FORUM ARTICLE

The GPS craze: six questions to address before deciding to deploy GPS technology on wildlife

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Published online: 28 July 2014

Abstract: GPS and satellite technology for studies on wildlife have improved substantially over the past decade. It is now possible to collect fine-scale location data from migratory animals, animals that have previously been too small to deploy GPS devices on, and other difficult-to-study species. Often researchers and managers have formatted well-defined ecological or conservation questions prior to deploying GPS on animals, whereas other times it is arguably done simply because the technology is now available to do so. We review and discuss six important interrelated questions that should be addressed when planning a study requiring location data. Answers will clarify whether GPS technology is required and whether its use would increase efficiency of data collection and learning from location data. Specifically, what are the required: (1) ecological question(s); (2) frequency and duration of data collection; (3) sample size; (4) hardware (VHF or GPS or satellite) and accessories; (5) environmental data; and (6) data-management and analysis procedures? This approach increases the chance that the appropriate technology will be deployed, budgets will be realistic, and data will be sufficient (but not excessive) to answer the ecological questions of interest. The expected results are important advances in ecological science and evidence-based management decisions.

Keywords: dispersal; ecological questions; fix-rate; migration; movement; resource selection; satellite technology; telemetry data

Introduction

GPS and satellite technology for use in wildlife research have skyrocketed. Fifty years since radiocollars were first used to study wildlife (e.g. Craighead 1982) there has been a revolution in GPS radiocollars, tags and transponders (Tomkiewicz et al. 2010), and in the quantitative methods to analyse these data (Morales et al. 2004; Schick et al. 2008). Early GPS collars were too big and heavy for use on small to medium-sized mammals and all species of birds (Cochran 1980). Not surprisingly, this biased telemetry studies towards large mammals of conservation or management concern, particularly in North America (Hebblewhite & Haydon 2010). Arguably New Zealand researchers (Sirtrack® notwithstanding) lagged behind in this technological revolution, primarily because large introduced wild mammals are managed as pests and GPS hardware was too heavy for deployment on priority species like native birds. However, given new micro-GPS technology (Recio et al. 2013), it is now possible to gain ecological insights into increasingly smaller animals.

The advent of GPS technology has resulted in a global proliferation of GPS deployment on animals. Sometimes this is done for essential monitoring of wildlife or to answer clearly articulated a priori biological questions, whereas other times it is done simply because the technology is now available to do so (Hebblewhite & Haydon 2010). For example, GPS units are often deployed to accumulate a large number of re-locations per day because that information may be useful, rather than to obtain a mechanistic understanding of why an animal chooses to migrate, disperse or hunt the way it does (Fagan et al. 2013). In this example, the latter approach puts emphasis on ecological questions, whereas the former does not.

There are numerous factors that researchers need to consider prior to deploying GPS units on individuals within an animal population. In response to the growing methodological questions about GPS units, many studies have assessed specific aspects of their function or performance. For example, studies have assessed the field performance of various makes and models, costs and benefits of VHF versus GPS, habitat-induced biases, influences of fix-rate on GPS performance, differences between animal species and their behaviours, and issues of database design and statistical approaches (e.g. Frair et al. 2010; Urbano et al. 2010; Recio et al. 2011). For any new project, however, sorting through this voluminous literature is challenging, and often, important factors to consider when initiating a study that requires GPS may go overlooked.

Our goal is to review and discuss six important interrelated questions that should be addressed when planning a study requiring location data. (1) What ecological question(s) will be addressed and answered? (2) What frequency and duration of data will be collected? (3) What are the sample size requirements? (4) What hardware (VHF or GPS or satellite) and accessories will be most appropriate? (5) What environmental data will be required? (6) How will the data be managed and analysed? We also discuss the budgetary implications of design choices, in the hope of increasing the likelihood that informative results will emerge from the project.

We use the terms 'GPS technology' or 'GPS units' to broadly include GPS-based systems and systems that combine GPS positioning with satellite-based data retrieval (Tomkiewicz et al. 2010). Further, most (but not all) GPS and satellite units also contain a VHF beacon transmitter that enables re-location of the device. Consequently, we define GPS or satellite units as any unit with those components irrespective of whether or not they have a VHF beacon transmitter.

1. What ecological questions will be addressed and answered?

The central thesis of this paper is that researchers considering using GPS technology must be driven by the data requirements of their research question, as opposed to being driven by technology or simple wildlife monitoring (Nichols & Williams 2006). Answering research questions advances ecological science and contributes importantly to management decisions. From a practical perspective and ensuring that money is well spent, clear and realistic research questions will inform data needs, which in turn will identify hardware requirements and specifications, logistical issues, and potential analytical tools. The research question should identify the biological process of interest (e.g. habitat use, dispersal, foraging behaviour), and the time over which the process occurs (e.g. minutes to months). Following Hebblewhite and Haydon (2010), we summarise the major questions and themes in ecology and conservation that can be addressed using location data, with emphasis on GPS (also see Table 1).

