itself is complex and generally high-priced (individual tags for some species cost upwards of $2,000), it can be costly to deploy tags given the expertise and equipment required, and there are recurring monthly or annual costs associated with data transmission. For example, satellite tag hardware can be ten times as expensive as a VHF tag of similar quality/longevity, even before the additional data transmission costs are considered (Palminteri, 2017). Although note that this comparison does not take into account the high labour costs of using VHF tracking devices, which require the constant presence of a tracker in the field in order to obtain data points.

Before commencing your study, carefully assess whether satellite tracking is sufficiently affordable to meet your monitoring needs (Thomas, Holland & Minot, 2011). Consideration of cost vs. sample size for is key to experimental design (Hays et al., 2016). The high cost of using satellite tags means that researchers are generally only able to collect data from a small number of animals (Cagnacci, 2010), limiting inference that can be made from the data. A minimum sample size of 30 collared or tagged individuals, not data points, is recommended to make inferences at the population level (Hebblewhite & Haydon, 2010), with greater sample sizes required where there is greater within-species variation, such as by sex, age, or geography (Hays et al., 2016). Insufficient sample size can have knock-on effects for conservation recommendations (e.g. when identifying critical habitats (Fraser et al., 2018)).

Estimating costs for satellite telemetry can be tricky, partly because of a lack of publicly available information on costs from tracking providers, and partly because cost varies with context (e.g. species being tracked, sample size and length of the study (Thomas, Holland & Minot 2011)). Hardware costs will also vary depending on volume ordered, and data transmission costs will vary with type of data, location resolution, and frequency of fixes required (Kemp, 2021). There are also additional costs for wildlife tagging studies in general, alongside those of physical hardware and data transmission, such as travel, vehicles, vets fees, anesthetic drugs, replacement parts, etc.

Below we provide a high-level comparison of the costs of different tracking technologies (VHF/UHF; GPS; Satellite telemetry), alongside indicative costs for different satellite network providers, based on rates seen in 2021. These costs will likely change so speak to providers for up-to-date numbers.

The good news is that satellite tracking is set to get less costly in future. Satellite technology is rapidly evolving, with new networks and providers entering the market, exploiting the cheaper costs of launching constellations to low earth orbits, and inexpensive small satellites. Emerging providers such as Hiber, Lacuna, and Kineis are competing to reduce hardware and data costs and provide smaller devices which operate for longer durations. These new solutions need to be evaluated for reliability before being used in wildlife studies but could make satellite tracking more accessible and scalable. A comprehensive list of providers can be found in Appendix 2.

## 7.3 Species specific constraints

If an animal is considered large enough to carry a device, biological and behavioural life history traits can make tracking challenging. Burrowing or hibernating behaviour, and time spent underwater or within thick forest, can reduce opportunities for devices to make contact with satellites, reducing the frequency and accuracy of location fixes. Species morphology can be an issue when attaching devices. For example, collars placed on species with tapering neck shape, such as equids and polar bears, can be difficult to fit and easily lost (Shoenecker et al., 2020; Perras and Nebel, 2012). When drop-off devices are used, there is a chance that they might fall off in a place where it is impossible to recover, especially for animals that spend time underground, in trees or on cliffs.

Tag orientation also plays a role in fix success and can be impacted by the behaviour of the study species. Fix rates for Grizzly Bears, for example, were higher when bears had higher rates of movement, potentially due to the vertical vs. horizontal position of tags when bears were moving or at rest (Graves & Waller, 2006). Bears also tend to forage in open areas and rest under forest cover, further reducing fix rates (Heard et al., 2008), demonstrating how multiple factors can combine to impact tracking error.

# Case study 3

Tagged green turtle (c) Miguel Varela

## Understanding Green turtle habitat use in West Africa

**Researcher:** Dr Ana Rita Patricio, Postdoctoral fellow, University of Exeter

**Species being collared:** Green turtles, *(Chelonia mydas)*

---

### What research question are the satellite collars being used to answer?

*Overall, the satellite tags are meant to assess the spatial distribution and marine habitat use of West African green turtles, and to explore the efficacy of marine protected areas (MPAs) in the region to protect them. Since 2018, we have deployed satellite tags on females (n=58), males (n=14) and juveniles (n=12), at two sites: the nesting beach/breeding area of the João Vieira-Poilão Marine National Park (PNMJVP), in the Bijagós archipelago, Guinea-Bissau, and the Banc d'Arguin National Park (PNBA), in Mauritania. Both sites are MPAs.*

*Tags are being used to investigate 1) home range and spatial distribution of breeding females, 2) migration routes of breeding male and females, 3) foraging grounds of breeding individuals, 4) priority areas for conservation. We are looking at differences between females and males in terms of migratory or foraging strategies, home ranges of males, females and juveniles to identify where 'no-take' zones could be usefully deployed and examining how environmental conditions such as sea surface temp, bathymetry and seagrass presence influence spatial distribution.*

### What are the challenges of tagging your species?

*Currently, there are no major challenges in the attachment of satellite tags on hard-shelled sea turtles, there are well-designed protocols and effective glues and resins that dry very fast and are waterproof. Deployments can be conducted while turtles lay their clutches of eggs or turtles can be temporarily restrained for a short period of time (20 minutes) without much effort for researchers and without stressing the animals.*

*The devices have a hydrodynamic shape, are lightweight and are relatively robust. Antennas on*

## Case study 3

*smaller-sized tags, which we applied for juvenile turtles with curved carapace lengths ranging from 55-68.5 cm looked more fragile.*

