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EFFECTIVE USE OF RADIOTELEMETRY FOR STUDYING TROPICAL CARNIVORES

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ABSTRACT. — Radiotelemetry has become one of the most valuable field techniques in wildlife ecology because it allows biologists to collect location and other data remotely. This method is an especially important tool for studying the behaviour and demography of species that are often secretive, traverse large areas, and occur at low densities. Although use of radiotelemetry for studying tropical carnivores has been limited, this is changing rapidly. However, to maximise the value of radiotelemetry for learning about and managing tropical carnivores, biologists need to understand this technique and important considerations in its application. Radiotelemetry studies can provide useful information when biologists clearly articulate their objectives, carefully select study designs, evaluate important assumptions, apply appropriate analytical methods, and interpret the results properly. The choice of equipment and methods often must consider challenges such as remote study areas dominated by dense vegetation. Appropriate methods of attaching transmitters are critical, as is the assumption that transmitters have no significant effects on study animals. The development of GPS radiotelemetry allows investigators to examine movements at high resolution, but VHF systems often remain the most appropriate or only feasible option for many studies of tropical carnivores. Methods for analysing radiotelemetry data also have expanded greatly in sophistication and explanatory power. Some of the most important analytical developments are in the shift from simple descriptive statistical approaches to process-based models that directly incorporate mechanistic hypotheses. Throughout this overview, we outline general advantages and disadvantages of various study options and emphasise the importance of testing key biological and methodological assumptions appropriate for each technique at all stages in the collection, analysis, and interpretation of radio-tracking data.

KEY WORDS. — carnivore, home range, movement, radiotelemetry, study design, tropical mammals

INTRODUCTION

To understand and manage wildlife species, biologists require appropriate information about animal demography, movements, space use, resource selection, and physiological activity. Radiotelemetry is a fundamental tool for obtaining this information (Mech, 1983; Kenward, 1987; White & Garrott, 1990). With this method, animals are equipped with tag units that transmit or receive signals to produce data about each animal's location, activity, and other attributes.

Radiotelemetry is often the most appropriate method, and in many cases the only effective option, for addressing many ecological hypotheses and management questions about wildlife (Miller et al., 2010; Millspaugh et al., 2012b). Moreover, continued technological and quantitative developments broaden the range of questions and species for which radiotelemetry studies are feasible (Millspaugh & Marzluff, 2001). This ever-increasing potential power of radiotelemetry is especially relevant to biologists studying and managing wide-ranging, elusive species occurring in highly challenging environments—species such as tropical mammalian carnivores.

Biologists using radiotelemetry should recognise that such investigations come with important assumptions, strengths, and limitations. Biologists must understand these issues, how this technique works, and how to choose among numerous options for equipment and methodology (e.g., Kenward, 1987, 2001a; Millspaugh et al., 2012a, 2012b). At the same time, radiotelemetry studies must be built on fundamental principles equally important in any scientific study (White & Garrott, 1990; Garton et al., 2001). Radiotelemetry is a tool, and in any situation investigators need to consider carefully whether it is the appropriate tool for obtaining the desired information (White & Garrott, 1990; Millspaugh et al., 2012b).

Our objective is to provide an overview of these interrelated aspects of applying radiotelemetry methodology to tropical carnivores. To help readers better understand the potential of the method as well as the current state of the field, we start by briefly discussing the past use of radiotelemetry for studying this group. We then focus on key study-design issues, basic technology and its field application, and analytical and software considerations. Our overview is a general and brief introduction to a complex topic, and should be seen as a gateway to more detailed coverage, including numerous key journal-length references as well as books and book chapters such as Mech, 1983; Kenward, 1987, 2001a; White & Garrott, 1990; Powell, 2000; Millspaugh & Marzluff, 2001; Fuller et al., 2005; Moorcroft & Lewis, 2006; Fuller & Fuller, 2012; and Millspaugh et al., 2012a, 2012b.