Resource selection – GPS data enable us to assess habitat preferences, i.e. resource selection by animals and their spatial relationships with other species – for management and conservation purposes (e.g. Frair et al. 2010; Latham et al. 2013a, b).

Behaviour – Behavioural studies have traditionally relied on direct observations of animals; however, this information can now be extracted remotely by coupling GPS technology with analytical approaches (e.g. Davis et al. 1999).

Home range – GPS units provide large amounts of highly precise and accurate location data necessary for detailed

Table 1. The major questions and themes in ecology and conservation that can be addressed using GPS technology (following Hebblewhite & Haydon 2010). Where possible we provide examples of New Zealand studies that have used GPS technology (or, for demography, VHF because we are unaware of GPS examples) to answer these major questions.

Question/ Theme	Example	Reference
Resource selection/use	Resource selection of sika deer (*Cervus nippon*) in mountain beech (*Fuscospora cliffortioides*) forest, Kaweka Forest Park, North Island	D. Herries, Dept. of Conservation, (unpubl. data)
	Resource selection of European hedgehogs (*Erinaceus europaeus*) in braided river systems, South Island	Recio et al. (2013)
	Den site use by brushtail possums (*Trichosurus vulpecula*) following density reduction, South Island	Whyte et al. (2014)
Behaviour	Foraging behaviour of black petrels (*Procellaria parkinsoni*) in relation to the ocean shelf-break off the coast of New Zealand	Freeman et al. (2010)
	Foraging behaviour of white-capped albatrosses (*Thalassarche steadi*) in relation to fishing vessels in subantarctic New Zealand	Torres et al. (2011)
Home range	Kererū (New Zealand pigeon, *Hemiphaga novaeseelandiae*), South Island	Powlesland et al. (2011)
	Home range estimation of five hosts of bovine tuberculosis to assess the dynamics of disease transmission, northern South Island high country	Yockney et al. (2013)
Demography	Survival and recruitment of captive-reared and wild-reared takahē (*Porphyrio hochstetteri*), Fiordland, South Island	Maxwell & Jamieson (1997)
	Survival of brown kiwi (*Apteryx mantelli*) following sustained exposure to brodifacoum poison, North Island	Robertson et al. (1999)
Migration / dispersal	Migration routes of juvenile northern royal albatrosses (*Diomedea sanfordi*), southern Pacific Ocean	Thomas et al. (2010)
	Extreme migration of eastern bar-tailed godwits (*Limosa lapponica baueri*) from New Zealand to breeding grounds in Alaska	Conklin et al. (2010)[1]
Movement ecology	Movement responses by wolves (*Canis lupus*) to footprint created by industrial activity, Alberta, Canada	Latham et al. (2011a)
	Effect of management options on brushtail possum movements, North Island	Pech et al. (2010)
Human–wildlife conflict	Avoidance of human activity by wolves on the eastern slopes of the Rocky Mountains, Alberta, Canada	Hebblewhite & Merrill (2008)
	Effect of a human-dominated land-use mosaic on African elephants (*Loxodonta africana*), north-central Kenya	Graham et al. (2009)

[1]Assessed using light-level geolocator dataloggers

descriptions of animal home ranges, and have been used worldwide for this purpose (e.g. Girard et al. 2002).

Demography – Telemetry technology (particularly VHF) has allowed researchers to follow individual animals from birth to death, allowing for improved estimates of survival, reproduction and recruitment (e.g. Haydon et al. 2008).

Migration/dispersal – GPS telemetry with satellite-based data retrieval systems have proven critical to furthering our understanding of many migratory or otherwise difficult-to-study species (e.g. Mueller et al. 2008).

Movement ecology – The use of GPS technology in the study of animal movement has opened up a whole world of possibilities and it is an area of research that is progressing rapidly (Morales et al. 2004; McClintock et al. 2012). To date, however, few studies in New Zealand have taken advantage of this technology to obtain a mechanistic understanding of animal movements.

Human–wildlife conflict – GPS technology has provided increased insights into how animals respond to human activity (such as tourism), urban or industrial development, and the footprint associated with that development (Hebblewhite & Merrill 2008; Hebblewhite & Haydon 2010).