*The major challenge that we face relates to animal behaviour: sea turtles spend most of their time underwater, only surfacing to breathe (in warm waters they do not need to surface to warm their body temperature), so the quantity of data is limited, as tags only transmit when the antenna is outside of the water. Increasing the transmission or repetition rate to 15 seconds enhances the possibility of data transmitting locations – we had this programming with Wildlife Computer tags, but not always with Lotek tags.*

*Another challenge is satellite cover, which is lower closer to the equator. At our study sites we have periods with no coverage (00:00 to 04:00 and 12:00 to 16:00) and tag programming needs to take this into account. One option is to disconnect tags during that period to save battery, but we recently had a problem as our tags were collecting summary DIVE data every 4 hours and were programmed to transmit these summaries during the following 4-hour periods, which meant that we have periods of blanks, which correlate with the absence of satellites.*

### What tags did you use & why did you choose them? What considerations and tradeoffs did you make?

*Our main considerations when choosing a supplier was price and technical support, i.e. how fast they respond to technical issues and how well situations are resolved. In terms of model, we initially used ARGOS tags to learn about migration and identify foraging sites, moving to FastGPS for finer scale spatial distributions [e.g. to assess boundaries of the MPA or distribution of seagrass.] TDR tags (time depth recorders) have allowed us to further explore how turtles user marine habitats.*

*In the past we have used Wildlife Computers Spot 375B ARGOS tags, Lotek F6G 376B and F6G 276F tags with FastGPS and more recently, Lotek DIVE tags – models F6G 376B and F6G 276F with depth sensors, usually deciding between them based on recommendations from colleagues, the functionality offered, the level of customer support and for specific features offered e.g. tags that can be switched on with a magnet but will also activate independently in contact with seawater if a user forgets to switch it on.*

### What have you learned from your work?

*We have greatly advanced the knowledge on the spatial distribution of West Africa green turtles, with data contributing to several scientific manuscripts in press and with more data yet to analyse.*

*In terms of working with the technology and suppliers, key learnings are:*

- *It is essential to discuss research questions and data needs with technicians to be sure that you are getting what you need, before compromising.*
- *Always test the tags before using them and before leaving for the field, particularly if there are no means of communication at your field site.*
- *If you are not tech-savvy then the best approach is to have satellite tags programmed to collect data non-stop with the highest repetition rate- Wildlife Computers can supply this and the battery life is still very good.*
- *Consider using TDRs (Time-Depth Recorders- a small and cost-effective data archiving tag) even if your current question only regards horizontal distribution, as you can accumulate data useful for future research.*

# 8. A potted history of satellite tracking

## Inception of satellite tracking

Satellite tracking is a relatively new technology that ultimately arose from the 1957 launch of the first space satellite – Sputnik – and the subsequent space race between the US and the Soviet Union, which led to the creation of GPS (Global Positioning System) [20].

Originally designed for military and intelligence applications, the US navy first brainstormed the idea of a GPS in the 1960s; however, it wasn't until 1973 that the outline of the current system was conceived by the US Department of Defense at the Pentagon. Testing began in 1974, and in 1978 the first experimental GPS satellite was launched to trial the tracking of fleet vehicles, amongst other uses. Initially, the launch of 18 satellites was planned to provide full GPS coverage but it soon became apparent that 24 would be needed. In 1989 the first of these operational satellites was launched. The final satellite was put in place in 1994 and the system was declared fully functioning in 1995[21].

Although initially intended for military use only, following the crash of a Korean aeroplane in 1983 the US announced that it would make GPS freely available for civilian use in order to improve navigation and increase air traffic safety. President Bill Clinton further strengthened the importance and relevance of GPS within the non-military world through an executive order that stated that civilian GPS was to become as accurate as military GPS from 2000 [22].

Other potential uses of GPS quickly became apparent when the technology was released for wider use. It revolutionized navigation, both at sea and on land, by providing position reports with unprecedented, pinpoint accuracy [23], and has gone on to be used to track parcel deliveries, enable emergency responders to reach casualties in remote locations, manage fleets of vehicles, track taxi journeys, and navigate walking routes.

## First applications to wildlife monitoring

During the early 1960s wildlife biologists created one of the first remote tracking technologies through the application of radio telemetry as very high frequency (VHF) collars or tags. These contain radio transmitters that continually send out a pulsed radio signal that can be picked up by a receiver and are used in conjunction with directional antennas (Evan et al., 2016). Although VHF tags revolutionised the field of animal tracking, through the provision of location data that wasn't previously possible, they weren't without their limitations. These constraints included the significant effort of the investigating scientist in terms of tracking the subject in the field (it may take a whole day or longer to track down a study animal), the limited number of data points, and the relative inaccuracy of the data collected, as well as the biases of data collection, which can be influenced by the weather, site accessibility, the presence of observers, and the occurrence of specific animal behaviours (Evan et al., 2016).

[20] https://www.wired.com/2007/10/dayintech-1004/

[21] https://www.wired.com/2011/02/0214gps-satellite-launched/

[22] https://www.wired.com/2010/12/1208-gps-open-civilians/

[23] https://www.wired.com/2011/02/0214gps-satellite-launched/

Consequently, when the world of satellite tracking began to open up to civilian use, wildlife biologists were keen to explore how it could be utilised. One of the first trials was by Craighead) in 1972, satellite tracking elk in Yellowstone National Park. Use of satellite telemetry started to become more widespread in the use of tracking large mammals from the mid 1980's (Hatch et al., 2000) and took off in the 1990's (Hofman et al., 2019).

