

Tracking Animal Location and Activity with an Automated Radio Telemetry System in a Tropical Rainforest

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How do animals use their habitat? Where do they go and what do they do? These basic questions are key not only to understanding a species' ecology and evolution, but also for addressing many of the environmental challenges we currently face, including problems posed by invasive species, the spread of zoonotic diseases and declines in wildlife populations due to anthropogenic climate and land-use changes. Monitoring the movements and activities of wild animals can be difficult, especially when the species in question are small, cryptic or move over large areas. In this paper, we describe an Automated Radio-Telemetry System (ARTS) that we designed and built on Barro Colorado Island (BCI), Panama to overcome these challenges. We describe the hardware and software we used to implement the ARTS, and discuss the scientific successes we have had using the system, as well as the logistical challenges we faced in maintaining the system in real-world, rainforest conditions. The ARTS uses automated radio-telemetry receivers mounted on 40-m towers topped with arrays of directional antennas to track the activity and location of radio-collared study animals, 24 h a day, 7 days a week. These receiving units are connected by a wireless network to a server housed in the laboratory on BCI, making these data available in real time to researchers via a web-accessible database. As long as study animals are within the range of the towers, the ARTS system collects data more frequently than typical animal-borne global positioning system collars (~12 locations/h) with lower accuracy (approximately 50 m) but at much reduced cost per tag (~10X less expensive). The geographic range of ARTS, like all VHF telemetry, is affected by the size of the radio-tag as well as its position in the forest (e.g. tags in the canopy transmit farther than those on the forest floor). We present a model of signal propagation based on landscape conditions, which quantifies these effects and identifies sources of interference, including weather events and human activity. ARTS has been used to track 374 individual animals from 38 species, including 17 mammal species, 12 birds, 7 reptiles or amphibians, as well as two species of plant seeds. These data elucidate the spatio-temporal dynamics of animal activity and movement at the site and have produced numerous peer-reviewed publications, student theses, magazine articles, educational programs and film documentaries. These data are also relevant to long-term population monitoring and conservation plans. Both the successes and the failures of the ARTS system are applicable to broader sensor network applications and are valuable for advancing sensor network research.

Keywords: sensor networks; animal tracking; environmental observing systems

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1. INTRODUCTION

Sensor networks have the potential to revolutionize our understanding of the natural and man-made environment by providing fine grained spatio-temporal data. This paper describes a sensor network designed to automatically, continuously and simultaneously track the locations and activities of radio-tagged wild animals living in a tropical rain forest. The developed system is not an in-laboratory research prototype, but a real-world working system that has been gathering science-quality data for over 6 years. This system is able to monitor the behavior of these wild animals at a much higher resolution than would be possible using traditional observational methods or other tracking technologies, including global positioning system (GPS) tracking. For this reason, we believe that the Automated Radio-Telemetry System (ARTS) system represents a significant advance in the use of sensor networks for animal monitoring.

2. SCIENCE MOTIVATION

Many important moments in an animal's life are difficult to study because they are rare, cryptic or occur over large spatial or temporal scales. One of the first obstacles any researcher studying wild animals must overcome is how to monitor and observe the behavior of mobile organisms. Attaching radio-tags to animals has been a primary method for studying animals in their natural environment for 50 years [1] and that vastly improved the quality and quantity of data that the biologists can collect [2, 3]. For example, our understanding of reproduction rates in many species is tied to an ability to find and monitor females during the birthing season, a feat that is often possible only through the use of radio telemetry [4–6]. In addition, much information on juvenile dispersal, a critical but poorly understood life stage, has come from radio-tracking studies [7–9]. Population density is notoriously difficult to quantify, and although dozens of methods are used to count individual animals, tracking is critical to any density estimate because it is the best way to quantify the areas used by the censused population. Finally, causes of mortality can best be determined by finding animals soon after their death, which typically requires animal tracking [10–12].

Radio-telemetry has greatly improved our ability to study rare behaviors and shy species. Traditional methods of radio-tracking, however, are inherently limited by the manpower that can be devoted to following study animals, and thus may not be adequate for addressing certain types of questions. In addition, many events such as predation are known to occur outside an animal's normal activity period and therefore are likely to be missed in traditional hand tracking studies [13]. The development of new tracking technologies capable of remotely, continuously and simultaneously monitoring the movements of a large number of study animals would provide a solution to these problems, allowing scientists to address previously

intractable questions. This in turn improves our knowledge of the dynamics of the natural world.

3. BACKGROUND

There are two basic ways to record animal motion [14]. The Lagrangian approach monitors a specific organism and records all the locations it passes over, while the Eulerian approach monitors a specific location and records the movement of all organisms across it. Eulerian studies are sometimes preferred because they do not require the capture of an animal, and so are less invasive [15]. However, they typically provide much less detailed data and therefore are more restrictive in the questions they can address. A Lagrangian approach (hereafter: tracking data), on the other hand, repeatedly records the locations of an animal moving through space. Observing the movement of an animal without tagging, it is rarely practical; so scientists have relied heavily on sensor technologies, especially radio-telemetry, and the GPS and Argos satellites (Table 1).

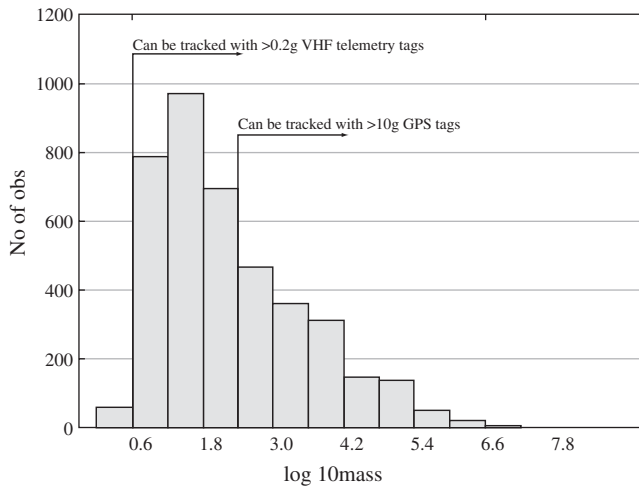
Radio-telemetry was the first technique developed to find and track free-ranging animals [1], and remains the most common method because of its low cost (300\$) and lightweight transmitters (>0.2 g [16]). Small transmitter size not only extends the range of species that can be tracked using radio-telemetry, but also minimizes the impact that the radio-tag has on the behavior of the study animal [2]. Because traditional radio-telemetry is collected manually, it is limited in the intensity and scale that data can be collected, typically <50 data points per day [2]. Automated tracking from satellites provides global coverage, but requires larger (usually >10 g) more expensive (few 1000s \$) tags, thus limiting the variety and number of animals that can be studied [17]. GPS- and satellite-based tracking technologies overcome many of these limitations, but Wikelski *et al.* estimated that 66% of mammal species and 81% of bird species were too small to be tracked by the smallest GPS tags available (Fig. 1) [17]. In contrast, VHF telemetry tags are so much smaller that they can be used on nearly all mammal species (Fig. 1). In addition, an obscured view of the sky by trees or mountains may limit the functionality of satellite-based systems [19]. The automation of data collection from VHF transmitters offers the potential of increasing the data resolution and scale of tracking projects [20] (Table 1). However, the promise of these systems has not been fully realized, in part, because of the difficulties in data acquisition and management.

3.1. Objectives

Here we describe an ARTS operating at the Smithsonian Tropical Research Institute field station on Barro Colorado Island (BCI), Panama. The ARTS uses standard VHF radio-tracking technology to monitor the movements of radio-tagged study animals automatically, continuously and simultaneously.

TABLE 1. Primary automated animal tracking methods.

Tracking method	Smallest tags, animal weight	Automated data collection?	Interference by vegetation
Traditional radio telemetry	0.2 g, 4 g	No	Low
GPS satellite tracking	10 g, 400 g	Yes	Medium
Satellite tracking (ARGOS)	10 g, 200 g	Yes	High
Automated radio telemetry (ARTS)	0.2 g, 4 g	Yes	Low

**FIGURE 1.** The body mass of Mammalia showing which species could be tagged by a 0.2 g VHF telemetry tag (animals >4 g) and those that could be tracked with a 10 g GPS tag (animals >200 g). Please refer to data from [18].

Because it relies on VHF technology, it can be used to track animals that are too small to be fitted with GPS transmitters. Additionally, ARTS is better able to track animals through the dense vegetation of a tropical rainforest than satellite-based tracking systems, which rely on UHF signals. In this paper, we provide a technical description of the ARTS system and report on its utility for studying the movements and activity of a variety of rainforest animals. The ARTS system has been used to track 374 individual animals from 38 species, including 17 mammal species, 12 birds, 7 reptiles or amphibians, as well as two species of plant seeds. The gathered data elucidates the spatio-temporal dynamics of animal activity and movement at the site. It is also relevant to long-term population monitoring and conservation plans.

4. SYSTEM DESIGN GOALS

Our field work was conducted at the BCI (9°10'N, 79°51'W) research station, which is managed by the Smithsonian Tropical Research Institute. BCI is a completely forested 1567 ha island

that was formed when the Chagres River was dammed to create Lake Gatun and complete the Panama Canal. Animals continue to move between the island and the surrounding national park land, which are separated by a distance of <400 m.