2. What frequency and duration of data will be collected?

Research questions for which GPS technology may be appropriate should describe a biological process and the spatial and temporal dimension over which that process occurs. This will help define the frequency and duration of data collection. For example, let us assume we are interested in how hunting and movement behaviour of feral cats (*Felis catus*) are influenced by habitat and time of day. For this question, it is critical that the location data be collected more frequently than the frequency at which the cats change their behaviours. This would mean that re-locations would have to be obtained at least once per hour (preferably more frequently) for several weeks or months, and from multiple animals. In contrast, it may be sufficient to obtain a location every 3–4 hours (or even less frequently) for a year or more if the research question is related to seasonal habitat use.

Programming fix-rate schedules (i.e. how often re-locations are obtained and for how long) results in trade-offs between the number of locations obtained per day and the length of time that the unit remains active (i.e. limitations associated with battery life). For example, the battery life of most GPS units will probably be insufficient to obtain enough fixes to answer questions about cat hunting and movement behaviour (a high intensity fix-rate) and describe annual resource use by cats (fixes obtained over a long period). Estimations of battery life may be based solely on the mean time taken per fix under factory conditions (although some units estimate best- and worst-case scenarios). If, however, actual mean time taken per fix in the field is longer (even marginally) than the estimated factory mean, when multiplied over the time that the device is deployed, battery life can be significantly shorter than initially estimated. One way of accounting for this uncertainty is to use the mean fix-rate time from previous studies conducted in similar habitats to calculate more realistic estimations of battery life.

Knowledge of natural history should also be foremost when deciding upon fix-rate schedules, particularly when battery life is a limiting factor. Schedules should be programmed so that fixes are obtained during appropriate times, biological season/s and, where more than one species is GPS-tagged to assess interspecific interactions, location data should be collected concurrently. For example, programming devices to obtain one fix per hour throughout the day and night for a nocturnal animal that sleeps in a burrow will probably yield no locations during the day and will unnecessarily waste battery life. Battery life can be substantially improved if GPS units include a 'smart' feature linked to an accelerometer. This feature omits fix attempts from the schedule if the accelerometer has not detected movement since the last time the GPS turned on to acquire a location (e.g. http://www.telemetrysolutions.com/track-wildlife/smart-GPS.php).

Once a fix-rate schedule has been chosen and GPS units have been programmed, it is critical to make sure they work before deploying them. This is easily done by leaving active devices outside overnight to collect fixes; devices are then checked the following morning to ensure they are operational. We recommend that habitat-induced biases and GPS measurement errors are also assessed at this stage. This can be done by placing units in habitats of interest for a couple of days, attempting to simulate the height and orientation that a unit would be in when deployed on an animal. Habitat-specific actual 'fix-rate' can be calculated from these data by dividing the number of successful fixes (stored locations) in each land-cover type by the number of attempted fixes. The precision of locations can be quantified by averaging the distance between each estimated location and the 'true' location of the device; the latter determined using fixed geodetic markers, differential-correction or a large-sample average (Frair et al. 2010). Habitat-induced bias in fix-rate and GPS measurement error can be particularly problematic for questions relating to resource selection, movement ecology and human–wildlife conflict.

Fix-rate schedule can also have implications for spatial and temporal autocorrelation of the data (Fieberg et al. 2010). A schedule that obtains GPS locations at shorter time intervals (e.g. five locations per second obtained during 'chase sequences') will usually result in significantly higher correlation of the data than locations obtained at longer intervals (e.g. four per day). In short, autocorrelation can produce deceptively low estimates of uncertainty, overfitted models and result in spurious conclusions (Fieberg et al. 2010). Although it cannot be discounted as a trivial issue, autocorrelation of the data can be assessed and, if found to be high, it can be modelled using sophisticated analyses like mixed-effects and state–space models (Fieberg et al. 2010).

Finally, researchers need to be aware that there is an inherent relationship between space and the time specified in the fix-rate schedule that can affect statistical analyses. For a given species, the disparity between the distance estimated from the GPS locations and the real distance moved increases as fix-rate declines (i.e. longer period between fixes). This means that at some threshold in fix-rate, which may differ across species, GPS data may not be accurate enough to estimate distance moved. For example, Pépin et al. (2004) showed that real movement distances of red deer (*Cervus elaphus*) could be estimated accurately only within the 15–240 min range. This has implications for combining different GPS datasets, and it is important to standardise them to the same fix-rate before conducting formal analyses. Moreover, many spatiotemporal analyses are inherently affected by the fix-rate because of the aforementioned autocorrelation of animal behaviours. Given the scalar nature of many ecological phenomena like habitat selection (DeCesare et al. 2012), and the relationship between fix-rate and movement rate, researchers will need to consider their study species and ecological question to identify the scale of fix-rates that will most closely correspond to a real biological move. For example, a 15-minute fix-rate might match the movement and behavioural scales of decisions made by a fast-moving predator, but a daily movement-scale might make more sense for slow-moving tortoises.

