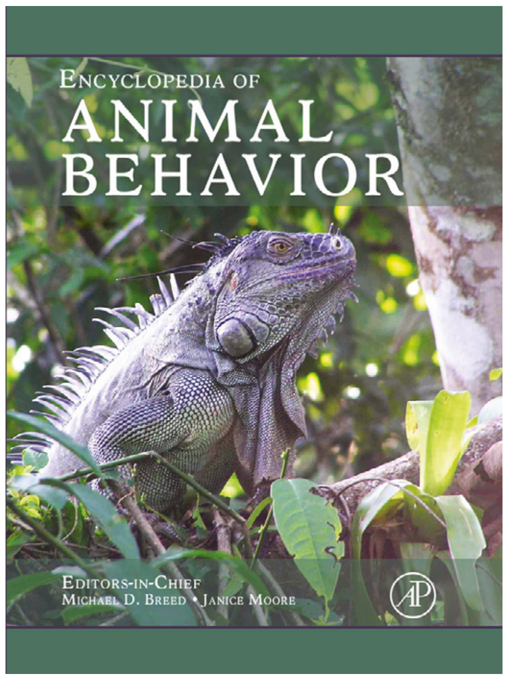

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Remote-Sensing of Behavior

N. Pinter-Wollman, Stanford University, Stanford, CA, USA
K. E. Mabry, New Mexico State University, Las Cruces, NM, USA

What Is Remote Sensing?

Remote sensing is information acquisition from a distance (without direct contact with the object observed). This term is often encountered in the fields of geography and ecology, where satellite data are used to infer topography, vegetation cover, system productivity, and other landscape attributes. Remote sensing usually provides large-scale data at the expense of detail (e.g., we can identify a habitat type as forest, but it would be difficult to determine the exact species of each tree). Similarly, remotely obtained behavioral data provide the big picture of animal movements, but usually do not address the fine details of the animal's motor patterns or exact behaviors, such as foraging. Still, much information about animals' behavior can be obtained remotely, with little interference to the study subject.

Why Use Remote Sensing to Study Behavior?

Spatial data from remote sensing may be used to answer a variety of behavioral questions. Early studies were primarily descriptive and focused on home range size, habitat use, survival, and movement patterns. Such descriptive data are still important for learning about the basic biology of cryptic, nocturnal, marine, migrating, and rare species that are not easily observed. However, researchers also use tracking data to test specific hypotheses about the relationship between an animal and its environment. For example, one can examine changes in spatial behavior as a function of life history stage (e.g., wintering sites of migrating birds) or competition pressure (e.g., the effect of population density on defendable territory size).

Studies of animal dispersal and migration have particularly benefited from advances in remote tracking of animals. Recent reductions in tag size have made it feasible to track extremely small animals such as dispersing juveniles. The ability to track an increasing number of migrating species has advanced our understanding of animal navigation, site fidelity, and population dynamics.

The study of animal movement also serves as a valuable link between animal behavior and conservation biology. Habitat conservation and restoration efforts and the design of wildlife corridors are often supported by data on animal movements. Increasing human populations around the world force many species into unfamiliar environments due to land use change (e.g., deforestation and expansion of agriculture) and wildlife management actions (e.g., reintroductions and translocations). Data on spatial behavior can greatly assist in determining which habitats to preserve and how different species and life stages cope with environmental change and teaching us about the mechanisms used for dealing with these changes (e.g., exploration patterns and changes in home range size or location).

One great advantage of remote sensing over direct observation is the ability to monitor the behavior of individual animals with minimal observer interference. After an initial tagging event, animals are left alone to behave naturally without further disruption. Remote sensing might be the only way for obtaining behavioral information about certain species, particularly those that are dangerous or difficult to see. Most tagging techniques allow individual identification of animals, which is especially useful for studying nocturnal animals or those that would be hard to distinguish using natural markings. The ability to continuously and reliably obtain information about a specific individual provides detailed information about certain life history events such as dispersal or migration.

What Do Spatial Data Look Like?

Remotely sensed animal location data consist of, at least, a series of X and Y coordinates coding the animal's location, and the associated time of each location. There are three primary types of spatial coordinate systems in use: longitude/latitude, Universal Transverse Mercator (UTM), and user-designed coordinate systems.