Tropical and sub-tropical environments are difficult for running a system of automatic electronic sensors because of the high rainfall and humidity. Although the temperatures on BCI are relatively stable throughout the year, there is a major variation in rainfall. The island receives an average of 2632 mm of rain per year, although roughly 90% of this falls during the ~8 month wet season (May–December). Because of the dense vegetation, humidity remains high year-round. At ground level in the forest, where most electronics are kept, relative humidity averages 80.6% in the dry season and 93.1% in the wet season [21]. Above the canopy, where some tower-based sensors are fixed, humidity is slightly lower (69.2% dry season, 80.2% wet season). In addition to the general risk of rain and humidity to electronics, rainy season storms bring an increased risk of lightning strikes to above-canopy towers. Finally, the increased cloud cover that characterizes the rainy season also decreases the potential for generating electricity from solar panels mounted on the towers. Sunny dry-season months average 19.5 MJ/m² day of solar radiation while rainy season months average only 14.0 MJ/m² day [21]. While these weather conditions are wetter than most temperate zone systems, they are typical of many tropical conditions, and represent a challenge to any tropical sensor network.

The ARTS system was designed to operate in the challenging conditions of BCI over multiple years with as little human intervention as possible. In designing the ARTS, we had seven primary design goals:

Robustness: The goal was to build a system that would operate effectively under these natural conditions (high rainfall, humidity and insect activity) and is robust to noise, signal-loss, multi-path effects due to forest-mountain environment.

Meet application-specific accuracy in harsh outdoor environments: In animal tracking studies, high accuracy of location estimates is always preferred. However, no remote tracking system is error-free. This system was designed to track a variety of animals that move over large areas (species that move multiple kilometers in a day). An accuracy of less than 50 m was desired to investigate both the large-scale

space-use patterns of study species and their finer-scale patterns of movement. In ARTS, the radio transmission range is typically few hundreds to a thousand meter.

Small form-factor for transmitters: The system was designed to track a wide variety of species, from insects to tapirs. We wanted to make sure that the behavior of a study animal is not altered by transmitter size or weight. Therefore, one of the goals was to use transmitters that are as inexpensive and light-weight as possible.

Scalability: An animal tracking study typically involves multiple animals being tracked at the same time. The system was designed to handle from one to at least twenty animals being tracked simultaneously. Because different users have different tracking requirements, the system needs to be programmable, allowing users to select sampling rates appropriate for their study question and study organism.

Spatial extensibility: Another design goal was the ability to change and augment the spatial coverage over time through the temporary deployment of additional receivers.

Remote command and control: Because sensors are spread throughout hilly terrain, the system was designed to stream live feed to monitor the performance of equipment. Additionally, we wanted to have an ability to modify programming from the central laboratory. In essence, the ability to remotely debug and control the system is a desirable property.

Multi-user functionality: Because a wide variety of researchers work on BCI, the system should be designed as a multi-user infrastructure to simultaneously and continuously track the movements of many radio-collared animals tagged for different studies. Each study might have different accuracy and power requirements.

5. AUTOMATED RADIO TELEMETRY SYSTEM INFRASTRUCTURE

In this section, we describe hardware and software elements of ARTS.

5.1. ARTS hardware

The ARTS system uses automated receivers to track the location and activity of transmitters mounted on animals, and relays these data to the laboratory in real time (Fig. 2). Biologists tracking animals with ARTS use standard radio transmitters (Fig. 3) available from a variety of commercial sources. However, each study must customize the design of the transmitters to not only be small enough to be carried by an animal without affecting its behavior, but also to securely attach to an animal that will probably try to remove it. Many mammals can wear a collar, which typically has few negative side effects. However, other

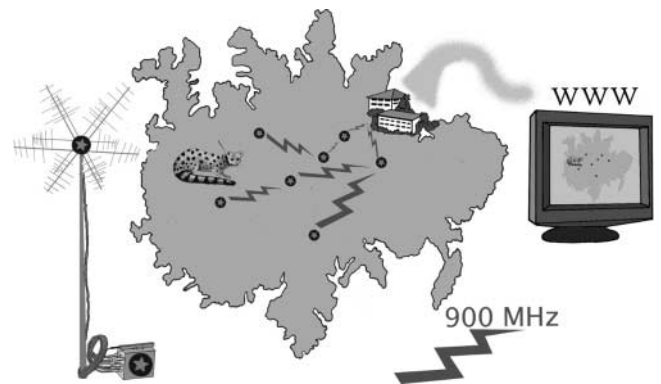


FIGURE 2. Schematic overview of the ARTS system. Radio transmitters placed on study animals emit 148–168 MHz radio signals, which are received by automated receiving units (red stars) connected to arrays of six wide-band Yagis antennas atop 40 m towers. The automated receiving units record the strength of the signal across the antennas array. The data are passed from the automated receiving unit to a filter box at the tower, which then sends it via a 900 MHz wireless network to the ARTS computer bank at the Smithsonian field station on BCI, Panama. The raw data (i.e. signal strengths), which are displayed real-time, are passed into SQL database on the ARTS server, which converts it into bearing estimates. These bearing data are then available to ARTS researchers anywhere in the world via the the Internet (art by Patricia Kernan).

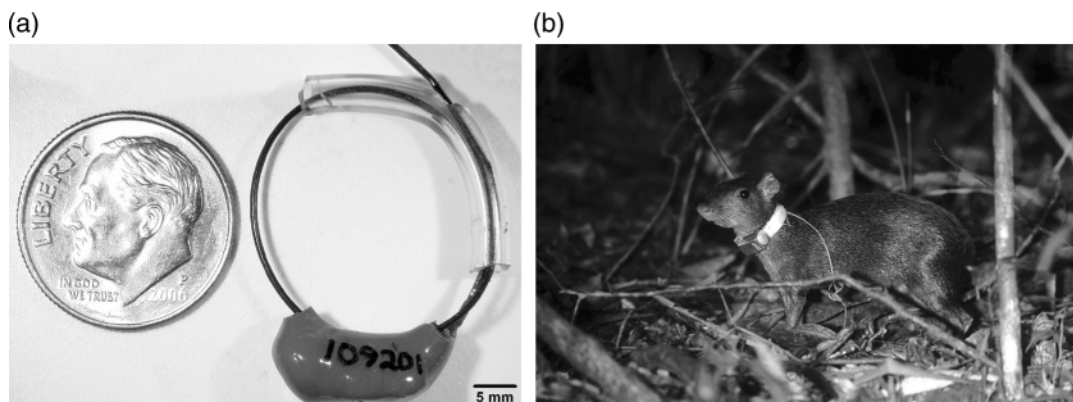


FIGURE 3. VHF Transmitters are tracked with the ARTS. (a) A small 1 g VHF radio collar designed to track small mice. (b) A Central American Agouti tagged with VHF tracking devices.

solutions must be found for animals that cannot wear collars (e.g. anteaters, birds), which sometimes include gluing the tags to the animals, attaching with a harness or even implanting them in the body cavity. Individual studies must carefully consider the anatomy and behavior of a particular species when customizing tracking tags.

The signals from the animal-borne transmitters are detected by one or more Automated Receiving Units (ARU), Sparrow Systems (<http://www.sparrowsystems.biz/>), Table 2, Fig. 4b, which comprise the core of the ARTS system. As shown in Fig. 4a, seven ARU's are deployed on 36 m radio towers constructed in the rainforest from Rohn 25 tower. These guyed towers manufactured by ROHN Products, LLC. are constructed with high strength steel tubing, and hot-dip galvanized after fabrication. The ARUs scan a user-selected list of radio-frequencies that correspond to the radio tags being worn by study animals, and record the signal strength of each frequency from each of six directional antennas in an array. The receivers are capable of searching over 200 channels in the frequency range, but time typically constrains the list to many fewer. The scan rate depends on the pulse rate of the transmitter. We typically set it to 1.5 s per antenna, or 9 s per frequency.

TABLE 2. Technical specifications for the ARU used in the ARTS system.

ARU specification	Values
Dimensions	15 × 15 × 15 cm
Weight	1000 g
Current 6 V	33 mA (1/5 W)
Current 12 V	35 mA (2/5 W)
Frequency range	148–170 MHz
Dynamic range	Variable standard calibration
Antenna input	BNC 50 Ohm, Unbalanced

An internal clock provides time stamps accurate to the nearest second over periods of many weeks. The receivers can record signal amplitude for continuous transmitters, in addition to pulse interval and pulse width from pulse transmitters. These receiving units are housed in water-proof containers to minimize the damage from the humid environment. The ARUs are located at the bottom of each of the 40-m radio towers that bear the antenna arrays. ARUs are connected to the antenna array on top of the tower by coaxial cables. A single ARU is sufficient to obtain temporal activity patterns, but at least three are needed to triangulate a location. In addition to streaming live data to the laboratory, data are recorded in exchangeable flash-memory modules, which we exchange every 1 or 2 weeks.