3. What are the sample size requirements?

Individual animals do not necessarily behave or move in response to spatial or temporal factors in the same way (Leban et al. 2001; Forester et al. 2007). This creates an important source of variation within a population that is likely to be most pronounced between sex and age classes (Aebischer et al. 1993). Consequently, sufficient individuals need to be radio-tagged to make robust population-level inferences about the spectrum of behavioural variability in the population (Girard et al. 2006). Thus, the animal (or depending on the question, a social unit like a pack or herd; Latham et al. 2013a) should be the sample unit and the location data a subsample of the animal's behaviour (Aebischer et al. 1993; Lindberg & Walker 2007).

Knowing the number of animals required (sample size) a priori is difficult but it can be guided by published work addressing the same or similar biological processes in which individual variation was explored. As a rough guide, previous studies have shown that about 30 animals are needed to estimate resource selection by a population (Aebischer et al. 1993; Leban et al. 2001); 50–100 animals are needed for survivorship analyses (Murray 2006); and 20–30 (or more) animals are needed to make statistical summaries of home-range size (Anderson et al. 2005; Börger et al. 2006). Importantly, the appropriate sample size will be dependent upon the question being asked and the variability in the population, and should be determined using an a priori power analysis. Although we contend that researchers must attempt to acquire adequate sample sizes (Girard et al. 2006), there may be certain situations in which smaller-than-desirable sample sizes may be acceptable. For example, information on resource selection by rare native species may be critical for the conservation of that species, but it might not be feasible to locate, capture or tag sufficient individuals to make robust population-level inferences. In this situation, some information about resource selection by this species is likely better than none, particularly if the smaller sample size is assumed to be representative of the total population size (Hebblewhite & Haydon 2010).

Researchers must also consider the possibility of GPS-unit failure (Tomkiewicz et al. 2010). This problem cannot be overcome by simply increasing the frequency at which a unit collects fixes because this only increases the subsample of a single animal's behaviour. Higher frequency of locations can increase precision and accuracy of, for example, home range estimation (Girard et al. 2002) and allow for a greater number of explanatory variables to be included in statistical models (Harrell 2001). However, for every GPS unit that fails (if data has not been retrieved prior to failure), sample size will decrease by one unless the unit (or units) are replaced on the same or other animals.

A good strategy for mitigating the practical weakness of sample size in GPS studies is to use a validation–design approach where GPS and VHF collars are both deployed in a study population. Then, for example, habitat or movement models derived from GPS data could be validated with coarser resolution VHF data.

4. What hardware and accessories will be most appropriate?

The different types of radio-telemetry or GPS units available and accessories for those devices are myriad. Not only must researchers decide upon the appropriateness of VHF versus GPS (store-on-board or remote downloadable) versus a satellite-based system, they must also consider whether products/features such as camera collars, proximity sensors, temperature or salinity sensors, activity accelerometers or other unit customisation features are required to answer the ecological or conservation question central to a study. Often, many customised features will provide critically important information to answer the ecological question. However, most unit accessories will also require a power source. Although these are usually powered by a battery additional to that powering the GPS and VHF, researchers should be aware of the specifics of their chosen make and model to ensure that the acquisition of location data is not compromised by any added accessories.

Although GPS units and their accessories are becoming more affordable, they are still expensive compared with VHF. For example, costs of GPS collars for ungulates or terrestrial carnivores can range from about USD$1,200 to $8,000 per unit, depending on the features of the collar and, for GPS/satellite-based data retrieval systems, the expense of satellite contracts to transfer data (Tomkiewicz et al. 2010; Kiwi Track, www.kiwitrack.co.nz). Conversely, VHF collars are an order of magnitude less, with a cost of about USD$150–$600 per unit (Tomkiewicz et al. 2010).

Clearly factors other than just the costs of the units need to be considered when assessing the utility of VHF or GPS for a study. Two factors are foremost among these. First, as a guideline, the weight of the telemetry unit should not be more than about 4–5% of body weight for mammals or 3–5% for birds (Cochran 1980). However, the behaviour and physiology of some species makes them more susceptible to body mass guidelines than others, and deploying units that are too heavy may result in location data that are not representative of the animal's "normal" behaviour. Thus this guideline should be considered on a species-specific basis (Casper 2009). Often GPS units might be too large to meet the body-mass criterion and VHF units might then become the default option. The weight of the units is not only critical for animal welfare, it also has implications for battery life (smaller and lighter devices will generally have shorter lifespans) and ultimately the question(s) that can be answered.

Second, not all ecological or conservation questions require location data; rather it may be sufficient that animals be re-located periodically for visual assessment (i.e. Judas individuals in a population undergoing control). In these cases, the use of VHF units may suffice. Because we are interested in questions that require location data from animals, we do not discuss alternative reasons for deploying telemetry units on animals further.