### Innovation and scaling

Initially, the use of satellite telemetry to gather data on wildlife was limited by the cost of the devices, the battery life of the units worn by the study animals (which was constrained by the size and weight of the battery), and the limited memory that the devices offered. However, a number of factors over the last ten to twenty years, including increased reliability, and reductions in cost and size, have converged to move satellite telemetry and animal tracking science into what is considered to be its 'golden age' (Kays et al., 2015).

Components have been miniaturised as a result of the demand for higher performance smartphones (Rahim, 2021), the benefits of which have carried over to the world of satellite tracking. This has resulted in reduced weight of collars and tags allowing use across a greater range of species and life stages and longer-term studies, and enabled the addition of other sensors, including accelerometers, gyroscopes, magnetometers and solar charging panels, prompting the generation of far richer, more valuable data sets. The technology has also reduced in cost as a result of these developments, leading to an increase in the use of satellite telemetry for wildlife research, as demonstrated by the huge uptick in the number of publications that use this methodology (Hofman et al., 2019.)

We are now able to track species at unprecedented spatial and temporal scales, in turn generating ever more data. The scientific community is coming together through the creation of collaborative infrastructures that allow the management and sharing of these sizable datasets (Curry, 2018), such as MoveBank (Hofman et al., 2019).

# 9. Further reading

Thomas, Holland & Minot (2011) provide information on: assessing potential approximate costs of differing methods so that they may be compared; areas for consideration with regard to sample size; Technology decision guides and a decision guide to determine if a solar powered tracking device would be suitable for your study.

Latham et al. (2014) provide information on: determining if satellite tracking is a suitable method for your study; broad considerations.

Hofman et al. (2019) provide a 'Recommendations' section with regard to practical steps of carrying out a satellite tracking study

Urbano et al. (2010) provide a detailed list of considerations and requirements regarding the management and storage of the data generated

Joo et al. (2020) provide a comprehensive list of software packages that can be used to analyse study data, and a summary of the main analyses types used for movement data.

This site [24] provides an overview of biologging, including satellite tracking.

---

[24] https://www.bio-logging.net/

# Appendix 1 - Common satellite tag providers

This is not an exhaustive review of all satellite tracking hardware providers but is intended to assist readers starting on their journey to determine where they can find technology suited to their needs.

| Brand | Notes | Website |
|---|---|---|
| **Advanced Telemetry Systems** | Provide a range of collars, backpacks, and ear tags<br>Species: birds, mammals, and marine animals | https://atstrack.com/index.html |
| **Africa Wildlife Tracking** | Provide custom made collars, ear tags and horn implants<br>Species: rhino, lion, pangolin, elephant, and others | https://awt.co.za/ |
| **Arribada** | Open-source, custom made hardware<br>Species: sea turtles, bears, elephants, sharks and others | https://arribada.org/ |
| **e-obs** | Provide a range of collars and tags<br>Species: birds, bats, crabs and others | https://e-obs.de/ |
| **Lotek** | Provide a range of hardware options that have features including the ability to take positional snapshots at predefined times and remote -release collars, to avoid the need for recapture<br>Species: wolves, caribou, mountain lion, moose, birds, sea turtles and marine mammals | https://www.lotek.com/ |
| **Microwave Telemetry** | Provide a range of solar and battery-powered transmitters.<br>Species: birds and fish | https://www.microwavetelemetry.com/ |
| **OpenCollar** | Open-source tracking collar hardware<br>Species: elephant, rhino, lion, cheetah, wisent, wild dogs, and others<br>Users can either have collars built, accessing design information through OpenCollar's open-source repositories on GitHub or purchase collars through Smart Parks | https://www.smartparks.org/opencollar-io/ |
| **Sea Mammal Research Unit** | Provide a range of bespoke hardware options that include features such as depth and temperature sensors.<br>Species: marine mammals | http://www.smru.st-andrews.ac.uk/Instrumentation/Products/ |

# Appendix 1 - Common satellite tag providers

| Brand | Notes | Website |
|---|---|---|
| **Telemetry solutions** | Provide custom made backpacks, collars, or implants<br>Specialise in the creation of very small GPS tags suitable for small mammals, herps and birds<br>They also make a limited range of larger devices for feral pigs, crocodiles, and alligators | https://www.telemetrysolutions.com/ |
| **Telonics** | Provide a range of options: backpacks, collars, necklaces, and tags<br>Species: birds, cetaceans, moose, lynx, wolf, turtles, and others | https://www.telonics.com/wildlife.php |
| **Vectronic Aerospace** | Provide several collar options each of which is designed to meet different needs<br>Species: bear lion, tiger, panda, boar, sika deer, elk, peccary, bison, reindeer, caribou, leopard, puma, jaguar, horse, tapir, and others | https://www.vectronic-aerospace.com/ |
| **Wildlife Computers** | Provide an extensive selection of hardware options and custom tags<br>Species: birds, pinnipeds, sea turtles, cetaceans, sharks, fish, penguins and others | https://wildlifecomputers.com/ |

# Appendix 2 - Emerging satellite location and communication providers

**Kineis:** A new subsidiary of CLS who will take over operation of the ARGOS system. Kineis are currently working on the development, production and launch into orbit of 25 nanosatellites, installation of 20 ground stations around the globe and upgrade of the IT infrastructures for this renewed system, which is planned to be operational by 2023.

Kineis will therefore be a hybrid system, using both satellite and terrestrial networks to enable connection to objects anywhere on Earth, with continual coverage. All existing ARGOS enabled devices will be able to connect to the new system to enable improved connectivity and coverage, whilst making data costs more affordable.