Longitude/latitude coordinates are based on a circular coordinate system that covers the globe. Location on the north–south axis is the latitude component and location on the east–west axis is longitude. These coordinates are measured in degrees, minutes, and seconds. This system provides continuous coverage of the entire globe. Therefore, it is the most suitable coordinate system for studying long-ranging animals.

UTM is a rectangular coordinate system, which is not continuous across our spherical globe. Between 80° S and 84° N, the earth is divided into 60 zones, within which the UTM system is continuous. An advantage of the UTM system is that each unit is 1 m, which simplifies the calculation of distance between locations in the field.

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If a field site spans the boundary between two UTM zones, a researcher may choose to use latitude/longitude coordinates instead, or to convert locations from one UTM zone so that they are compatible with those collected in the other zone. Conversion between the UTM and the longitude/latitude systems is possible but not straightforward.

Finally, researchers may create their own coordinate systems for use in small field sites or lab studies. This approach is usually taken when the spatial resolution of a GPS is large relative to the spatial activity of the study animal. For example, if the movements of a 1-cm long insect are being tracked, the 5-m error associated with the locations from most handheld GPS units will be too large. The main disadvantage to this approach is its inconsistency across studies. Furthermore, for maximum accuracy, one should use proper distance measuring tools in the field, which may not always be possible.

How Do We Study Behavior Remotely?

There are many methods for gathering behavioral data remotely. All methods reviewed here involve affixing a tag to an animal and tracking the signals emitted from the tag, or downloading data stored on a tag. There are several types of tags, categorized by the wavelengths they transmit. A tag may contain more than one type of tracking mechanism. For example, a GPS recording tag can also be equipped with a VHF transmitter. The suitability of each tag type will depend on the study species, habitat, and the study aims. Here, we present several tagging methods, explain how they operate, and provide some advantages and disadvantages of each tag type. We will summarize this section with general considerations relevant to all tags.

Radio Tracking (VHF)

Radio tracking is probably the most widely used method for acquiring behavioral data remotely. Radio tags constantly transmit a radio signal at a set frequency in the very high frequency (VHF) range (142–230 MHz). Each tag transmits a unique radio frequency (e.g., 150.020, 148.800 MHz) used for distinguishing between different tagged individuals; these signals are detected using a receiver (Figure 1). Both tag and receiver are equipped with antennas, the size of which will determine the distance from which the tag can be detected.

Receivers can tune into different frequencies either manually or automatically (using a programmable receiver). When a tagged animal is within the range of the receiver, a beeping tone is heard and its strength is used to determine the direction of the animal. The antenna connected to the receiver is used for scanning the landscape by carefully 'sweeping' it from side to side. The direction in which the tone is strongest is recorded as the bearing to the animal. Researchers can determine the location of a tagged animal using the following techniques.

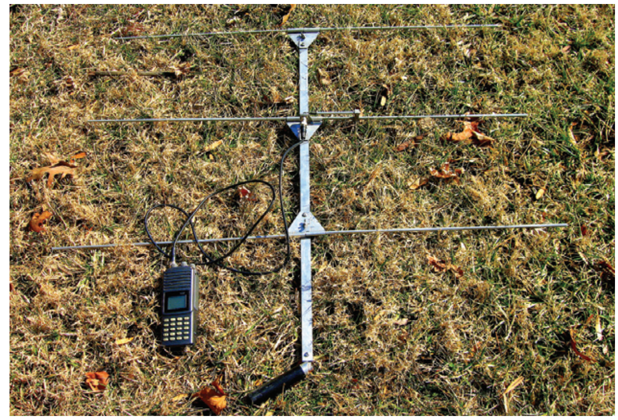

Figure 1 R1000 Communications Specialists handheld receiver connected to a three-element Yagi antenna. Photo by Karen Mabry.

Ground tracking

One simple method for locating a tagged animal is homing in to its signal. This is achieved by following the strength of the tag's signal until the animal is seen. This method is not always feasible because the animal may hear the observer approaching and move away, or the terrain may be impassable. In addition, this tracking method is likely to disturb and alter the tagged animal's behavior. Thus, researchers may choose to obtain the location of a tagged animal indirectly, using triangulation.