An obvious benefit of using GPS over VHF units is the ability to collect fine-scale spatio-temporal location data, particularly on many previously difficult to study species such as long-distance migratory birds and mammals (Mueller et al. 2008). However, this does not mean that GPS units should be chosen as the default option for questions requiring location data. There is a case to be made that behaviour, migration, movement ecology and human–wildlife conflict questions will benefit from the deployment of GPS units on animals (Hebblewhite & Haydon 2010). First, it may be impossible to collect data to answer these types of questions, for some species, without GPS units and a satellite-based data retrieval system. Second, the frequency with which VHF units would need to be monitored to acquire sufficient telemetry re-locations would be considerable and probably exceed the purchase cost of the GPS units. Conversely, although resource-selection and home-range questions would benefit from the increased precision, accuracy, and reduced sampling bias offered by GPS, VHF units may yield adequate data to answer these types of questions for some species but at considerably less cost (e.g. Whyte et al. 2014). VHF transmitters also have much longer battery life than GPS. Consequently, for studies where individual animals need to be followed infrequently for a long period, using VHF on animals will mean that they do not need to be recaptured as often to replace batteries, resulting in reduced project costs and animal welfare concerns.

A final consideration when deciding between VHF and GPS is sample size. GPS units have many attractive advantages to VHF, and consequently researchers often opt for the former over the latter. The main disadvantage of this is that the current high cost of even the cheapest GPS units can result in prohibitively high costs to achieve required sample sizes to make reliable statistical inferences. For example, using the sample of 30 animals described above for estimating resource selection by a population (Aebischer et al. 1993; Leban et al. 2001) would result in minimum costs of about USD$36,000–$240,000 for lower and upper end GPS units, respectively. Where collar accessories are needed, the price per unit could be even higher. The cost of using GPS to estimate demographic parameters such as survival would be even more expensive, and these types of ecological studies would benefit from having more individuals radio-tagged with VHF or new hybrid GPS technology designed specifically for survival studies (e.g. LifeCycle GPS collars; http://www.lotek.com/) rather than more location data from fewer individuals (Murray 2006). Clearly trade-offs must be made between small sample sizes and the possibility of weak population-level inference, and the advantages of large amounts of location data required for some ecological questions.

Researchers weighing telemetry options must decide upon data requirements and estimate the costs of the study conducted using VHF versus GPS, i.e. estimate the net cost per datum. As a rough guide, it can be assumed that (1) costs of animal capture and deploying units on those animals are roughly equal for VHF and GPS; (2) a GPS unit is at least an order of magnitude more expensive than a VHF unit; and (3) monitoring costs for VHF will usually exceed the cost of monitoring GPS – all else being equal, the difference in monitoring costs will depend upon how frequently VHF-tagged animals need to be monitored.

Importantly, a proportion of the initial cost of purchasing GPS units should be recovered upon retrieval of devices. Often however, units (and consequently cost) are not recovered because units fail (GPS being far more likely to fail than VHF) or tagged animals disperse and cannot be re-located. This is particularly problematic for devices that store data on-board (i.e. data cannot be accessed remotely via UHF or satellite communications) because it results in a substantial loss of investment (i.e. the data). Thus, researchers should consider the biology (movement distances and likelihood of dispersal) of their study species, how important the retrieval of the units is to the study and how likely it is that they will be retrieved.

5. What environmental data will be required?

GPS units provide fine-scale data on animal movement and distribution; however, to answer the ecological question this information needs to be matched with environmental data. In fact, environmental data are often the most important to answer why animals do something. In this sense, environmental data refer to any data concerning those resources that influence the use of a location by an animal (Beyer et al. 2010), and can vary from data collected meticulously in the field to spatial layers derived from remotely-sensed satellite data. For example, it has been common practice in resource selection studies to describe habitat characteristics around GPS locations using land-cover maps derived from satellite imagery (Hebblewhite & Merrill 2008; Recio et al. 2013) or from digitised aerial photographs (Latham et al. 2013b). In studies of wildlife–human conflict, anthropogenic disturbances have been frequently measured not only as the area they occupy on the ground (Dussault et al. 2012), but also in terms of distance to the feature, i.e. to assess the area of biological influence beyond the actual footprint of the disturbance (Hebblewhite & Merrill 2008; Latham et al. 2011a). In studies of predator–prey dynamics, resources available to predators have been quantified as seasonal prey abundance layers derived from field surveys (Latham et al. 2013a) or by using GPS units deployed concurrently on the prey species (Bastille-Rousseau et al. 2011). Resource selection has also been linked to measures of fitness such as calf survival (Dussault et al. 2012).