Each tower supports an above-canopy network of two sets of six log-periodic antennas vertically stacked 1.2 m apart, with six azimuth directions separated by 60°. These antennae allow the scanning of the frequency range of 148–170 MHz. This is the typical range for VHF animal tracking because the signals are able to penetrate the dense vegetation better than higher frequencies. Directional VHF antennas provide the strongest signal when pointed directly at the source, dropping off steeply when angled away. The specific directionality pattern of our antennas are shown in (Fig. 5). When manually tracking animals, these antenna are physically rotated while listening to the signal to determine the compass bearing from the receiver to the transmitter. To automate this process without requiring the mechanical movement of antennas, we use six stationary antenna, but space these out evenly across 360° so that their directionality patterns overlap. Comparisons of the two strongest signals allow us to estimate the compass bearing to the transmitter. For example, in Fig. 5a, an animal sitting at a bearing of 100° from the receiver would have its signal registered most strongly by antenna 6 and its second strongest signal from antenna 5. The ratio of these two signal strengths can thus be used to estimate compass bearings to radio transmitters.

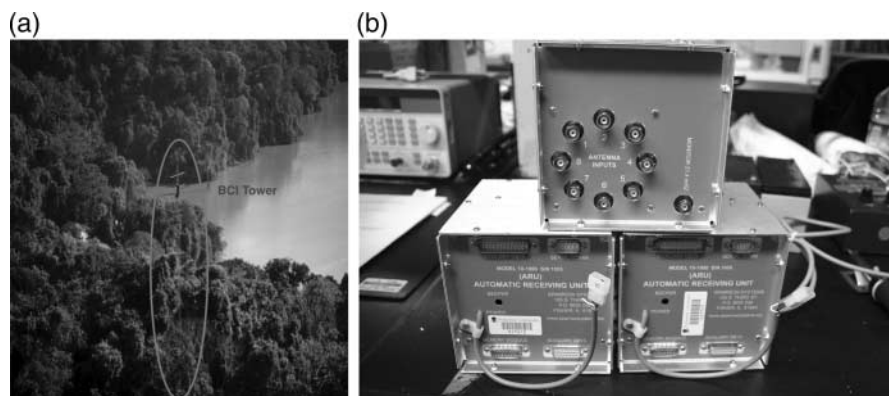


FIGURE 4. BCI hardware infrastructure-based around ARU. (a) An aerial view of an ARTS tower extending above the rainforest canopy on BCI, near the shore of the Panama Canal. (b) An automated receiving unit with connections for up to eight separate antenna (we use six for the ARTS). The unit scans each antenna to record the strength of a radio-tagged animal's signal from each one.

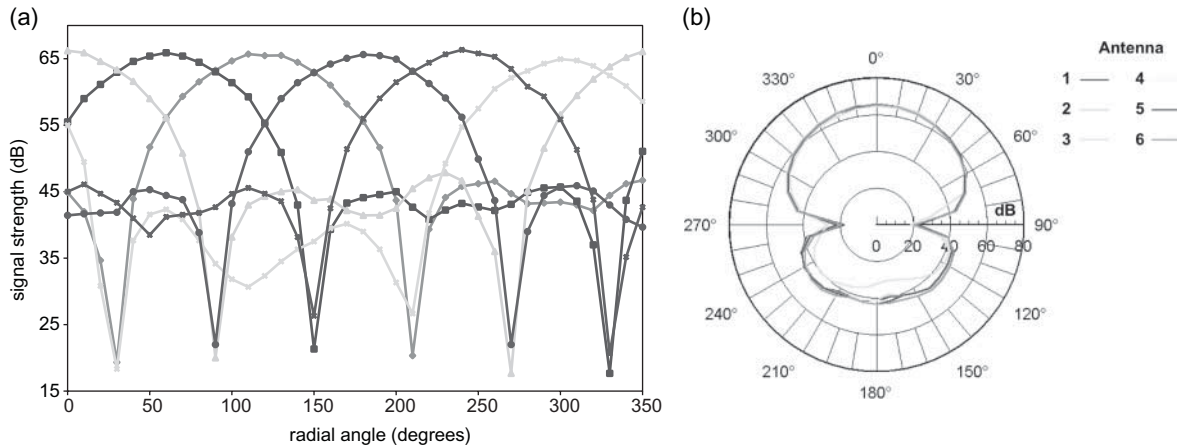


FIGURE 5. Directionality patterns for VHF antennas used by the ARTS towers showing the strength of signal received relative to the orientation of the transmitter to the compass bearing of the antenna. (a) The overlap of directionality patterns for the six antennas as they are mounted on the ARTS towers, pointing in 6 different directions. The bearing to a transmitter can be estimated by comparing the strength of the signal received from the two strongest antennas. (b) The overlap of directionality pattern of six antennas showing their consistency and symmetrical decline to either side of 0°.

Data from the receivers are streamed live to the laboratory via a 900 MHz network using waterproof FreeWave radios (www.freewave.com). We use a filter box between the receiver and the FreeWave radio to manage communications by buffering the output of the ARUs and tagging them with a unique tower identifier. The FreeWave radios are mounted on our above-canopy towers and set up as a multi-point network feeding into a master radio at the laboratory. Upon reaching the laboratory, data are received by a Linux machine that automatically loads them into a Web-accessible PostgreSQL database and it is also sent to a Windows machine, where it is plotted in real time (Fig. 6a). The researchers can monitor these real-time plots of radio signal strengths to determine approximately where an animal is, and recognize when a malfunction that stops data collection has occurred.

The electronics used at each ARTS tower (receiver, filter box, FreeWave) are powered by standard 12 V car batteries located at the bottom of each tower. Without a charger, these 12 V car batteries last about a month with just the ARU recording data to exchangeable flash memory, or a week with the added draw of the FreeWave network and filter box. However, solar panels mounted on the towers above the forest canopy are able to recharge the batteries and allow uninterrupted operation of the equipment. We also supplement this tower network with two movable understory receiving units consisting of one antenna array and ARU components mounted 3–6 m above the ground on one or two tower sections. Understory units do not have the same range as tower-mounted antenna, but are useful to obtain more detailed coverage of small areas. For example, we set up two understory units to supplement one nearby tower in tracking frogs visiting a localized breeding pond in the wet season [22]. Solar panels are not functional in the shady understory; thus it is necessary to manually recharge the power

supply for these portable sub-units. The 900 MHz radio link can typically connect to a nearby tower, thus relaying live data from these understory units.

5.2. Software infrastructure

Here we outline the software components used to program the receivers and do the initial data processing to convert radio signals into usable information about animal activity and location. The ARUs are programmable through a manufacturer-provided software suite (Sparrow Systems, <http://www.sparrowsystems.biz/>), which allows users to set the sequence of frequencies to be searched by the ARUs. Once designed using their software, these programs can be loaded into the receivers via the flash memory, or live over the FreeWave Network (Over The Air Programming). The data recorded by ARUs can also be either extracted from the flash memory units or retrieved live through the FreeWave network. In both cases, the real-time data are then loaded into a PostgreSQL database. This ability to remotely program and control the ARUs as well as the data acquisition is crucial since working in the field is not always easy due to challenges posed by the harsh physical environment.

To estimate animal locations, we must first convert signal strength into bearings, and then use the bearings to triangulate animal locations. We calculate bearings from signal strength data with a database trigger programmed using a formula derived from the directionality pattern of our antenna array (Fig. 5). Antennas receive their strongest signals when pointed directly at the transmitter, and this decreases at a predictable rate as the source moves away from the central direction of the antenna. Therefore, by comparing the relative signal strength of the two strongest antenna, we can estimate the true

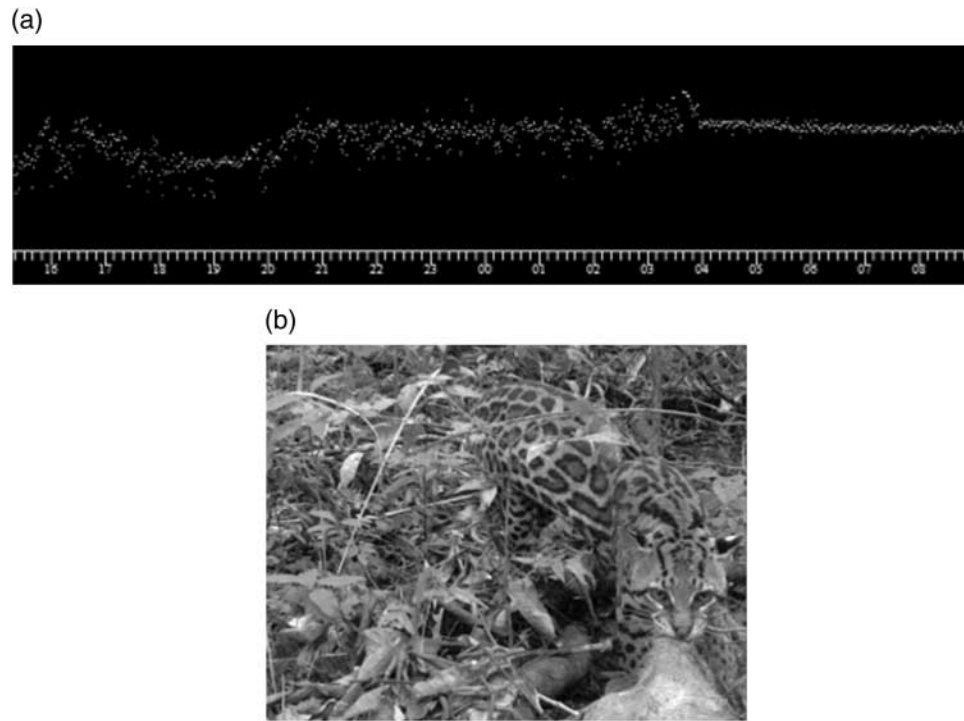


FIGURE 6. ARTS live data stream at BCI (a) allows us to quickly detect the death of a tagged animal and go investigate the cause. In this case, we placed a motion-sensitive camera (b) at the carcass of a recently killed agouti to capture the return of the predator, an ocelot. (a) Real-time data stream received at the laboratory depicting the change of radio-signal (y-axis) received by one ARU over time (x-axis showing time of day). This example is from a transmitter attached to an agouti that died during the night. The signal is relatively dynamic during the day (<20:00) compared with the resting animal (20:00–3:45). At approximately 3:45, the animal was killed by a predator, and the radio-signal changes very little because the collar is laying on the forest floor. (b) Motion-triggered cameras set at the remains carcasses show ocelots to be the primary of agoutis.