Triangulation requires at least two directional bearings toward a tag from known locations. The estimated location of the tagged animal is based on the intersection of the bearings (Figure 2(a)). Bearings are obtained using a handheld antenna, vehicle-mounted antenna, or antennas on fixed towers. The simplest way to obtain a bearing is to rotate the antenna 360° and record the direction in which the signal is the strongest, using a compass. When using a handheld compass, it is important to account for magnetic declination – the difference between true north and magnetic north, which varies across the globe. Just two intersecting bearings are needed to generate an estimated location, but at least three bearings are needed to estimate the associated location error (Figure 2(a)). However, more bearings are not necessarily better; rather than resulting in a more accurate location, too many bearings may create confusion (Figure 2(b)). Location accuracy will depend on the intersection angle of the bearings, the number of bearings, and the time interval between them. Note that animals may move while obtaining bearings. Thus, the size and speed of the study animal should be carefully

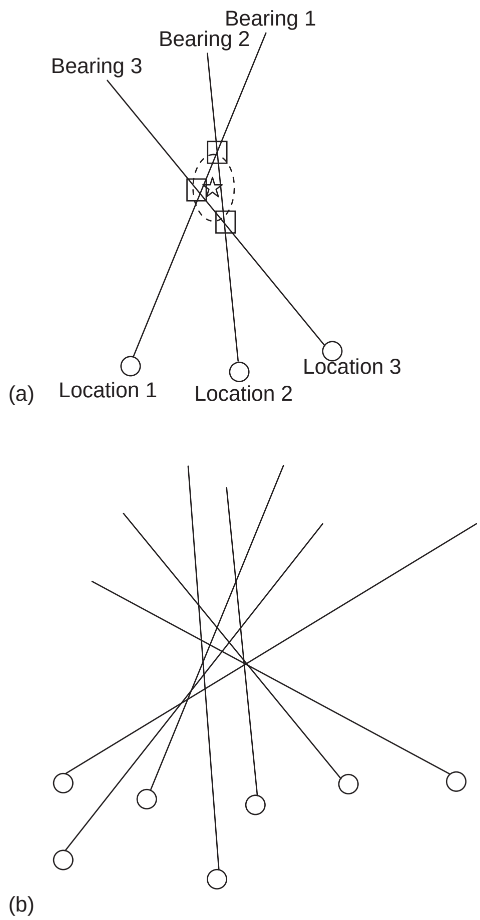

Figure 2 Triangulation to VHF tags. (a) Two bearings might be enough for obtaining an estimate of the animal's location, but notice that different bearing pairs may produce different locations (squares). Therefore, at least three bearings are needed for estimating a more accurate location and its measurement error (star – location and oval – error). (b) Too many bearings might not always be helpful – removing some of the bearings in this figure will not affect the estimated location of the animal.

considered when deciding on the number of bearings to use and the spatial and temporal distance between them. LOCATE III is a useful computer program for estimating an animal's location using triangulation.

Aerial tracking

When animals move large distances, are in inaccessible terrain, or many animals need to be tracked at once, aerial tracking may be used. Similar to homing in from the ground, an aircraft can be used to home in on a tagged animal. Light aircrafts used for wildlife telemetry are usually mounted with two antennas, one on each wing (Figure 3). A switch box connected to the two antennas is used for activating them. Initially, both antennas are activated. Once a signal is detected, the listener can alternate between the antennas to determine the signal's direction, depending on its strength. When the signal is very strong from

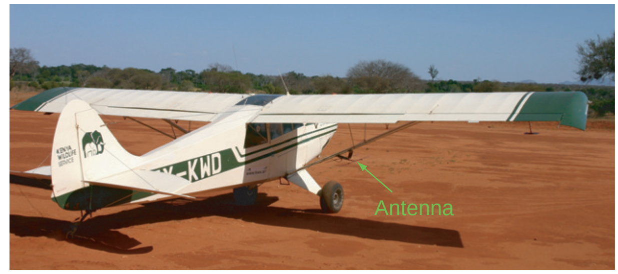

Figure 3 Light aircraft with antennas connected to each wing for wildlife tracking. Photo by Roy Wollman.

both sides, the aircraft can begin circling to visually search for the tagged animal.