A key consideration to collecting environmental data is what spatial and temporal resolutions are required to complement the fine-scale location information provided by GPS technology? For example, if resources are characterised at a coarse spatial resolution and at one snapshot in time there is likely to be a discrepancy between what the animal was experiencing at a given GPS location and what is actually captured in the environmental data. In turn, this will influence the strength of associations that are discovered during the analysis phase (Boyce 2006). It is important to note, however, that not all of the environmental data need to be collected at the same temporal and spatial scales as those of the location data. Some resources might show very little variation in biological time (e.g. elevation), in which case a one-time snapshot of their spatial distribution will suffice. Conversely, resources that show high temporal variation in their abundance and/or distribution (e.g. available forage/browse or prey) will need to be quantified at a scale that best matches their patterns of availability to the temporal scale of the GPS data (Hebblewhite & Haydon 2010). Likewise, when mapping resources in space, consideration needs to be given to the level of detail or resolution that is needed in order to reliably characterise their heterogeneous distribution in the environment (Hebblewhite & Haydon 2010).

Important breakthroughs in the collection of multi-scale, multi-temporal satellite imagery now allow better integration between environmental and animal GPS data. For example, instead of having to use 'static' land-cover models, numerous satellites can now provide information on resources on a monthly, weekly or daily basis (e.g. Normalized Difference Vegetation Index (NDVI), Pettorelli et al. 2005). Likewise, datasets on ocean primary productivity, temperature and salinity are all available in equally fine spatial and temporal scales (McClain 2009; Roberts et al. 2010). These advances have improved our ability to predict and understand the drivers of animal movements across species.

The costs of gathering the necessary environmental data are not trivial. In general, data that need to be collected in the field will come at a higher cost than spatial layers that are readily and in many cases freely available online (e.g. koordinates, http://koordinates.com/; LRIS portal, http://lris.scinfo.org.nz/; NASA LP DACC, https://lpdaac.usgs.gov/products/). However, even online data will need some level of processing to derive the attributes of interest for a given study. This can vary from a simple clipping to the outline of a study area to time-consuming classification and post-processing of satellite imagery. Satellite imagery itself comes at a cost depending on the extent of the study area and the desired resolution of the image. In essence, there are numerous ways in which resources can be described and myriad sources of data, each with its associated cost. We encourage researchers to give careful consideration to what environmental data will be needed to complement the GPS data and answer the ecological question.

6. How will the data be managed and analysed?

There are numerous question-specific analytical approaches to deal with telemetry data. At one end of the spectrum, various statistics can be summarised from location data, e.g. habitats in which animal locations occurred, the distances animals moved over a given period, or home range size. At the other end, there are numerous sophisticated mechanistic models with which to assess behaviour and animal movement (Cagnacci et al. 2010). Regardless of the complexity of the analyses required, consultation with quantitative ecologists or biostatisticians should occur at the onset of asking the question and designing the study. As a general guideline, we indicate when simple summary statistics may be sufficient to answer management questions and when they are not. Where summary statistics are limited or may be misleading, we provide a brief overview of more appropriate statistical methods.

Often, managers and conservationists do not have the expertise, money or need to conduct sophisticated analyses. If, for example, we are interested in the average home range size of male versus female Himalayan tahr (*Hemitragus jemlahicus*) or in the distance that they move in winter versus summer, we can obtain this information by using simple analyses. There are a number of useful analytical packages for summarising this type of information (e.g. Geospatial Modelling Environment: http://www.spatialecology.com/gme/; Home Range Tools for ArcGIS (Rodgers et al. 2007); adehabitat (Calenge 2006)). These ready-to-use tools can estimate home range size, distances between consecutive locations, and habitat characteristics at GPS locations. Where these types of measures are sufficient to answer the ecological question we encourage their use. If, however, we are interested in what habitats male tahr prefer compared with females or we want to infer behaviour from their location data, more sophisticated methods are required.

Telemetry yields information about used locations, i.e. places that tagged animals were when a GPS fix was taken. It does not yield information about unused locations, because tagged animals may have been in innumerable places between GPS fix attempts. This is not problematic for home range and demographic studies, but it can create a dilemma for other types of studies, particularly resource selection ones. In these instances, typical used–unused statistical methodology is inappropriate because there are no 'unused' locations (Manly et al. 2002). If an analysis is conducted without giving consideration to areas that are unused by GPS-tagged animals, limited inferences can be made about the resource preferences of those animals. In our tahr example, it means that we can summarise what habitats telemetry locations occurred in, but we cannot infer what habitat they preferred (or selected).