Other new satellite tracking providers include Hiber, Lacuna, Starlink and Swarm. Each of these companies have launched a number of low-cost nano or cube satellites in low orbits (500-600km). Currently these providers largely focus on IoT solutions rather than wildlife tracking, often requiring antenna sizes that are too large to use on wildlife. However, with reductions in antenna sizes, they have potential to provide a much lower cost solution compared to the data costs of traditional satellite providers.

**Lacuna**: Has low-cost cubesats flying at 500km orbits, circling the Earth 14 times each day. Low-cost, battery powered sensors transmit signals using LoRaWAN protocols (this requires low power, so conserves battery life) to these passing satellites, which store the data until they pass over a ground station where messages are relayed to the cloud platform and the user. In this way, Lacuna provides an ultra-low power tracking and connectivity service for short data messaging based on open source LPWAN protocols, that works everywhere, enabling the tracking of remote sensors or assets. Lacuna have so far launched 4 cubesat gateways so have a way to go until full service is provided and there is no option for downlink information currently. However, the service allows for existing LoRaWAN devices to be converted with modified antennas which means many devices can be connected quickly and easily, and devices can be small and low power. At present there would still be antenna size issues. Lacuna offers a super low-cost pay model (similar to LoRaWAN terrestrial networks) which offers significant data cost reduction compared to traditional satellite tracking technology.

**Hiber:** Is the world's first Low Power Global Area Network (LPGAN), with tiny, low-cost nano satellites orbiting just 600km above Earth. Hiber have low data costs, at just 4 to 6 euro a year for 4 fixes a day, and low device costs. However, Hiber devices currently require an antenna size of 280x280x27mm which means it is only applicable to non-animal devices.

**Starlink:** Is similarly focused on developing a low latency, broadband internet system to meet the need of broadband consumers across the globe, but again, antenna size is currently prohibitive for wildlife tracking solutions.

**SWARM Technologies:** is a private company based in the USA building a low Earth orbit satellite constellation for Internet Of Things (IOT) communications. They have a Federal Communications Commission (FCC) licence for low bandwidth communications satellites in low Earth orbit and have launched 9 test satellites and 36 low Earth orbit satellites to provide communication with IOT devices. They plan to launch a total of 150 LEO picosatellites. (CubeSats with a 0.25U form factor).

# Appendix 3 - High-level overview of the differences between the tracking technologies

High-level overview and comparisons of the differences between the tracking technologies available (VHF/UHF; GPS; Satellite telemetry).

| | VHF or UHF | GPS | ARGOS |
|---|---|---|---|
| **Hardware costs** | Relatively low, $200—600 approximately a tenth of the cost of satellite telemetry hardware | High cost, $2-8,000 unit & loss and repairs need to be factored in | High, typically each unit costs $2-8,000 & loss and repairs need to be factored in |
| **Cost to deploy** | Costs that may need to be covered: travel, vehicle, drugs to anaesthetise, vet & other ad hoc costs | Costs that may need to be covered: travel, vehicle, drugs to anaesthetise, vet & other ad hoc costs | Costs that may need to be covered: travel, vehicle, drugs to anaesthetise, vet & other ad hoc costs |
| **Cost to receive data** | High costs, labour intensive process, requires a person to visit the site & spend time locating the animal to acquire each data point | Ranges in cost dependent on method used, generally cheaper than satellite telemetry & VHF or UHF | High costs, ranges in cost depending on provider and number of fixes required |
| **Data transfer reliability (from device to user)** | Most accurate & reliable method | Variable as there are several different download methods available | Least reliable method, should expect for the loss of some fixes & account for this in the study design |
| **Advantages** | Low hardware costs<br>Lightweight collars/tags | No observer bias | No observer bias<br>Ability to track animal location as frequently as required |
| **Disadvantages** | Observer bias in data collection- human disturbance; weather; locations checked for presence etc.<br>Considerable amount of time can be spent locating the animal just for 1 data point | High hardware costs can reduce study sample size.<br>Can reduce connection between scientist to the field<br>Collars/tags are heavy and so are restricted in what they can be used on<br>Larger antennas required which increase overall size<br>GPS fixes can be slower to achieve than ARGOS | High hardware and data transmission costs – can reduce study sample size.<br>Can reduce connection between scientist to the field<br>Collars/tags are the heaviest of the options and so are restricted in what they can be used on |

# Reference list

Alfred, R. (2010). Dec. 8, 1993: Location, location, location. https://www.wired.com/2010/12/1208-gps-open-civilians/

ARGOS. (2020). FAQ Localisation Argos. https://www.argos-system.org/support-and-help/faqlocalisation-argos/ Accessed 30th January 2021.

Bartlam-Brooks, H. L. A, & Beck, P.S.A & Bohrer, G & Harris, S. (2013) In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. Journal of geophysical research: biosciences, vol. 118 https://doi.org/10.1002/jgrg.20096

Berger, J. (2004). The Last Mile: How to Sustain Long-Distance Migration in Mammals. Conservation Biology - CONSERV BIOL. 18. 320-331. 10.1111/j.1523-1739.2004.00548.x.

Bjørneraas, K. & Van Moorter, B. & Rolandsen, C.M., & Herfindal, I. (2010). Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics. The Journal of Wildlife Management 74, 1361-1366, https://doi.org/10.1111/j.1937-2817.2010.tb01258.x.