A major advantage to radio tracking is its common use as a tracking method. There is a great deal of information about radio tracking in the scientific literature. It is possible that radio tracking has become so widely used because of its simplicity. VHF tag and receiver architectures are simple and therefore relatively inexpensive compared with other tags discussed later. In addition, the tag's simplicity allows for small tags that can be attached to small animals such as mice, frogs, and even large beetles. Despite its widespread use, radio tracking does have some disadvantages. The tracking equipment itself is relatively inexpensive, but tracking in the field may become very costly in terms of researcher time and fuel costs, especially if aerial tracking is needed. In addition, if triangulation is used, locations might be inaccurate. Terrain and vegetation cover can greatly influence signal accuracy because VHF signals may bounce off from hills, disappear in valleys, or be absorbed by heavy forest cover. Finally, accessibility should be carefully considered when planning ground tracking – extensive road or trail systems and high topographical features for bearing stations can be useful.

Ultrasonic Telemetry

In aquatic environments, radio frequencies (VHF) can be greatly distorted and are hard to detect. Therefore, tags for tracking aquatic animals utilize ultrasonic frequencies (30–80 kHz, 75 kHz being the most popular). These frequencies can be used only in fresh water environments.

Tracking ultrasonic tags is similar to radio (VHF) tracking, with the primary difference being that tracking is conducted by boat, or by using fixed underwater receiver stations, because the tagged animal is underwater. Water-submerged antennas are often used to avoid signal distortion arising from the transition between water and air. In addition, homing in on the tagged animal, as described for radio tracking, can be used to position a boat or an aircraft directly above the tagged animal. The advantages and disadvantages of ultrasonic telemetry are similar to the ones mentioned for radio tracking.

Satellite Tracking

Some animals, such as migrants, cannot be feasibly tracked using radio telemetry because of their large-scale movements. Platform Transmitter Terminals (PTTs) are tags used for satellite-based tracking. The 'Argos system' is used for detecting the locations of PTTs and for transmitting these locations directly to researchers, with no need for tracking the animals in the field. PTTs transmit a signal at a specific ultra high frequency (UHF) (401.650 MHz). Currently, five polar-orbiting satellites are equipped with receivers for this particular frequency. Based on how often a tag transmits a signal and the speed of the passing satellite, the tagged animal's location is calculated using the Doppler effect. Animals are distinguished from one another based on identification numbers that are specific to the tag's transmission electronics. In addition to calculating location, the satellite can also download data recorded by other devices attached to the tag such as a GPS, pressure sensor, and others discussed later. The satellites transmit the data to a receiving station on the ground which in turn sends the information to a processing center. The processing center consolidates the data and prepares them for presentation to the end user, the researcher. Data can be viewed on the internet, received by email, text message to a cell phone, and other communication channels.

PTTs are often deployed on marine and migrating animals (Figure 4). When aquatic animals are deep in the ocean, the satellites cannot receive the UHF signal. Therefore, PTTs for aquatic animals are often equipped with a device that activates them only when the animal surfaces, thus preserving battery power. This may reduce the number of locations per day that can be obtained for these animals.

A great advantage of satellite tracking is that animals can be tracked under all weather conditions, and at all times of day. Furthermore, once the tag is attached, there is no need to follow the animals in the field, thus greatly reducing the expenses of field work. This point is particularly important for long-ranging animals, such as migrants that can travel from pole to pole and for which VHF tracking is not practical. However, the location accuracy varies (from 250 m to 1.5 km error) depending on the number of fixes the satellite obtained when passing over the tagged animal. In addition, the number of locations obtained per animal depends on its position around the world. At the poles, a tag can be detected up to 14 times a day, but this number declines at lower latitudes. Another disadvantage to satellite tracking is its price. Because PTTs use a very specific frequency, manufacturers are under stringent technical constraints. As a result, PTT tags are larger and more expensive than VHF tags. Still, PTT tag sizes are getting smaller and the cost of tags and the associated data processing fees should be carefully weighed against the expenses of tracking a VHF tag.

Figure 4 A satellite-tagged Franciscana dolphin. Chicago Zoological Society's Sarasota Dolphin Research Program. Courtesy of Randall S. Well.