To overcome this issue, a used–available design is applied, where availability is represented by those sites where the species' presence is uncertain (i.e. it may or may not have been there) and can be quantified at a wide range of spatial and temporal scales (Beyer et al. 2010). Resource selection using GPS data has been estimated using various statistical approaches including resource selection functions (RSFs; Manly et al. 2002), resource utilisation functions (Marzluff et al. 2004), generalised estimating equations (Koper & Manseau 2009) and compositional analysis (Aebischer et al. 1993). Despite differing analytically, these resource selection models all yield fundamental information regarding the distribution and abundance of organisms, such as Himalayan tahr habitat preferences.

One area of research that has benefitted from GPS technology is the study of predator–prey interactions (conducted within a resource selection framework; Merrill et al. 2010), albeit largely from studies conducted outside of New Zealand. Spatio-temporal interactions between prey and predators have been inferred from concurrent locational data using latent selection difference functions (Latham et al. 2011b), RSFs (Bastille-Rousseau et al. 2011) and Cox proportional hazard models (Whittington et al. 2011). However, these approaches are correlational, and the key link between predators and their prey remains in quantifying kill rates to estimate functional response curves (Merrill et al. 2010). Spatially-explicit estimates of functional responses have been derived using space–time clustering algorithms, ratio estimators, and movement models (Hebblewhite et al. 2003; Morales et al. 2010). Given the large number of invasive mammalian predators and threatened indigenous prey in New Zealand, we foresee broad applicability for these methods.

High-frequency location data derived from GPS technology present opportunities to study questions related to animal behaviour and movement. For example, the technology can allow us to identify areas where feral cats focus their foraging effort (i.e. profitable places from unprofitable places) and assess whether these coincide with areas used by prey species of conservation concern. There are numerous complex and rapidly evolving statistical methods that address these types of questions. Different behavioural states (e.g. foraging) have been inferred using state–space models (Morales et al. 2004; McClintock et al. 2012), the first passage time method (Fauchald & Tveraa 2003) and the residency time method (Barraquand & Benhamou 2008). Behavioural states can then be associated with environmental characteristics to understand how the environment controls the behaviour of animals, and ultimately the behavioural mechanisms underlying space use and animal distribution (Schick et al. 2008; Beyer et al. 2010; Morales et al. 2010).

Movement models have also been used to understand environmental factors driving migratory behaviour. For example, Sawyer et al. (2009) used Brownian bridge movement models to identify and prioritise movement corridors for mule deer (*Odocoileus hemionus*), and Singh et al. (2012) used net squared displacement to study how environmental variation and risk of predation from hunters and brown bears (*Ursus arctos*) interact to affect the probability of migration in moose (*Alces alces*). Corridors for maintaining connectivity between populations may be identified by combining least-cost path analysis with fine-scale habitat selection (Squires et al. 2013). Movement models and RSFs have also been used extensively to infer the effects of human-induced habitat alteration on wildlife (e.g. Hebblewhite & Merrill 2008; Latham et al. 2011a).

An area of research that has sparked recent interest is that of individual variability within populations (Bolnick et al. 2003). GPS technology allows us to track the locations of individual animals, infer their individual habitat preferences and movement behaviour, and describe how these differ from population-level patterns (Latham et al. 2013a, b). Furthermore, changes in individual preference as a function of availability allow for the study of 'functional responses' in resource preferences (sensu Mysterud & Ims 1998). Importantly however, prevalence of individuality in a population still requires a large sample of tagged individuals to be able to make valid inferences about variability within a population and ultimately understand the emergence of population-level patterns (Bolnick et al. 2003).

In summary, analytical approaches to deal with telemetry data vary widely in their complexity and in the types of questions that can be addressed. Likewise, the costs associated with each approach vary according to their complexity, but also depend on whether the researcher has the expertise to carry out analyses in-house or whether these need to be outsourced. An additional consideration is the time it takes to organise and prepare large datasets that are downloaded from GPS units.

Some minor yet non-trivial considerations related to the format in which the data are retrieved from GPS collars can save processing time. Most commonly, data obtained from GPS collars are exported as 'text' files (.txt) or 'comma separated value' files (.csv), which can be imported into database management, statistical or GIS software. At minimum, retrieved files will contain *x*/*y* coordinates, date and time. Column (or field) names within files can be problematic because some software does not allow the use of spaces or underscores. To overcome this, the researcher can request that column names be adjusted by the manufacturer before collar deployment, usually at no extra cost. Researchers should also explicitly inform the manufacturer about their preferred coordinate system and time standard. Although these components can be adjusted post-data-acquisition, careful planning will help reduce data processing time.