bearing of the source of the signal as an offset to the central direction of these two antennas. The following equation shows our bearing calculation formula.

$$\text{Bearing} = \psi \pm (2.9015 * \Delta_s) + 30.0. \quad (1)$$

Where ψ is the angle of strongest antenna, Δ_s is the difference in signal strength between the two strongest antenna, and \pm is determined by which side (right or left) of the strongest antenna lies the second strongest signal. Numbers 2.9015 and 30 are based on directionality patterns of antennas [23] (Fig. 5).

We estimate animal locations by triangulating with bearings from at least three different towers using standard wildlife software (LOAS Ecological Software Solutions). Bearing data from towers are often noisy, with erroneous bearings caused by interference and multipath propagation. These problems are not unique to automated systems, but plague all radio telemetry projects [2]. However, because the ARTS collects data constantly over long periods of time, we have a greater ability to extract the real signal out of a messy, scattered data set.

Our signal processing approach makes use of a hand-smoothing technique commonly used in physiological studies [24], and involves visualizing the bearing data from each

animal, from each tower, and interpolating a line through the weighted center of the points (Fig. 7). This manual process is analogous to calculating a running median, which is a more appropriate measure of the true signal than the mean bearing because it is relatively uninfluenced by outliers caused by signal bounce and interference. Although this approach to signal processing is labor-intensive (It takes about 30 min to smooth 1 week of data for one animal), the circular nature of bearing data make automating a running median function difficult, and we have found human pattern recognition to perform better than any of the automated smoothing techniques we have tried. This not only removes outliers, but also fills small gaps in the data and improves triangulation [25].

ARTS data are also useful for estimating the activity of an animal. Activity can be monitored using data from a single receiver and antenna, making it useful even for animals living where ARTS coverage is not sufficient to obtain data from the three towers needed to estimate locations. The strength of signals received by the automated receiving units from active animals are dynamic, while those from resting animals are relatively constant. This is obvious to the human eye when inspecting plots of live data (Fig. 6a), and also simple to calculate to quantify animal activity levels [26, 27]. The strength

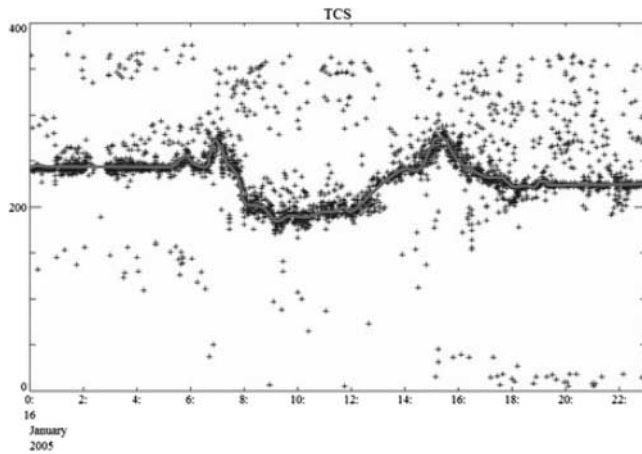


FIGURE 7. The smoothing of bearings (black dots) from one tower to one radio-collared animal over one day. A red line is drawn through the central data cloud to smooth the bearings and eliminate the erroneous bearings caused by interference and multipath propagation.

of sequential signals Δ_s can be used to determine whether an animal is active or not. We use a query to extract the strongest signal for a given animal from a given tower over a period of time, use standard statistical techniques to produce the absolute value of the difference between two signals and then code each time point as active (1) if $|\Delta_s| > \text{Threshold}$ or inactive(0) if $|\Delta_s| < \text{Threshold}$. These values can then be averaged over different time periods to produce an Activity Index that can be compared between species or between experimental treatments.

5.3. System design space and ARTS design choices

In this section, we describe related research on localization and tracking and explain the motivation behind ARTS system design choices. Great Duck Island [28] project was a pioneering effort for the habitat and environmental monitoring using a large-scale network. However, their deployment consisted of static sensors. The ZebraNet system includes custom tracking collars that include GPS, Flash memory, wireless transceivers and a small CPU; essentially each node is a small, wireless computing device [29]. These collars form a peer-to-peer network to deliver logged data back to researchers. Since it uses a GPS, it is mainly limited to tracking large mammals. Recently, Dyo *et al.* [30] proposed a RFID-WSN hybrid system to monitor European badgers (*Meles meles*) in a forest. This is a RFID-based monitoring solution and has a very short range such that it is only useful for knowing, for example, if an animal is within 1 m of a sensor, such as on a nest or not. The ARTS is a unique solution for collecting a dense set of activity and location data in real time for small animals. The physical environment (heavy rains, dense tree canopy etc.) and science requirements (ability to track small-size animals) had a heavy influence on our infrastructure design. For example, we used the following

asymmetric approach for hardware design. Because animals are very hard on the tags attached to their body, and because of weight limitations, we use very light-weight, low-cost and dumb devices (tags) that fit on animal bodies. Since towers have relatively lower constraints on power (because of solar panels) and form factor, we adopted a centralized architecture in which the receivers transmit data to a base station. This approach allows us to estimate animal locations in a place where computation power is easily available.

In this project, we focus on tracking a mobile sensor (animal), rather than locating a stationary sensor. We reduce the problem of tracking mobile sensor to a sequence of location estimation problem for a nearly-stationary sensor. Localization has received a lot of attention in the context of static sensor networks. We now mention some of the state-of-the-art techniques that can be used for localization for static networks. He *et al.* [31] have classified existing localization techniques into two categories: *range-based* and *range-free*. In range-based techniques, information such as distances (or angles) of a receiver are computed for a number of reference points using one of the following signal-strength- or timing-based techniques and then position of the receiver is computed using some multilateration technique [32]. However, range-free techniques do not depend upon the presence of any such information.

Localization techniques typically require some form of communication between reference points (nodes with known coordinates) and the receiver (node that needs to localize). Some examples of communication technologies are RF-based and acoustic-based communication. In RADAR system [33], RF-based localization is suggested, where distance is estimated based on the received signal strength. Cricket [34] uses concurrent radio and ultrasonic sounds to estimate distance. Some researchers have used time-based techniques such as Time-of-Flight (TOA) [32], Time-Difference-of-Arrival (TDOA) [34, 35] between reference point and the receiver node as a way to estimate distance. Niculescu and Nath [36] proposed using angle-of-arrival to estimate position. Recently He *et al.* [31] proposed range-free techniques for localization. In our work, we use the Received Signal Strength Indicator (RSSI) to localize. The RSSI-based method has advantage since it is readily available in practically all the receivers in market. However, its accuracy is severely hampered by nonlinearities, noise, interference and absorption due to walls in indoor environments. Since our target deployment is an outdoor environment, we believe that the RSSI-based approach is a reasonable choice for localization. However, forests are notoriously difficult environments for radio-based signaling networks, due to issues of signal attenuation and multipath. A key question we seek to answer is: how accurate a signal-strength-based localization/tracking system will perform in this environment? Our results show that within the range of ARTS towers the signal-strength-based approach meets the accuracy requirement of our application.

Although acoustic ranging systems [37] provide precise range estimates, we believe that they are not a good fit for our application due to the nature of the physical environment (e.g., animal sounds, environmental noise due to rain etc.). Bulusu *et al.* [38] studied signal-strength-based and connectivity-based techniques for localization in outdoor environments. Nodes localize themselves to the centroid of their proximate reference points. Their outdoor testbed consisted of five Radiometrix RPC 418 (radio packet controller) modules connected to a Toshiba Libretto running RedHat Linux 6.0. Although the paper presented several insights, the work of adapting their localization method to noisy environments and large-scale deployments was left for future work. In addition, the paper did not focus on mobile sensor networks.