RADIOTELEMETRY STUDIES OF TROPICAL CARNIVORES

The use of radiotelemetry for studying tropical carnivores has been limited due to harsh field conditions in many study areas (e.g., in dense tropical forests), technological limitations, budgetary constraints, and possibly lack of general familiarity with the technique's potential. However, there has been a gradual increase in the number of successful applications and the number of species studied, a trend that should accelerate rapidly. For example, consider the use of this technique in studying the carnivore fauna of selected regions in the Asian tropics. Based on published studies, 10 of 36 carnivore species have been radio-collared in Thailand's tropical forests: leopard cats (*Prionailurus bengalensis*), clouded leopard (*Neofelis nebulosa*), Asiatic golden cat (*Catopuma temminckii*), marbled cat (*Pardofelis marmorata*), leopard (*Panthera pardus*), binturong (*Arctictis binturong*), common palm civet (*Paradoxurus hermaphroditus*), masked palm civet (*Paguma larvata*), dhole (*Cuon alpinus*), and yellow-throated marten (*Martes flavigula*; Rabinowitz, 1990, 1991; Rabinowitz & Walker, 1991; Grassman, 1998, 1999, 2000; Grassman et al., 2004, 2005a, 2005b, 2005c; Austin et al., 2007; Simcharoen et al., 2008). Of 29 carnivore species in Peninsular Malaysia, only the short-tailed mongoose (*Herpestes brachyurus*) and Malay civet (*Viverra tangalunga*) have been studied using radiotelemetry (Jennings et al., 2010a, 2010b). In Borneo, five of 25 carnivore species (leopard cat, common palm civet, Malay civet, Sunda clouded leopard [*Neofelis diardi*; Fig. 1], and sun bear [*Helarctos malayanus*]) have been studied with radiotelemetry (Colon, 2002; Wong et al., 2004; Fredriksson, 2005; Rajaratnam et al., 2007; Nakashima et al., 2010).

We believe that the use of radiotelemetry for tropical carnivores is following a trend similar to the patterns shown repeatedly within other specific taxonomic groups (e.g., bats: Amelon et al., 2009), and mirroring major advances in technology (e.g., GPS radiotelemetry; Hebblewhite & Haydon, 2010). Initially, several factors have tended to produce a strong focus on somewhat exploratory, descriptive studies usually characterised by low sample sizes: the novelty of technology, challenges and expense of adopting this technology to difficult taxonomic groups, and high value of basic natural history and behavioural information (White & Garrott, 1990; Kenward, 2001b). After this initial exploratory phase, a stronger focus on rigorous study designs using sufficient sample sizes and modern analytical methods to assess mechanistic ecological hypotheses has developed (White & Garrott, 1990; Moorcroft & Lewis, 2006; Millspaugh et al., 2012a, 2012b).

For most tropical carnivores, the use of radiotelemetry has been in the initial exploratory phase. For example, in studies of Asian tropical carnivore species cited earlier in this section the median number of individuals followed

Fig. 1. Sunda clouded leopard (*Neofelis diardi*) anesthetized and equipped with a neck-collar radiotransmitter (biologists from left to right: Joanna Ross, Siew Te Wong, and Andrew Hearn).

per species per publication is 5 (range = 1–20). This is small even in comparison to average sample sizes obtained in radiotelemetry studies of tigers (*Panthera tigris*) in India, Nepal, and Russia (Miller et al., 2010). Certainly these studies already have provided considerable insights regarding social structure and scale of space use (Jennings et al., 2010a), important ecosystem roles (Nakashima et al., 2010), and habitat requirements (Wong et al., 2004). We also do not wish to under-emphasise the difficult challenges in obtaining higher sample sizes for tropical carnivores, particularly with limited funding or study populations that sometimes may include only a dozen or fewer individuals (e.g., Núñez-Pérez, 2011). However, there are tremendous opportunities for more powerful uses of radiotelemetry. For this to occur, biologists need continued advances in technology and funding. However, fundamental general considerations not unique to tropical carnivores will be even more important in determining the value of radiotelemetry for understanding and managing this group. This value can accelerate most rapidly if biologists understand and build on powerful study design and analytical frameworks developed for radiotelemetry studies during the last several decades.