Finally, exciting new approaches that ease the assembly and management of both animal and environmental data are freely available in online platforms such as MOVEBANK (Kranstauber et al. 2011; www.movebank.org) and OzTrack (http://oztrack.org/). For example, these platforms have built-in functions for simple descriptive summary statistics and study designs, and increasingly provide a powerful spatial data management system for integrating animal telemetry locations with environmental data. Many New Zealand biologists are already using these platforms, with data from, for example, kea (*Nestor notabilis*), long-tailed cuckoo (*Eudynamys taitensis*), and sooty shearwater (*Puffinus griseus*) currently listed. MOVEBANK allows flexible permissions, meaning that data owners have full control over who can view and download their study metadata and data. OzTrack, on the other hand, provides two options: immediate 'open access' or 'delayed open access', whereby metadata for the project are made public immediately but location data become open access after a maximum of 3 years. Overall, these platforms facilitate data-sharing between researchers and allow the wider scientific community to be aware of what is being done and where, benefiting wildlife ecology and conservation research worldwide.

Other considerations

Often there are a number of studies in a given area that have deployed units (including GPS units containing VHF) with VHF beacon transmitters on wildlife. This has implications for choosing VHF frequencies for any units that you aim to deploy, because duplications between studies can occur whereby two or more animals have units operating on the same (or very similar) frequencies. This can result in field staff tracking the wrong animal (particularly if animals are re-located from an aircraft), and is a waste of time and money. The area that can be affected by this problem can be large and extend well outside a study area. This can happen for two reasons. First, tagged animals can disperse from one area to another. Second, some VHF beacons have signals that are detectable at considerable distances under optimal conditions. For example, a wolf in Alberta, Canada, had a beacon that was occasionally detectable from an aircraft at about 50 km (A.D.M. Latham, unpubl. data) and a kea in Kahurangi National Park had a beacon that was detectable from 15 km (I. Yockney, Landcare Research, pers. comm.). To avoid this problem, we recommend that VHF frequencies from all studies across organisations be kept in a centrally-managed national database (recognising that this information should not be made publicly available) and consulted as required. Further, the VHF band width within which units may legally be deployed for wildlife studies can differ between countries. Consequently, researchers must ensure that purchased units are within the permissible national or regional band-width range.

Finally, studies using GPS technology will have additional costs that can be difficult to estimate and budget for accurately. For example, there are the expected costs of retrieving spent units, either by recapturing the animal or picking the unit up from the field if they have a timed-release or radio drop-off option. There are the probable costs of searching for missing or failed units and, if the project is ongoing, having to replace those units that are confirmed lost or failed. In some instances a unit may be retrieved from an animal and, once its battery has been changed and the unit tested to ensure it is functioning correctly, it may be in a condition that is adequate for immediate redeployment. Other times this is not the case, and many units will require extensive and expensive refurbishment.

Summary

We have emphasised that the ecological or conservation question(s) should be the starting point for determining the appropriateness of GPS or satellite-based systems, not the current availability of high-tech hardware. Once the question has been posited and GPS deemed appropriate, sampling frequency, sample size, environmental data, and statistical requirements should be determined a priori. Giving careful consideration to all of these components will increase the likelihood that useful inference will be attained from expensive GPS data.

Critical to this assessment are budgetary considerations and logistical trade-offs. In other words, are there sufficient funds and expertise to purchase enough units for the required sample size; to capture and tag animals; and to collect and analyse environmental and location data? If the budget is not sufficient to do these things, then either more funds need to be obtained or the question has to be changed. Further, we emphasise that researchers must be cognizant of the budgetary requirements for data management and statistical analysis as these can be a significant proportion of the total budget of a project.

Although GPS technology has contributed substantially to our understanding of many biological processes, it should not be considered a substitute for knowledge of natural history or field biology but rather complementary to them. Throughout this paper we have emphasised the importance of the 'question'. Insightful questions can only be asked by those who have a sound understanding of the species (singular or plural), system, and their ecology. Quantitative analyses are also an indispensable component to GPS studies. Consultation with quantitative ecologists should not arise after location data have been collected, but rather at the onset of asking the question and designing the study.

Studies using GPS telemetry still need to make or advance important links such as connecting habitat selection and movement to individual fitness and population consequences (Gaillard et al. 2010). Our understanding of some of these links may come through judicious use of GPS units and long-term ecological studies (Hebblewhite & Haydon 2010). 'Judicious' clearly implies that the question that will further our understanding of ecological processes is foremost in a study design. Applying this philosophy will maximise the utility of GPS technology for wildlife studies.

Acknowledgements

This work was funded by core funding provided to Landcare Research by the Ministry of Business, Innovation and Employment. We thank Christine Bezar, Clare Veltman, Nate Webb, Phil Cowan, and Ivor Yockney for their input. Isabel Castro and her graduate students, and two anonymous reviewers provided useful comments on an earlier version of this manuscript.

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