GPS

All the earlier-mentioned tags can be equipped with a global positioning system (GPS) unit. GPS units automatically record the animal's location at fixed, predetermined, time intervals and store the data on-board the unit. The frequency at which locations are obtained will determine the battery life of the unit and therefore the tracking duration. To preserve battery life, GPS units must have a clear view of the sky, to enable communication with the GPS satellites (Figure 5(a) and 5(b)). Heavy vegetation cover (e.g., thick forests) and aquatic environments may distort or disable the use of a GPS unit.

There are several ways to retrieve the data stored on-board the GPS unit.

Manual retrieval

One straightforward method for data retrieval is to remove the tag from the animal at the end of the study and directly connect to the GPS unit (using hardware and software provided with the tag). If recapture is impossible or unwanted, tags can be equipped with a drop-off device (Figure 5(c)). The drop-off device is scheduled to detach a tag at a predetermined time, and the researcher is left to find it. Having a VHF unit on such tags is useful for successfully locating them. After detaching from aquatic animals, tags float to the surface and can either be retrieved by the researcher or the data can be remotely downloaded through a satellite link (see below).

Remote retrieval

An alternative method to retrieve data from a GPS unit is linking to it remotely. Remote download permits multiple

Figure 5 African elephants collared with VHF/GPS collars with a drop-off unit. (a) A collared female elephant and her calf. The GPS unit is on top, between her ears, and the VHF unit is hanging below the elephant's chin. The drop-off unit is behind the elephant's ear and cannot be seen. (b) The GPS unit can be seen between the elephant's ears, facing the sky to allow easy connection with the GPS satellites. (c) An anesthetized elephant immediately after collar deployment. The VHF unit can be seen at the bottom with black cloth covering the VHF unit's antenna. The silver box is the drop-off unit and the GPS unit cannot be seen. Photos by Noa Pinter-Wollman.

data downloads throughout the study period, allowing adaptive management decisions and troubleshooting of data acquisition rate. Furthermore, remote downloading eliminates the need for recapturing an animal or depending on unreliable drop-off mechanisms. It also eliminates the challenge of finding a dropped tag in dense vegetation. Three ways to remotely link and download GPS data are:

UHF: Short-range receivers which rely on UHF remotely connect to the GPS unit and download the data, requiring a stable connection for several minutes.

Satellite: A satellite link can be used for downloading data from GPS units mounted on PTT tags, through the 'Argos system.' The data are relayed to the researcher in a similar manner to that described earlier in the satellite-tracking section. For downloading data using a satellite link from aquatic animals, the tag must be at the water surface to allow a stable connection.

GSM: Recent advances in the cellular phone technology allow remote downloading using the Global System for Mobile communications (GSM) network. The location data are then received as a Short Message Service (SMS) to a cell phone. This remote download method is available only in field sites with GSM coverage.

The major advantage to using a GPS unit is the excellent location accuracy (5–55 m error) at high temporal resolution. In addition, GSM and satellite retrieval methods allow obtaining real-time location of tagged animals, which is especially useful for making adaptive management decisions.

Some disadvantages to using GPS units include the tradeoff between data temporal resolution and battery lifetime, distorted or missing locations in dense habitats, and the GPS unit size, which currently constrains their use to animals heavier than 2 kg. Some potential problems with manual data downloading include inability to recapture the animal, failure of the drop-off mechanism, inaccessibility to the drop-off location, or inability to find the tag. For these reasons, GPS units should always be deployed along with VHF/PPT/Ultrasonic units to allow tag retrieval. These other tracking devices can also be used for obtaining spatial data at a lower temporal resolution, as backup for GPS failures.

Additional Data Collection Devices

In addition to a GPS unit, other sensors can also be attached to tags for collecting information about the environment and the animal's physiology. The data are often stored on-board these devices and can be retrieved using the techniques mentioned in the GPS section. Sensors may record water salinity, pressure, air and body temperature, heart rate, and activity. Marine animals are often equipped with pressure sensors to provide information on the animal's swimming depth, which is an additional spatial measure. The study of social behavior can also benefit from these devices. For example, microphones attached to tags record vocalizations, and recently developed proximity loggers record instances and duration of social interactions between tagged individuals.