Bodey, T & Cleasby, I & Bell, F & Parr, N & Schultz, A & Votier, S & Bearhop, S. (2017). A Phylogenetically Controlled Meta-Analysis of Biologging Device Effects on Birds: Deleterious effects and a call for more standardized reporting of study data. Methods in Ecology and Evolution. 9. 10.1111/2041-210X.12934.

Burnside, R.J., Guilherme, J.L., Collar, N.J. et al,. Backpack-mounted satellite transmitters do not affect reproductive performance in a migratory bustard. Eur J Wildl Res 65, 98 (2019). https://doi.org/10.1007/s10344-019-1332-0

Cagnacci, F & Boitani, L & Powell Roger, A & Boyce Mark S.(2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challengesPhil. Trans. R. Soc. B3652157–2162

Census of Marine Life website (2009) http://www.coml.org/investigating/movement/acoustic_tags.html Accessed 20th January 2022.

Cheshire, J & Uberti, O. (2016.) Where the animals go. Particular Books.

Clements, S & Ballard, B & Eccles, G & Sinnott, E & Weegman, M. (2022). Trade_offs in performance of six lightweight automated tracking devices for birds. Journal of Field Ornithology. 10.1111/jofo.12392.

CLS, (2020). Collecte Localisation Satellites. https://www.cls.fr/en/ Accessed 28th December 2020.

Cooke, S.J. & Midwood, J.D. & Thiem, J.D. & Klimley, P. & Lucas, M.C. & Thorstad, E.B. & Eiler, J. & Holbrook, C. & Ebner, B.C. (2013). Tracking animals in freshwater with electronic tags: past, present and future. Animal Biotelemetry 1, 5. Doi: 10.1186/2050-3385-1-5.

Cooke, S.J. & Woodley, C.M. & Eppard, M.B & Brown, R.S. (2011). Advancing the surgical implantation of electronic tags in fish: A gap analysis and research agenda based on a review of trends in intracoelomic tagging effects studies. Reviews in Fish Biology and Fisheries 21, 127-151.

Craighead et al., (1972). Nasa website: https://ntrs.nasa.gov/api/citations/19720017418/downloads/19720017418.pdf See this paper for write up: https://www.jstor.org/stable/3830437?refreqid=excelsior%3A822dff06ec47e118cf4beefc296ba564

Curry, A. (2018). The internet of animals that could help to save vanishing wildlife. Nature 562, 322-326 doi: https://doi.org/10.1038/d41586-018-07036-2

Cushman SA, Elliot NB, Bauer D, Kesch K, Bahaa-el-din L, Bothwell H, et al.,. (2018) Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. PLoS ONE 13(7): e0196213. https://doi.org/10.1371/journal.pone.0196213

Cyr, A. & Nebel, S. (2013). Satellite and Data Logger Telemetry of Marine Vertebrates. Nature Education Knowledge 4(2):4

Deguchi, T & Suryan, R & Ozaki, K & Jacobs, J & Sato, F & Nakamura, N & Balogh, G. (2014). Translocation and hand-rearing of the Short-tailed Albatross Phoebastria albatrus: early indicators of success for species conservation and island restoration. Oryx. 48. 195-203. 10.1017/S0030605313000094.

Dodd, N.L. et al.,. (2007). Assessment of elk highway permeability by using global positioning system telemetry. Journal of Wildlife Management 71, 1107-1117

Dodge, S., Toka, M., Bae, C.J., (2021). DynamoVis 1.0: an exploratory data visualization software for mapping movement in relation to internal and external factors. Movement Ecology 9, 55, 10.1186/s40462-021-00291-5.

Dodge, S., Bohrer, G., Bildstein, K., Davidson, S.C., Weinzierl, R., Bechard, M.J., Barber, D., Kays, R., Brandes, D., Han, J. and Wikelski, M., 2014. Environmental drivers of variability in the movement ecology of turkey vultures (Cathartes aura) in North and South America. Philosophical Transactions of the Royal Society B: Biological Sciences, 369(1643), p.20130195.

Donaldson, M & Hinch, S & Suski, C & Fisk, A & Heupel, M & Cooke, S. (2014). Making connections in aquatic ecosystems with acoustic telemetry monitoring. Frontiers in Ecology and the Environment. 12. 565-573. 10.1890/130283.

Fleming, C.H &, Drescher-Lehman, J. & Noonan, M.J. & Akre, T.S.B. & Brown, D.J &, Cochrane, M.M. & Dejid, N. & DeNicola, V. & DePerno, C.S. & Dunlop, J.N. & Gould, N.P. & Harrison, A.L. & Hollins, J. & Ishii, H. & Kaneko, Y. & Kays, R. & Killen, S.S. & Koeck, B. & Lambertucci, S.A. & LaPoint, S.D. & Medici, E.P. & Meyburg, B.U. & Miller, T.A. & Moen, R.A &, Mueller, T. & Pfeiffer, T. & Pike, K.N. & Roulin, A. & Safi, K. & Séchaud, R. & Scharf, A.K. & Shephard, J.M. & Stabach, J.A. & Stein, K. & Tonra, C.M. & Yamazaki, K. & Fagan, W.F. & Calabrese, J.M. (2021). A comprehensive framework for handling location error in animal tracking data. bioRxiv 10.1101/2020.06.12.130195, 2020.2006.2012.130195, 10.1101/2020.06.12.130195.

Frair, J.L. & Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N. & Pedrotti, L. (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical transactions of the Royal Society of London. Series B, Biological sciences. 365. 2187-2200. 10.1098/rstb.2010.0084.