Stoleru *et al.* [39] proposed Spotlight—a novel localization system for high-accuracy (sub-meter localization error) and low-cost localization in WSNs. The Spotlight system also employs an asymmetric architecture in which field-deployed sensors do not include any additional hardware for localization, and all sophisticated hardware and computation resides on a single Spotlight device. The authors assume that sensor nodes are deployed from an unmanned aerial vehicle. Upon deployment, nodes run a time-synchronization protocol and self-organize. An aerial vehicle such as a helicopter equipped with Spotlight device then flies over the network and generates light events. Sensors report these events along with timestamps, which are then used for calculating their locations. Once the sensors have determined their own location, they could be used analogous to the ARTS towers, e.g. the animals would still be tagged by radio transmitters, but instead of sending their signals to the towers, the tags would send to the neighboring sensors. This requires that the sensors are equipped with additional hardware, which in turn raises the cost and increases the form factor of sensor nodes. Also, if sensors on ground are used, the advantages offered by the tower height are lost. In addition, sensor nodes are likely not designed to withstand the high humidity in a rainforest environment such as BCI. Long-term monitoring is a key goal of ARTS. We believe that the Spotlight system is suitable for a campaign-style deployment rather than a long-term deployment for the following two reasons: (1) sensors can be easily moved compared with guyed towers. Given the nature of the physical environment, we do not believe that once deployed the sensors will remain unperturbed for extended time periods. (2) the Spotlight system uses battery-operated sensors, whereas the ARTS system uses electricity generated from solar panels mounted on the towers.

Solutions that require RSSI and do not need beacon nodes essentially use a mobile beacon node [40–42]. Sensors that hear the beacon node use various localization algorithms. Beacon nodes can range from human operators to unmanned vehicles. Given the nature of the physical environment (heavy rains, dense tree canopy etc.) and the frequent mobility of sensors, these protocols are not suitable for our environment. The design space of a sensor-network-based tracking application is quite rich.

It has many dimensions such as modes of tracking (active vs. passive), placement of computation (centralized vs. distributed), placement of functionality (smart collars and dumb receivers vs. dumb collars and smart receivers) etc. The science requirements and real-world challenges led to the aforementioned design goals, which in turn provided the basis for our architectural design decisions, technology selections and system deployment.

6. EXPERIMENTAL RESULTS

In this section, we describe the results of 6 years system deployment of the ARTS designed to track animal movements and activity patterns. We evaluated the ARTS system across various dimensions including accuracy, data quality, scalability etc. We now describe some of the key questions that we used during our system evaluation. How does ARTS compare to the traditional localization/tracking technologies such as GPS? What are the tradeoffs between tracking accuracy, cost and energy efficiency? What are the true ecological and infrastructure limitations for various animal tracking technologies? What is the impact of the physical environment (rain, tree canopy), animal size (large tags vs. small tags) and position (tags in the canopy, on the forest floor, in underground burrows etc.) on system performance? What are the major bottlenecks in operating the system in real-world over an extended time period? Finally, does the system generate science equality data and enable new research that was not possible before? We now describe our experiments that seek to address the above questions.

6.1. Radio propagation in forests

Forests are notoriously difficult environments for the successful employment of radio-based signaling networks, due to the issues of signal attenuation and multipath. The first question we seek to answer is: How much impact does this environment have on the propagation of radio signal?

A radio wave radiated by a point source, propagating in free space (an empty space free of reflecting or absorbing boundaries), loses intensity in proportion to the inverse square of the distance traveled. This is simply a result of spherical geometrical dilution. For example, if the distance from the source to a receiver is doubled, the intensity in the wave (the power in a square meter of the spherical wave front) is reduced by a factor of four, or about 6 decibels (dB). This rule would apply, for example, for signals propagating above the forest canopy, as from a flying bird to a tower, or for the free-space component of a more complex path, which also involves vegetation or other obstacles.

Within the forested environment, the situation is considerably more complicated. Not only are radio waves scattered and absorbed by foliage and tree trunks and branches, but also by the ground. These effects control the signal strength in a forest

with a well-established canopy and considerable undergrowth, such as a lowland tropical rainforest or a temperate deciduous forest, up to distances from source to receiver of 500 m. At longer distances the signal strength between two points on or near the ground beneath the canopy is typically governed by losses along a path from the transmitter up through the canopy, then to a more or less horizontal path above the canopy toward the receiver, then down through the canopy to the receiver. As may be imagined, the situation is much more complicated than this simplified scenario, but experiments have shown that at short ranges the strength of a received signal is dominated by attenuation caused by the vegetation and the ground, while at long ranges it is dominated by the inverse square law attenuation of the path above the canopy [43]. In fact, at distances of more than a kilometer, say, one might say that the forest has negligible effect. These arguments apply broadly to frequencies over the range from 100 to 1000 MHz.

We conducted experiments in two forest types: lowland tropical rainforest on BCI in Panama and a second growth cottonwood plantation in Illinois (ref. Table 3). Both had fairly dense undergrowth. In each case, a transmitter with antenna at one to two meters height was moved through the forest while its signal strength was recorded at a fixed location with an antenna positioned and polarized similarly to that of the transmitter. The transmitting antenna was moved to several positions one or two meters apart while multiple measurements were made and averaged at each geographical station. Measurements were generally repeatable over intervals of a few days; there were no significant differences between dry and wet foliage and no systematic differences between vertical and horizontal antenna polarizations (though in all cases, receiving and transmitting antennas were similarly polarized). In the Illinois tests, there was only minimal difference between summer and winter.

To permit comparisons with free-space spherical spreading, these measurements were converted to the losses encountered when the distance from transmitter to receiver is increased from 100 to 200 m. In free space, this would result in a loss of 6 dB; the differences (ref. Table 3) are due to the vegetation and the ground. Given that these results clearly show that radio signal propagation is significantly impacted by the physical

environment (Table 3), we now investigate how accurate a signal-strength-based localization/tracking system will perform in that environment.

6.2. Localization error comparison

When an animal is within the range of three or more towers, its location can be estimated through triangulation. We evaluated the accuracy of these location estimates by comparing them with known locations of test transmitters moved along marked paths on BCI (Fig. 8a). More specifically, we conducted test walks to assess the accuracy of the ARTS. A researcher carried a radio transmitter along trails that had already been geo-referenced with a handheld GPS unit (Garmin 60CSX) at 100 m intervals. These bearings were processed as described already, with bearing smoothed using PV-Wave software, and locations triangulated from three or more bearings using an Andrew's M-estimator [44, 45] implemented in LOAS. Since the standard least-squares method is unstable if there are outliers present in the data, we used Andrew's M-estimator. We calculated the distance between the ARTS estimate and the trail to produce a measure of system accuracy (Fig. 8a). As shown in Fig. 8a, ARTS accuracy varied by location on the island: error was smallest in central portions of the island and largest towards the periphery. Average error for the entire island was 73 m (s.d. = 71 m, range = 0–590 m), but average error within the center of the island (box drawn around towers was 42 m (s.d. = 34 m, range 0 to 200 m. Ref. Fig. 8a). Our tests show that within the range of ARTS towers, we collect data more frequently (~5 m) than typical animal-borne GPS collars with lower accuracy (~50 m) but at much reduced cost (10× less expensive animal tags) and power consumption.

6.3. Accuracy of activity estimates

Patterns of activity and inactivity are one of the most basic measures of animal behavior. To determine an appropriate threshold for distinguishing between inactivity and activity, we tested the correlation between a standard definition of activity and what is detected by the ARTS system. To do this, we calibrated ARTS estimates of activity levels by having human

TABLE 3. Experimental signal strength loss in forest as distance increases from 100 to 200 m.

Frequency, MHz	Environment	Season	Distance doubling loss, dB
462	Zetek trail, BCI	Dry	16
154.6	Zetek trail, BCI	Dry	8.2
462	Armour trail, BCI	Dry	18
154.6	Armour trail, BCI	Dry	10
150	Illinois cottonwoods	Spring and Winter	16
302	Illinois cottonwoods	Spring and Winter	13

Free space loss would be 6 dB, local vegetation and ground caused the amount to be greater in these tests.

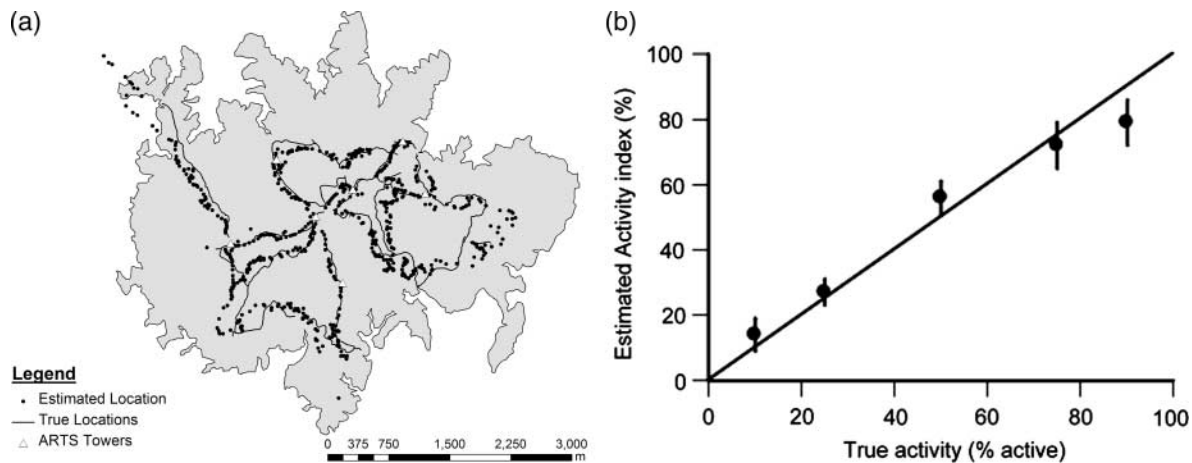


FIGURE 8. Study of Accuracy of Localization and activity measurement of ARTS. (a) Estimated and true locations of a radio transmitter in a test-walk on trails of BCI. (b) Calibration of activity levels estimated by the ARTS as tested on human subjects following different presubscribed activity exercises.

subjects (20 total) carry a radio transmitter around their waist while walking back and forth on a short forest path. Subjects were active for different amounts (10, 25, 50, 75 or 90%) of time during subsequent 10-min periods. As shown in Fig. 8b, the activity index estimated by the ARTS was tightly correlated with the true activity protocol being executed by the subjects. Calibration between ARTS activity measures and observations of animal behavior was likewise highly correlated [27].