These sensors provide additional useful and interesting data on the tagged individuals and by collecting data automatically, they can reduce the time required for behavioral observations. However, the more sensors placed on the tag, the heavier and larger it will be. In addition, note the advantages and disadvantages relating to data retrieval, mentioned earlier for GPS units.

RFID and PIT Tags

Radio frequency identification (RFID) tags are some of the smallest tags currently available. These tags encode information electronically (e.g., tag ID) and transmit it via radio waves. RFIDs utilize a wide range of frequencies (LF: 30–300 kHz; HF: 3–30 MHz; UHF: 300 MHz–3 GHz). Higher frequencies allow the information on the RFID to travel further using smaller tag antennas. Two types of RFIDs exist: active and passive. Active tags contain a battery that allows a constant transmission of the information on board the RFID. Passive tags do not contain a battery and the information on them is transmitted only when in proximity to a reader that 'wakes up' the tag by sending an electronic pulse to charge-up the tag. Because passive tags do not contain a battery, they can be very small, but this small size comes at the expense of reading range. Passive RFID chips can be as small as 0.3 mm^2; however, the read range of such a chip without an antenna is only 2–3 mm, connecting an antenna to the RFID chip increases its size (to several square centimeters) and read range (depending on antenna structure).

Passive Interrogated Transponders (PIT) tags are glass-encapsulated passive RFID tags that often utilize the low frequency range and can be as small as 8 mm (read range of ~20 cm). These tags are now widely used in wildlife studies, especially when studying small mammals, fish, amphibians, reptiles, and insects (**Figure 6**). The tag is usually injected into the animal (except for insects), thus enhancing its durability in the field. Because the read range of PIT tags is relatively short, the animal has to pass very close to the reader for data to be gathered. This often allows studies only on the presence/absence of an animal at a certain location (e.g., a nest site or feeding station). Thus, animals that routinely use certain locations, and study questions that rely on these locations would be good systems for deploying PIT tags. Certain tracking systems can provide spatial information as well. For example, a series of readers along a river enables researchers to record the movements of fish up and down the river.

The obvious advantages of RFIDs and PIT tags are their small size and low price. These features increase the range of species that can be remotely studied and reduces the financial burden of tagging large numbers of individuals. Furthermore, the injection of PIT tags into to animal's body eliminates the need to attach external, potentially disturbing tags. However, the small size of these tags comes at the cost of read range. In addition, while the tags are cheap, tag readers are expensive, and obtaining many of them might not be feasible, thus limiting the number of reading points available. In addition to field use, RFIDs and PIT tags may be implemented for tracking small animals in controlled lab environments.

Figure 6 A paper wasp tagged with a passive RFID. The tag shown is an insert of a PIT tag, without the outer glass casing. Photo by Aidan Weatherill.

Harmonic Radar

For tracking the flight path of insects, some researchers have used radar technology. The insects are tagged with very small and lightweight tags emitting super high frequencies (SHF) (3–30 GHz) that allow a radar detector to distinguish the flying insect from the background noise of moving objects (e.g., plants moving in the wind). The tagged insect can be detected at a radius of up to 400 m from the radar, depending on the insect's flight height (if it is flying above the horizon, it can be detected at longer distances).

These tags are extremely light and small but the radar detectors are large, bulky, expensive, and difficult to move. Furthermore, tagged insects cannot be individually identified, and radar error can be up to 7 m. Tracking insects using radar is uncommon and little information is available about it.

Bird flocks, flying bat groups, and very large insect swarms can also be detected using radar. In these cases, the animals are not tagged and the flight patterns of the entire group are detected by radars used for weather forecasting, similar to detecting rain clouds. This technique is used for tracking movements of large animal groups at large geographical scales. Radar technology does not allow distinguishing between individual animals or even between species (e.g., birds and bats). It can often be difficult to differentiate the signal of moving animals from background noise (e.g., clouds and vegetation).

Attachment Methods

There are many ways to attach tags to study animals. Researchers seek attachment methods that minimize interference to an animal's activities but ensure that the tags remain on until the end of the study. Tag manufacturers, veterinarians, and researchers working on similar species should be consulted when choosing the appropriate attachment method. Listed below are some available attachment methods.