Franklin, C. E & Read, M.A & Kraft, P.G. & Liebsch, N & Irwin, S.R. & Campbell, H.A. (2009). Remote monitoring of crocodilians: Implantation, attachment and release methods for transmitters and data loggers. Mar. FW. Res. 60:284–292

Fraser, K & Davies, K & Davy, C & Ford, A & Flockhart, T & Martins, E. (2018). Tracking the Conservation Promise of Movement Ecology. Frontiers in Ecology and Evolution. 6. 150. 10.3389/fevo.2018.00150.

Geen, G. R. & Robinson, R. A., & Baillie, S. R. (2019). Effects of tracking devices on individual birds–a review of the evidence. Journal of Avian Biology, 50(2).

Gill, Jr, R & Tibbitts, T. & Douglas, D & Handel, C & Mulcahy, D & Gottschalck, J & Warnock, N & McCaffery, B & Battley, P & Piersma, T. (2008). Extreme endurance flights by land birds crossing the Pacific Ocean: Ecological corridor rather than barrier? Proceedings. Biological sciences / The Royal Society. 276. 447-57. 10.1098/rspb.2008.1142.

Graves, T. A.& Waller, J. S. (2006). Understanding the causes of missed global positioning system telemetry fixes. J. Wildlife Manage. 70, 844–851.

Gupte, P.R. & Beardsworth, C.E. & Spiegel, O. & Lourie, E. & Toledo, S. & Nathan, R. & Bijleveld, A.I. (2022). A guide to pre-processing high-throughput animal tracking data. Journal of Animal Ecology 91, 287-307, https://doi.org/10.1111/1365-2656.13610.

Hammerschlag, N & Gallagher, A & Lazarre, D.M.(2011). A review of shark satellite studies. Journal of Experimental Marine Biology and Ecology - J EXP MAR BIOL ECOL. 398. 10.1016/j.jembe.2010.12.012.

Harris, Grant & Thirgood, Simon & Hopcraft, J. Grant C. & Cromsigt, Joris & Berger, Joel. (2009). Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research. 7. 55-76. 10.3354/esr00173.

Hatch, S.A. & Myers, P.M & Mulcahy, D,M & Douglas, D.C. (2020). Performance of implantable satellite transmitters in diving seabirds. Waterbirds 23, 84-94

Hays, G & Ferreira, C & Sequeira,L & Meekan, A & Duarte, M & Bailey, C & Bailleul, H & Bowen, F & Caley, W. & Costa, D & Eguíluz, V & Fossette, S & Friedlaender, A & Gales, N & Gleiss, A & Gunn, J & Harcourt, R & Hazen, E & Heithaus, M & Thums, M. (2016). Key Questions in Marine Megafauna Movement Ecology. Trends in Ecology & Evolution. 31. 463-475. 10.1016/j.tree.2016.02.015.
Hazen, E & Maxwell, S & Bailey, H & Bograd, S & Hamann, M & Gaspar, P & Godley, B & Shillinger, G. (2012). Ontogeny in marine tagging and tracking science: Technologies and data gaps. Marine Ecology Progress Series. 457. 221-240. 10.3354/meps09857.

Heard, D. & Ciarniello, L & Seip, D. (2008). Grizzly Bear Behavior and Global Positioning System Collar Fix Rates. The Journal of Wildlife Management. 72. 596 - 602. 10.2193/2007-175.

Heathcote, A. (2017). Everything you need to know about the megamouth shark. Australian Geographic. https://www.australiangeographic.com.au/topics/wildlife/2017/08/everything-you-need-to-know-about-the-megamouth-shark/.

Hebblewhite M, & Haydon DT (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Phil Trans R Soc B 365:2303–2312. doi:10.1098/rstb.2010.0087

Hebblewhite, M, & Percy, M, & Merrill, E.H. (2007). Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the central Canadian Rockies. Journal of Wildlife Management. 71(6): 2026–2033. Doi: 10.2193/2006-238.

Hebblewhite, M,& Merrill, E, & McDermid, G. (2008). A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population.. Ecological Monographs 78, 141-166, https://doi.org/10.1890/06-1708.1.

Hofman M.P.G, & Hayward M.W, & Heim M, & Marchand P, & Rolandsen C.M, & Mattisson J, et al. (2019) Right on track? Performance of satellite telemetry in terrestrial wildlife research. PLoS ONE 14(5): e0216223. https://doi.org/10.1371/journal. pone.0216223

Hussey, N.E, & Kessel, S.T, & Aarestrup, K, Cooke, S.J, Cowley, P.D, Fisk, A.T, Harcourt, R.G, Holland, K.N, Iverson, S.J, Kocik, J.F, Mills Flemmin, J.E, & Whoriskey, F.G et al.,. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. Science 348(6240), 1-10.

Joo, R. & Boone, M.E. & Clay, T.A, & Patrick, S.C, & Clusella-Trullas, S, & Basille, M, (2020.) Navigating through the r packages for movement. Journal of Animal Ecology 89, 248-267, https://doi.org/10.1111/1365-2656.13116.

Joo and Basille (2022) CRAN Task View: Processing and Analysis of Tracking Data. Version 22.01 (2022-01-27). URL: https://cran.r-project.org/view=Tracking

Kays, R, & Crofoot, M. C, & Jetz, W, & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. Science 348(6240), aaa2478.

Kemp, R (2021) UKSA Sat4Wildlife use case report. Unpublished

Khan, 2022. How collaring cheetahs reduced human-wildlife conflict in Namibia. Reset. https://en.reset.org/how-collaring-cheetahs-reduced-human-wildlife-conflict-in-namibia/

Kough, A & Jacobs, G & Gorsky, D & Willink, P. (2017). Diel timing of lake sturgeon (Acipenser fulvescens ) activity revealed by satellite tags in the Laurentian Great Lake Basin. Journal of Great Lakes Research. 44. 10.1016/j.jglr.2017.10.008.