6.4. Localization error vs. transmitter and receiver distance

The primary ARTS infrastructure consists of seven 40-m towers with receiving units, but can be expanded through the use of mobile, understory units. We wanted to study the impact of mobile understory units for improving coverage and accuracy of the system. We also wanted to investigate the overall infrastructure needed for higher-accuracy tracking. The objective of this study was to understand the tradeoff between accuracy and cost (including labor and maintenance) of the ARTS tracking system.

The permanent towers of the ARTS, spaced approximately 800 m apart, are well suited to track the location of larger terrestrial animals (weight greater than 10 kg) or smaller arboreal animals (weight between 0.5 and 10 kg) but are too far apart to triangulate the locations of smaller animals. The size of the animal that can be tracked and the accuracy to which they can be located is limited by the distance between receiver stations. We decrease our inter-receiver distances by temporarily setting up two understory units to fill gaps in our coverage. This denser network of receivers also inherently has better accuracy in locating an animal because the effects of angular error increase with linear distance between the transmitter and the receiver.

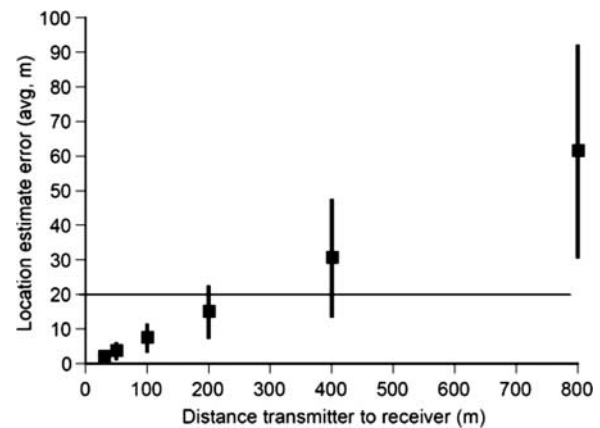


FIGURE 9. Modeled location estimates as a function of transmitter-receiver distance.

To evaluate the added location accuracy provided by an even denser networks of receivers, we used the location error simulation model in the triangulation software LOAS (www.ecostats.com). Setting an estimated bearing error of 4° (our estimated error after bearing smoothing), we simulated system configurations with different between-receiver distances. The results show the extent to which location accuracy would improve by having more receivers over a smaller area (Fig. 9). Equally important is the decrease (by a factor of 4) in the variance of the location error. Location accuracy improves to as much as <5 m when the receivers are spaced 50 m apart. Such a resolution would be sufficient to record the movement of small understory rodents or large insects at sufficient resolution to map them onto individual tree crowns.

However, achieving such a dense receiver network would be a major challenge. For example, we estimated that it would take another 30 understory receiver units, in addition to the existing

above-canopy towers, to give us this accuracy over about 75 ha. Achieving this density of receivers would be very expensive and incredibly complex.

6.5. Geographic coverage model

For ARTS to function, transmitters worn by study animals must be within the range of the ARU and their associated antenna arrays. This presents a challenge as the transmitters used in radio telemetry are low-power, and animals can move over large areas. To maximize coverage, we mounted antennas atop above-canopy radio towers set on hilltops. Preliminary tests suggested that placing antennas on towers 10 m above the forest canopy roughly doubled the range at which a ground level transmitter could be detected in comparison with antennas in or below the tree canopy. Thus, tree-mounted antennas would not be nearly as efficient as tower-mounted ones.

We tested the actual range of our system by walking all the trails on BCI while holding radio transmitters at 1 m height. We recorded the strength of signal received from each of the seven tower-mounted receivers and then related this to the specific location of the transmitters to test for relationships of elevation, angle of the slope relative to the receiver, distance to the tower and distance to the nearest area with line-of-site to the receiver.

Using these data, we made a model to predict the strength of signal received by an ARTS tower based on the strength of the transmitter and the surrounding landscape ($r^2 = 0.39$, df: 5, $P < 0.0001$). All variables were included in the final model, which we used to predict island-wide coverage for different types of transmitter (Table 4).

Our model predicts the range of animals walking on the forest floor (Fig. 10a), but does not take into account the effect of their movement up into trees, or down into underground holes. Our experience shows that the effect of going underground depends

on exactly how far down an animal goes, but radio-tagged animals sleeping in very deep holes can sometimes only be heard within a few dozen meters of the hole. Transmitters in the forest canopy can be detected from a greater distance than those at ground level. We quantified this by raising test transmitters into trees and found an increase in signal strength of 25–35 dB between the forest floor and 40 m high in a canopy tree (Fig. 11). This difference can be incorporated into our model to predicting the coverage for arboreal animals (Fig. 10b).

6.6. Radio interference

Detecting the faint signal of a radio-tagged animal can be impossible if there is strong interference from other radio transmitters on or near the same frequency. We discovered that the two-way communication networks of local taxis, television stations and other unknown sources of radio-traffic caused

TABLE 4. Variables used in function to predict the strength of signal received by a tower-mounted receiver from an animal-mounted radio transmitter, based on local landscape characteristics.

Variable	Coefficient
Transmission power of radio-tag (dBm)	1.18055670
Distance to tower-mounted receiver (m)	−0.01218720
Distance to nearest area with line-of-site to tower (meters, 0 if in line of site)	−0.00244816
Elevation (meters)	−0.03867165
Angle of the slope of the hill related to the receiving antenna (0 = facing towards tower, 180 = facing away)	−0.02403199
Intercept	−98.9454675

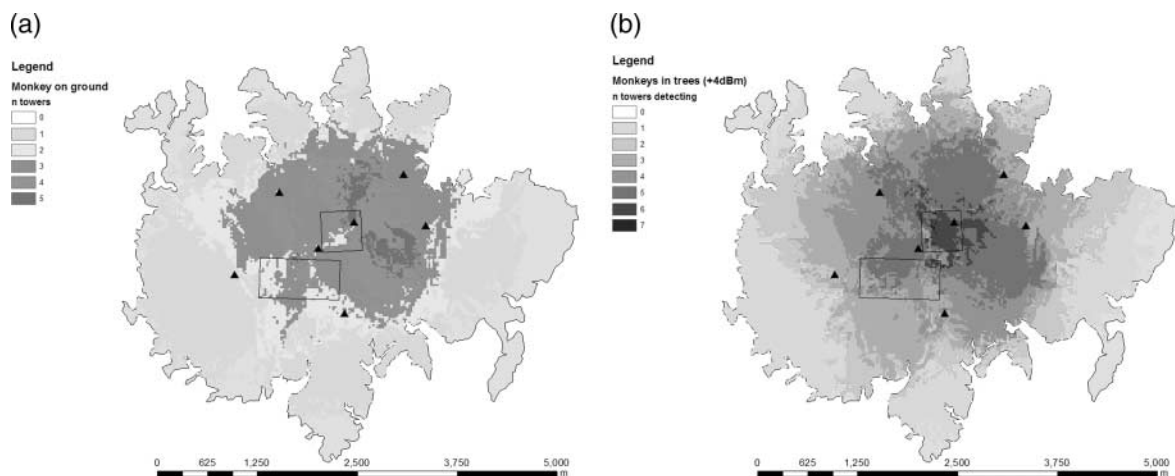


FIGURE 10. The predicted range of ARTS towers to detect different types of radio-collars. Triangles represent the location of the towers and the colors show the number of towers expected to receive the radio signal from an animal at a given location for (a) a monkey-sized collar on the forest floor or (b) in the trees. (a) Tower overlap when monkey is on the ground. (b) Tower overlap when monkey is in trees.

significant radio-interference. This is a common problem for all animal tracking studies near human settlements, but in our case we could use the automated receivers to map this interference

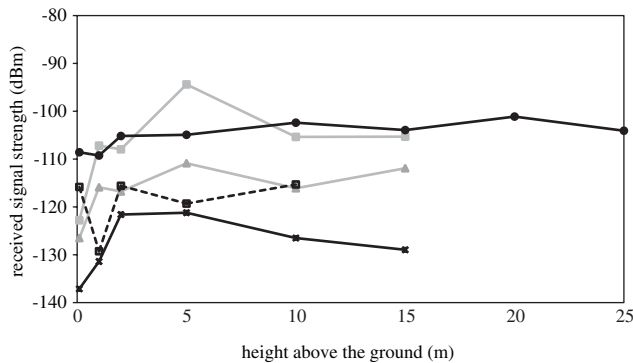


FIGURE 11. Change in signal strength recorded by a telemetry receiver from a radio-transmitter at different heights above the ground. Each line represents a different location where a radio-collar was hauled into the rainforest canopy. The biggest increase in signal strength comes in moving the collar off the ground and up above of first few meters of understory vegetation.