Collars

Mostly used for tagging terrestrial mammals, collars attach the tag around the animal's neck (**Figure 5**). Collars should be loose enough to allow an animal to swallow but not so loose that it gets hung on vegetation. The space left between the collar and an animal's neck usually follows some rule of thumb specific to the species.

Harnesses

Animals whose necks are larger than their heads (including many birds, reptiles, and amphibians) cannot be fitted with collars and are instead fitted with harnesses. A harness is mounted on the animal's body like a backpack.

Tail Mounts

Tags are sewn into the shaft of a bird's tail feathers. The tag then falls off with the feather when it molts; therefore, this attachment method is usually for a short time period.

Glue On

When collars and harnesses will not work, because of the animal's body shape, or the environment, glues such as epoxy, cyanoacrylate (superglue), or eyelash glue may be used. It is important to ensure the glue does not cause skin irritation. Glues are commonly used to attach tags to aquatic animals (**Figure 4**), crustaceans, reptiles, insects (**Figure 6**), and some birds.

Implants

PIT tags and very small radio tags can be implanted in the animal. Implantation can be carried out through injection, ingestion, or incision. An incision will require anesthetizing the animal and keeping it under supervision for a few days after the surgery.

Ear tags and leg mounts are two additional less commonly used attachment techniques.

What Should One Consider When Choosing a Tracking Device?

Certain feasibility considerations apply to all of the aforementioned tags. The study objectives will guide how many animals and which individuals should be tagged, at what time of year they should be tagged, and the duration of the study. Funding availability often limits the number of animals that can be tracked. Thus, it is important to carefully design a tracking study to ensure that the data collected will actually address the study questions. Too often, researchers tag as many animals as they can afford and only later realize that a larger sample size is necessary to achieve sufficient statistical power or that the age and sex structure of the tagged animals restrict the study results.

Animals must be captured and sometimes anesthetized to allow the attachment of a tag. Capture equipment and anesthesia can be costly and should be considered in the project's budget. Capturing an animal can be difficult and time consuming; it might take a researcher several days or even weeks to locate and capture an appropriate individual. Anesthetization can be risky for the animal and should be conducted in consultation with a veterinarian or other experts. For some animals, anesthesia could be more risky than the stress of being tagged while awake. A variety of local, national, and institutional regulations and laws will apply to most capture and tagging procedures. The appropriate personnel (e.g., the Institutional Animal Care and

Use Committee (IACUC) at US universities) should be consulted to ensure that all research is consistent with the applicable laws, and that appropriate capture and anesthesia protocols are followed.

How large can a tag be? The rule of thumb used by most researchers allows for tags that weigh less than 5% of a terrestrial mammal's body weight and less than 2% of body weight for birds and bats. Aquatic animals can carry slightly heavier weights, but the tag's effect on their hydrodynamics is usually the confounding factor. Battery weight usually contributes the most to tag weight, and is positively correlated with the tag's life span and thus with the study duration. GPS and PTT fixes require considerable battery power, leading to a negative correlation between the number of GPS or PTT fixes and the tag's life expectancy. The development of solar-powered PTT and GPS units may increase tag life span. It is also important to match the battery life with the longevity of the attachment method. It makes little sense to invest in a large tag that can last for 2 years if the animal can remove it after 1 week.

Finally, once the study is completed, the tags should be removed to ensure the animal's well-being. Tags are often deployed for short periods of time, but may adversely affect the animal if left on for too long. Drop-off mechanisms and pop-off units are one way to achieve tag removal, but animals may need to be recaptured and even anesthetized for removing their tag. It may not always be possible to remove the tag at the end of the study, but every effort should be made to do so. As a practical consideration, many tags can be refurbished and reused, thus reducing the cost of tracking in future studies.

See also: Amphibia: Orientation and Migration; Bat Migration; Bats: Orientation, Navigation and Homing; Bird Migration; Fish Migration; Habitat Selection; Insect Migration; Insect Navigation; Irruptive Migration; Magnetic Compasses in Insects; Magnetic Orientation in Migratory Songbirds; Maps and Compasses; Migratory Connectivity; Pigeon Homing as a Model Case of Goal-Oriented Navigation; Sea Turtles: Navigation and Orientation; Spatial Orientation and Time: Methods; Vertical Migration of Aquatic Animals.

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