Latham, A. D. M, & Latham, M. C & Anderson, D. P. & Cruz, J & Herries, D & Hebblewhite, M. (2014). The GPS craze: six questions to address before deciding to deplpy GPS technology on wildlife. New Zealand Journal of Ecology. Vol 39

Levikov, N. 2014. To Migrate or to Forage? The Where, When and Why Behind Grevy's Zebra Movement. Thesis submitted to Imperial College London

Long, T. (2011). Feb. 14, 1989: GPS enters orbit. https://www.wired.com/2011/02/0214gps-satellite-launched/

Matley, J.K, & Klinard, N.V, & Barbosa Martins, A.P, & Aarestrup, K, & Aspillaga, E, & Cooke, S.J, & Cowley, P.D, & Heupel, M.R, & Lowe, C.G, & Lowerre-Barbieri, S.K, & Mitamura, H, & Moore, J-S, & Simpfendorfer, C.A, & Stokesbury, M.J.W, & Taylor, M.D, & Thorstad E.B, & Vandergoot, C.S, & Fisk, A.T. (2022). Global trends in aquatic animal tracking with acoustic telemetry. Trends in Ecology & Evolution, 37(1), 79-94. https://doi.org/10.1016/j.tree.2021.09.001

Matthews, A, & Ruykys, L, & Ellis, B, & Fitzgibbon, S, & Lunney, D, & Crowther, M. S, & Glen, A. S, & Purcell, B, & Moseby, K, & Stott, J, & Fletcher, D, & Wimpenny, C, & Allen, B. L, & Van Bommel, L, & Roberts, M, & Davies, N, & Green, K, & Newsome, T, & Ballard, G, & Wiggins, N. (2013). The success of GPS collar deployments on mammals in Australia. Australian Mammalogy, 35(1), 65-83. https://doi.org/10.1071/AM12021

Maxwell, S. M, & Breed, G. A. et al.,. (2011) Using satellite tracking to optimize protection of long-lived marine species: Olive ridley sea turtle conservation in Central Africa. PLoS ONE 6 (5), e19905.

Miller, M.R, & Takekawa, J.Y, & Fleskes, J.P, & Orthmeyer, D.L, & Casaza, M.L, & Perry, W.M. (2005). Spring migration of Northern Pintails from California's Central Valley wintering area tracked with satellite telemetry: routes, timing, and destinations. Canadian Journal of Zoology 83, 1314-1332 (2005).

Ministry of Environment, Lands and Parks Resources Inventory Branch for the Terrestrial Ecosystems Task Force Resources Inventory Committee (1998). "Wildlife Radio-telemetry". Ser. 2.0. Victoria, B.C.: Resources Inventory Committee. Archived from the original on 17 September 2016. Retrieved 3 April 2016.

Moen, R. & Pastor, J. & Cohen, Y. & Schwartz, C. C. (1996). Effects of moose movement and habitat use on GPS collar performance. J. Wildlife Management. 60, 659–668 doi:10.2307/3802085

Naidoo, R. & Chase, M. & Beytell, P. & Du Preez, P. & Landen, K. & Stuart-Hill, G. & Taylor, R. (2014). A newly discovered wildlife migration in Namibia and Botswana is the longest in Africa. Oryx. 50. 1-9. 10.1017/S0030605314000222.

Naidoo, R. & Chase, M. & Landen, K. & Beytell, P. & Du Preez, P. & Stuart-Hill, G. & & Taylor, R.(2017). Namibia and Botswana's zebra migration: Still the longest, but for how long? A reply to Schapira et al.,. Oryx, 51(1), 20-20. doi:10.1017/S0030605316000867

Oliver, R.Y. & Mahoney, P.J, & Gurarie, E, & Krikun, N, & Weeks, B.C, & Hebblewhite, M & Liston, G & Boelman, N. (2020). Environ. Res. Lett. 15 045003

Palminteri, S. 2017. Location, location, location goes high-tech: Facts and FAQs about satellite-based wildlife tracking. Mongabay https://news.mongabay.com/2017/05/location-location-location-goeshigh-tech-facts-and-faqs-about-satellite-based-wildlife-tracking/ Accessed 28th February 2021

Perras, M. & Nebel, S. (2012). Satellite Telemetry and its Impact on the Study of Animal Migration. Nature Education Knowledge 3(12):4

Pimm, S & Ayres, M & Balmford, A & Branch, G & Brandon, K & Kitching, R & Bustamante, R & Costanza, R & Curran, L & Dobson, A & Farber, S & Fonseca, G & Gascon, C & Brooks, T. (2001). Can we defy nature's end?