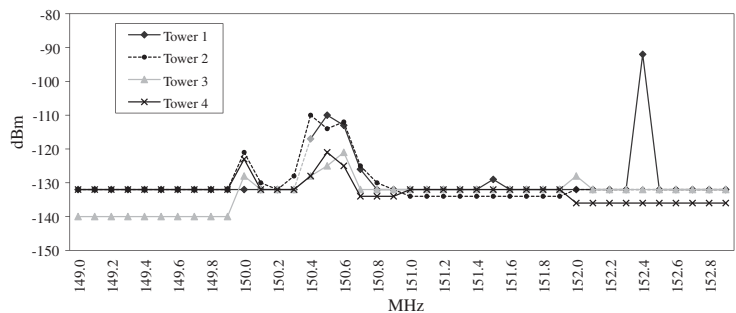
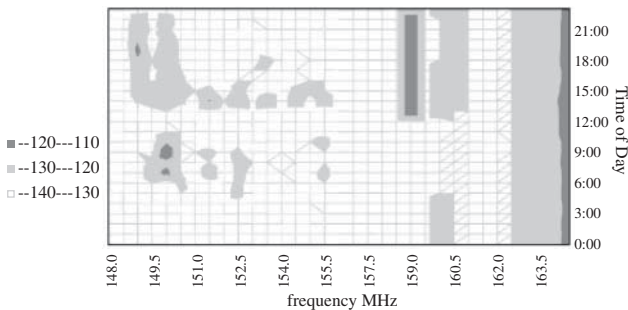


FIGURE 12. The background radio interference at BCI, levels above -130 dBm interfere with our ability to track radio-tagged animals. (a) shows how interference varies over a broad-band (16 MHz) across the course of one day. (b) shows a more fine-scale view of interference over the 4 MHz used for most animal tracking, and how this varies across four different tracking towers. (a) Broad scale radio interference over the course of one day from one tower. (b) Fine-Grained-Interference at BCI from four different ARTS towers.

TABLE 5. ARTS: repairs and maintenance details.

Equipment	Problem type	Frequency	Solution
Towers (7)	Large tree fall on guy wires	Two times total	Replacement of bent tower sections (\$500)
Towers (7)	Small branches growing on guy wires	Once per year per tower	Trim branches once per year
Towers (7)	Corrosion at guy wires, bolts and nuts	performed 6 years	General tower maintenance (\$6500)
ARU (7)	Lightning strike	Three times total	Units repaired by vendor (\$250)
FreeWave 900 MHz radios	Lightning strike	Four times total	Units must be replaced (\$1000)
RG-8 Cable	Broken in middle	One time total	Cable was replaced (\$500)
RG-59 Cable (42)	Connectors go bad	Replaced after 4 years	Cable replaced (\$4 each)
PL-259 connectors (64)	Corrosion and bad connectivity	Replaced after 4 years	Replaced with custom built aluminum mounts
Solar panel mounts (7)	Corrosion	Replaced after 4 years	Connectors replaced (\$5)
Antennae (42)	Corrosion	Replaced after 4 years	all antenna replaced

on BCI. Normal background signal for our system was -130 dB, and anything above this was considered man-made interference.

We first made a broad scale survey scanning 33 channels from 148 to 164 MHz across one entire day (Fig. 12a). This showed an extensive interference at higher frequencies which we later tracked to a television repeater, which does not transmit early in the morning. We also conducted a more fine-grained scan for interference at BCI across the 4-MHz that we primarily use for research (Fig. 12b). Most channels are clear, although there are scattered frequencies that we avoid when purchasing radio-transmitters to attach to animals.

7. REAL-WORLD DEPLOYMENT CHALLENGES

7.1. Tower repair and management

Table 5 enumerates the technological and maintenance challenges that we have faced with the ARTS system, as well as the solutions we have employed. The environment has a significant impact on the system ranging from lightning strikes, to tree falls and corrosion (Fig. 13a). However, so far, we have

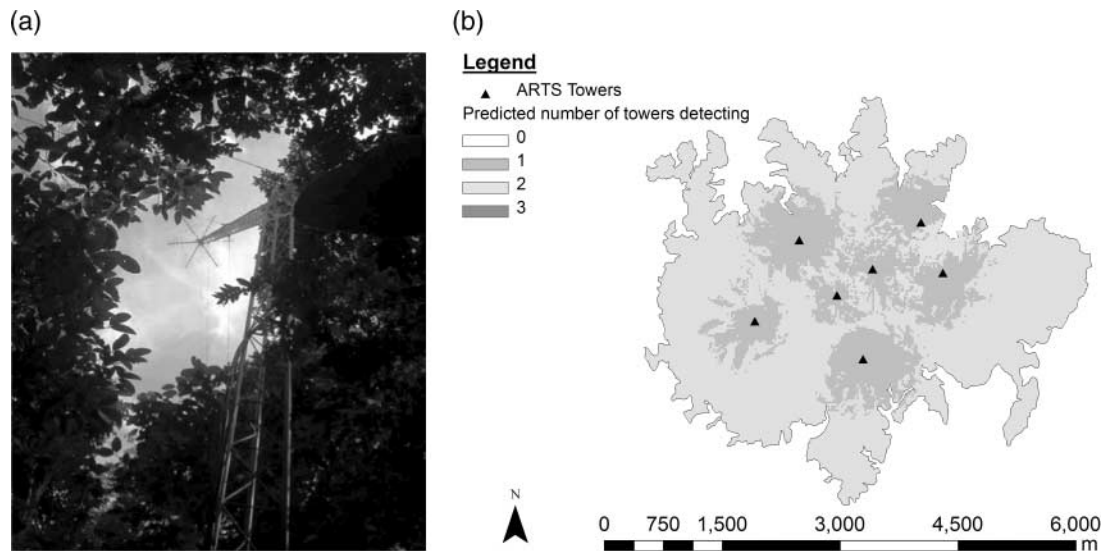


FIGURE 13. Real world challenges of tracking animals in the rainforest include towers damaged by falling trees (a) and the limited detection range for small animals on the forest floor (b). (a) Tower at BCI broken by tree falling on guy wires and (b) ARTS tracking a rat species (animal with small body size).

been quite satisfied with ARTS in terms of its maintenance effort and cost.

7.2. System power consumption

Power management in a real-world deployment is always a challenging issue. Each ARTS tower is equipped with one solar panel as a renewable source of energy. We now describe the system power consumption statistics. The ARU Drain Current is 37 mA. The Filter Box power consumption is 20 mA and the Freeway radio power consumption is 64 mA. We typically use 90 Ah rated batteries. At 75% of discharge ($90 \times 0.75 = 67.5$ Ah), the battery can last in the field for ~ 76 days ($67.5 \text{ Ah} / 37 \text{ mA} \times 24 \text{ h}$). As batteries get older or if they get fully discharged and charged again, they tend to accumulate less charge.

If the subunit also has a radio (in addition to an ARU discussed already), then the total power consumption is as follows:

$$E_{\text{ARU}} + E_{\text{Filter Box}} + E_{\text{FW}}. \quad (2)$$

This translates to ~ 23 days of battery life ($67.5 \text{ Ah} / 121 \text{ mA} \times 24 \text{ h}$). If we constantly monitor the batteries and avoid them to get fully discharged (aka its voltage does not go below 10 V), they could last up to 2 years. However, in practice this level of monitoring is unrealistic, and the batteries last less than this.

As mentioned before, in addition to the above-canopy tower, we also have understory units. These units do not have solar panels, as a renewable source of energy since sunlight can hardly penetrate through dense tree canopy, and use batteries as their sole source of energy. We typically change the subunit

batteries every 3 weeks. The system had been engineered to ensure a positive energy balance, and never experienced a case of insufficient power in 6 years of operation.

7.3. Deployment barrier

One drawback of the ARTS system is that it is large and complex. The complete ARTS system is best suited for use at well-funded, easily accessible research sites, although components of the system may also be useful in smaller temporary studies. However, once operational, the system is able to quickly collect huge quantities of high quality data, and thus promises to provide an enormous leap forward in our ability to describe and understand the ecology of animal movement.

7.4. Tracking error for animals with small body size or large home range

Using ARTS for tracking small animals is challenging. For example, Fig. 13b shows the predicted signal reception by the ARTS system for a rat-sized transmitter. This is due to the fact that since small animals cannot carry large batteries, transmission power has to be kept low, which in turn generates a weak signal. This weak signal, coupled with environmental factors such as dense tree canopy, makes it hard to detect. For the cases where localization and tracking from at least 3 towers is not possible, determining whether an animal is active or not is still very feasible using signal strength changes observed at one tower. In addition, tracking animals with very large home ranges is challenging since the animals can come and can go in and out of the coverage area. Nonetheless, ARTS is still a viable

and attractive option for tracking small animals compared with a GPS-based system, which are too large to attach to most species (Fig. 1).

8. SUMMARY OF SCIENTIFIC IMPACTS

Many behaviors that have a major impact on the survival and reproduction of wild animals are difficult to study because they are infrequent, cryptic or occur over large spatial or temporal scales. Our lack of data on important biological processes, including predation, dispersal, migration and intergroup competition, is slowing the development and testing. Compared to traditional methods, including direct observation and manual telemetry, ARTS allows scientists to collect more data on the activity and locations for a greater number of study animals for longer periods of time, and over larger areas. In addition, the availability of live data allows scientists to make more efficient use of their field time, and recognize and act on rare but important events. These functions have facilitated new scientific discoveries on topics that have

proved difficult to study, using traditional observational or telemetry methods.

Traditional methods of observation are limited in studying many important biological processes, including predation, dispersal, migration and intergroup competition. Our lack of data on these is slowing the development and testing of ecological theory, and interferes with our ability to develop effective conservation and management strategies in the rapidly changing world.

8.1. Activity and mortality of animals

The activity of an animal is one of the most basic descriptors of animal behavior, revealing daily rhythms that are one of the three basic dimensions of an ecological niche (along with diet and locomotory mode) [46]. In addition, variations in activity patterns are related to individual physical and social condition. Because the ARTS records data constantly and continuously, these data can provide details on both daily activity (Fig. 6a) as well as long-term patterns (Fig. 14). These document one key dimension of an animal's ecological niche, and have also

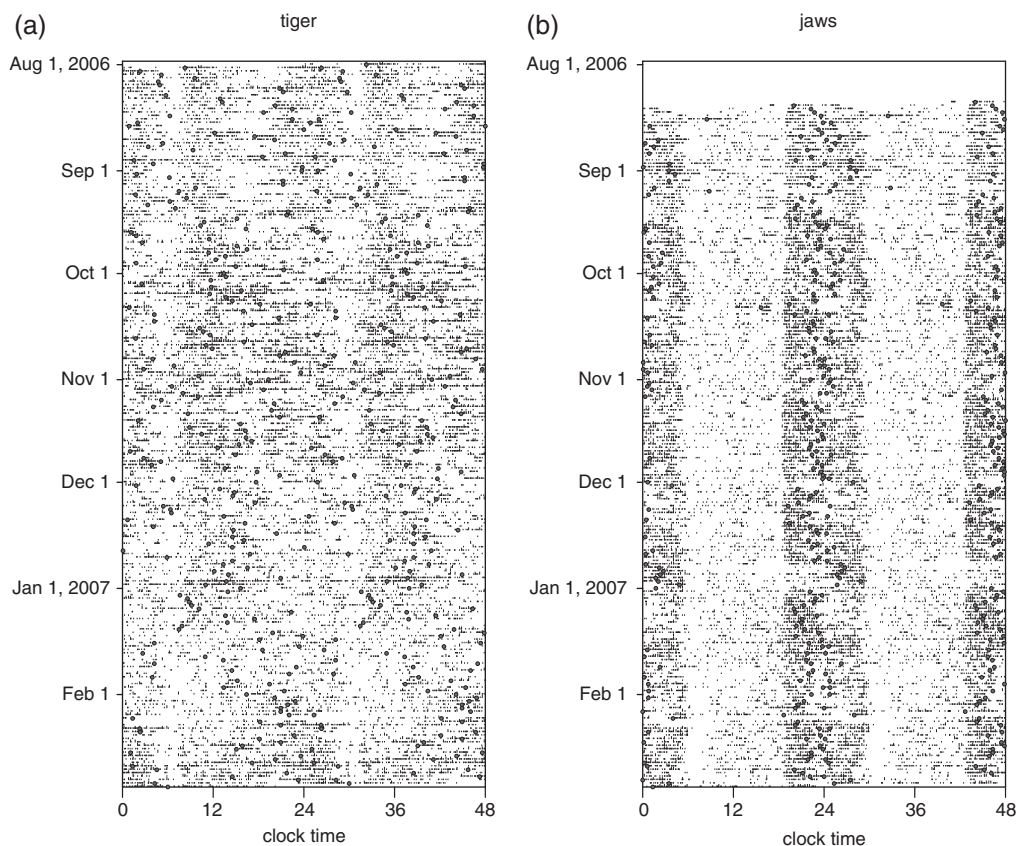


FIGURE 14. Actograms showing the patterns of daily activity over 7 months for a three-toed sloth with almost no daily rhythm (a) and a two-toed sloth with strong nocturnal activity (b). Each row represents two continuous days of data, with dark color indicating activity and white indicating inactivity at 4-min intervals. The long term data also allows the determination of finer-scale patterns such as the early AM rest period of the three-toed sloth, and a regular effect of the lunar cycle on the nocturnal activity of two-toed sloths. (a) Actogram of a three-toed sloth. (b) Actogram of a two-toed sloth.

been used to model how environmental variables, such as weather and food availability, affect animal activity [27]. As with the mortality data, results are often surprising. For example, Holland *et al.* [47] used ARTS to find that Pallas' Mastiff Bats were active flying and foraging for only 82 min per night, spending the rest of their time hiding in a roost. This suggests that this species is a very efficient forager, and is probably not limited by food abundance.

8.2. Movement ecology

Being able to determine how animals use their habitat is critical for understanding their ecology, behavior and evolution, as well as for planning effective conservation strategies [25]. Animal movements are influenced by a wide range of factors, including the distribution of important resources such as food and water, and interactions with members of their own and other species. Investigating how these factors interact to shape patterns of space-use and resource access has been problematic because of the logistical challenges involved in simultaneously tracking the movements of many animals. ARTS provides a means of overcoming this obstacle. For example, simultaneous and continuous tracking of six white-faced capuchin (*Cebus capucinus*) social groups over a six month period demonstrated that areas that were shared by multiple groups (i.e. areas of home-range overlap) were underused compared with non-shared areas [48]. This heterogeneous pattern of space use was not necessarily the result of intense intergroup aggression, but could also be explained by the economics of memory-based foraging [49]. Simultaneous tracking of multiple social groups also elucidated the factors that determined the balance of power between neighboring social groups. As expected, large group size conferred a competitive advantage in this population, but surprisingly, this effect was less important in determining the outcome of aggressive inter-group encounters than the location of the fight [25]. This strong home-field advantage may be the key to understanding how small social groups are able to persist in the face of intense, between-group competition.

In another study, Crofoot *et al.* [49] tested a critical assumption of animal behavior studies: that habituated groups do not move more when followed by a human than they do when left alone. This has been assumed by thousands of studies, but never tested empirically. ARTS movement data allowed them to compare the distance and speed moved by habituated animals accompanied by a ground-based observer with other days when they were not being followed. No effect was found, offering the first real field confirmation of an age-old assumption.

8.3. Species interaction studies

The seeds are most commonly removed by a 2–4 kg caviomorph rodent, the Central American agouti (*Dasyprocta punctata*).

Agoutis typically scatterhoard seeds under a few centimeter of dirt which protects the seeds from parasitic insects and other seed predators. During periods of food scarcity, agoutis return to their cached seeds to consume the seed. We developed a tagging method, which allowed researchers to turn the transmitters off of buried seeds without digging up the seed [50]. This has allowed us to quantify secondary dispersal of seeds, and plot where individual seeds have moved over time. This method also ensured that the transmitters turned on when the seed was moved or eaten by an animal. The ARTS allowed researchers to know if seed transmitters were active in real time, which led to a major reduction in field effort and increased the life of the transmitters.

9. CONCLUSIONS

Networks of sensors deployed in natural areas are increasingly being used to collect data at the scales and rates needed to address modern environmental challenges [51–56]. However, these are typically focussed on measuring abiotic conditions, or attributes of sessile plants. Here we describe a unique ARTS designed to track the movements and activity patterns of animals. The results of this 6 years system deployment are relevant not only because of the biological results, but also because of the more general challenges of maintaining electronic sensors in real-world rainforest conditions. The strength of the ARTS for science application lies in its ability to simultaneously stream real-time data on animal location and activity from dozens of animals tagged with inexpensive radios as small as 0.2 g. GPS offers an alternative tracking technology to ARTS style systems that is not limited by range or accuracy, but suffers from other shortcomings including large, expensive tracking tags and complicated data retrieval options. In fact, our 6-year long experience shows that ARTS system collects data more frequently than typical animal-borne GPS collars (~12 locations/h) with slightly lower accuracy (~50 m) but at much reduced cost per tag (~10X less expensive). The success of ARTS across the relatively small scales of Barro Colorado Island shows the scientific importance of real-time, high-resolution tracking data and why it is important to continue to refine tracking technology to make these studies possible on the smallest animals, at the largest scales [17]. We hope that the experience gained and lessons learned during our deployment of the ARTS system are applicable to the broader sensor network applications and help push for the advancement of the animal tracking technology.

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