Power, R.J, & Rogan, M.S, & Naude, V.N. (2021) Mountain refugia limit anthropogenic suppression in a re-established felid population: the case of the Magaliesberg leopard population in South Africa, African Zoology, 10.1080/15627020.2021.2011411, 56, 4, (292-302)

Putman, N.F, & Mansfield, K.L.(2015). https://www.cell.com/current-biology/pdfExtended/S0960-9822(15)00328-0 Current Biology 25, 1221–1227 May 4

Rabaiotti, D. & Woodroffe, R. Coping with climate change: limited behavioral responses to hot weather in a tropical carnivore. Oecologia 189, 587–599 (2019). https://doi.org/10.1007/s00442-018-04329-1

Rahim, S. (2021) Washington Post. https://www.washingtonpost.com/climate-solutions/2021/10/11/high-tech-low-cost-push-track-sharks-rhinos-other-species-amid-climate-change/

Read, M. A & Grigg, G.C. & Irwin, R & Shanahan, D & Franklin, C.E. (2007). Satellite Tracking Reveals Long Distance Coastal Travel and Homing by Translocated Estuarine Crocodiles, Crocodylus porosus. PLOS ONE 2(9): e949. https://doi.org/10.1371/journal.pone.0000949

Regehr, E.V., Hunter, C.M., Caswell, H., Amstrup, S.C. and Stirling, I. (2010), Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice. Journal of Animal Ecology, 79: 117-127. https://doi.org/10.1111/j.1365-2656.2009.01603.x

Regehr, E.V., Laidre, K.L., Akçakaya, H.R., Amstrup, S.C., Atwood, T.C., Lunn, N.J., Obbard, M., Stern, H., Thiemann, G.W. and Wiig, Ø., 2016. Conservation status of polar bears (Ursus maritimus) in relation to projected sea-ice declines. Biology Letters, 12(12), p.20160556.

Robertson, (Thomas), B & Holland, J & Minot, E. (2012). Wildlife tracking technology options and cost considerations. Wildlife Research. 38. 653-663. 10.1071/WR10211.

Rowat, D & Gore, M. (2007). Regional scale horizontal and local scale vertical movements of whale sharks in the Indian Ocean off Seychelles. Fisheries Research. 84. 32-40. 10.1016/j.fishres.2006.11.009.

Ryan, P.G. & Peterson, S.L. & Peters, D.G. (2004). GPS tracking a marine predator: the effects of precision, resolution and sampling rate on foraging tracks of African penguins. Marine Biology, 145 (2004), pp. 215-223.

Sawyer, H., Nielson, R.M., Lindzey, F. and McDONALD, L.L., 2006. Winter habitat selection of mule deer before and during development of a natural gas field. The Journal of Wildlife Management, 70(2), pp.396-403.

Schapira,P & Monico, M & Rolkier, G & Bauer, H. (2016). Wildlife migration in Ethiopia and South Sudan longer than 'the longest in Africa': a response to Naidoo et al.,.. Oryx. 51. 1. 10.1017/S0030605316000363.

Skomal, G & Zeeman, S & Chisholm, J & Summers, E & Walsh, H & Mcmahon, K & Thorrold, . (2009). Transequatorial Migrations by Basking Sharks in the Western Atlantic Ocean. Current biology : CB. 19. 1019-22. 10.1016/j.cub.2009.04.019.

Thirgood, S & Mosser, A & Tham, S & Hopcraft, J. & Grant C. & Mwanogmo, E & Mlengeya, T & Kilewo, M & Fryxell, J & Sinclair, A. & Borner, M. (2004). Can parks protect migratory ungulates? The case of the Serengeti wildebeest. Animal Conservation. 7. 10.1017/S1367943004001404.

Tomkiewicz, S.M. & Fuller, M.R. &, Kie, J.G. & Bates, K.K. (2010) Global positioning system and associated technologies in animal behaviour and ecological research. Philosophical Transactions of The Royal Society B 365, 2163-2176.

Väli, U & Bergmanis, U. (2017) Apparent survival rates of adult Lesser Spotted Eagle Clanga pomarina estimated by GPS-tracking, colour rings and wing-tags, Bird Study, 64:1, 104-107, DOI: 10.1080/00063657.2016.1271395

Urbano, F. & Cagnacci, F. & Calenge, C. & Dettki, H. & Cameron, A. & Neteler, M. (2010). Wildlife tracking data management: a new vision. Philos Trans R Soc Lond B Biol Sci 365, 2177-2185, 10.1098/rstb.2010.0081.
Viana, D.S. & Granados, J.E. & Fandos, P.(2018). Linking seasonal home range size with habitat selection and movement in a mountain ungulate. Movement Ecology, 6

Villepique, J.T, & Bleich, V.C, & Pierce, B.M, & Stephenson, T.R, & Botta, R.A, & Bowyer, R.T. (2008). Evaluating GPS collar error: a critical evaluation of Televilt POSREC-Science (TM) collars and a method for screening location data. California Fish and Game, 94(4), 155-168

Wall, J & Wittemyer, G & Klinkenberg, B & Douglas-Hamilton, I. (2014). Novel opportunities for wildlife conservation and research with real-time monitoring. Ecological Applications. 24. 593-601. doi:10.1890/13-1971.1.

Wilson, R.P. & Gremillet, D. & Kierspel (2002). Remote-sensing system and seabirds: their use, abuse and potential for measuring marine environmental variables. Marine Ecology Progress Series 228, 241-261.

Witt, M.J. & Akesson, S. & Broderick, A.C. & Coyne, M.S. & Elick, J. & Formia, A. & Hays, G.C. & Luschi, P. & Stroud, S. & Godley, B. J. (2010). Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. Animal Behaviour 80 (3) 571-581 https://doi.org/10.1016/j.anbehav.2010.05.022

WWF/UNEP. A future for all: the need for human-wildlife coexistence. (2021). https://www.unep.org/resources/report/future-all-need-human-wildlife-coexistence

Yurkowski, D.J., Semeniuk, C.A.D., Harwood, L.A., Rosing-Asvid, A. and others.(2016) Influence of sea ice phenology on the movement ecology of ringed seals across their latitudinal range. Mar Ecol Prog Ser 562:237-250. https://doi.org/10.3354/meps11950