GENERAL STUDY-DESIGN CONSIDERATIONS

As a general technique, radiotelemetry is unique in the diversity of research and management questions it can help address. Radiotelemetry allows assessment of daily and seasonal movements, dispersal and migration, home-range and core-area utilisation, and intra- and inter-specific interactions (see Kernohan et al., 2001 and Millspaugh et al., 2012a for overviews; examples with tropical carnivores include Wong et al., 2004; Grassman et al., 2005c; Jennings et al., 2010a, 2010b). Radiotelemetry locations, along with habitat and other environmental data, often form the basis for estimating resource use and selection (e.g., Wong et al., 2004; Simcharoen et al., 2008). When location data are combined with suitable layers in geographic information systems (GIS), resource selection can be examined simultaneously at multiple spatial scales. With sensors integrated into radiotags (e.g., mortality or activity sensors), biologists can quantify survival, causes and timing of mortality events, and activity patterns (e.g., Janis et al., 1999; Grassman et al., 2005b). Radiotelemetry can be a primary or supporting tool in estimating abundance and density (White & Shenk, 2001; Núñez-Pérez, 2011), and radiotelemetry data can play a joint role with other data sources in integrated demographic analyses (Skalski et al., 2005). Moreover, with careful study design and sufficient resources, biologists may address multiple questions in a single field study.

Because of this diversity of potential questions, it is easy to make the mistake of spreading limited effort across multiple objectives such that the study does not address any objective conclusively. Similarly, it is easy to forget that radiotelemetry technology is simply a tool for addressing well-defined questions (White & Garrott, 1990). These and similar pitfalls can be avoided by paying careful attention to fundamental questions throughout all stages of a study. Here, we briefly highlight a few relevant issues, and refer readers to other sources (e.g., Garton et al., 2001) for more extensive discussion.

Why is the study being conducted, what are the specific objectives, and how do the proposed objectives serve the overarching purpose? — Is the intention to provide specific information for which there is a clear intended management use, to address poorly understood aspects of basic life history and behaviour, to test specific ecological hypotheses and predictions, or to evaluate untested technology or key assumptions as a step towards implementing fuller studies? The underlying purpose provides the context for developing and justifying meaningful objectives.

Regardless of whether the study is focused on conservation management questions or basic ecology, the objectives should be phrased in terms of specific parameters to be estimated (e.g., mean home-range size and mean difference in home-range size in different areas, based on some precise definition of "home-range size"). The objectives should define the spatial, temporal, and demographic domains (i.e., target universe or target population) of interest. For example, is the focus on all ages classes of both sexes throughout some protected area at all times of the 24-h cycle year-round, or on some subset of these dimensions? The objectives should specify the desired information quality, which may be defined in terms of precision, statistical power, ability to distinguish among competing ecological hypotheses, or whatever other metric is most relevant (Reynolds, 2012). If there are multiple objectives, (e.g., estimating average 95% probability-contour home-range sizes for females during each season of the year, comparing habitat characteristics at dens vs. random sites, and estimating female annual survival), what is the relative priority of each objective? The objectives should guide all subsequent decisions about sampling designs, equipment, and analytical methods (Mech, 1983:82; Kenward, 1987; White & Garrott, 1990; Garton et al., 2001). Even if an investigation is intended to be an initial pilot study of an elusive tropical carnivore, time spent defining and prioritising objectives will pay off.

How will major potential sources of bias be quantified and addressed? — This question involves integrated consideration of factors such as how study individuals are selected to be radiotagged, the schedule for collecting observations from them, the degree to which they may be affected by radiotags, and whether location accuracy or ability to get a location fix varies with respect to factors (e.g., habitat type, Frair et al., 2010) under investigation in the study. The impacts of tags on animals obviously are of concern from animal-welfare and conservation standpoints, but also because of fundamental study-design principles. If radiotelemetry tags cause non-trivial changes in behaviour, survival, or reproduction, resulting data will be unrepresentative of the broader population of interest (White & Garrott, 1990). This potential risk needs to be minimised through suitable equipment choices and, when appropriate, by not using data collected from an individual until it has acclimated to the radiotag. Such actions do not guarantee that the problem has been avoided. Therefore, it is critical to evaluate the assumption that this source of bias truly is inconsequential in your study situation (e.g., Winterstein et al., 2001; Withey et al., 2001). Testing transmitters on captive individuals or surrogate species (White & Garrott, 1990; Biggins et al., 2006), along with other pilot studies, are invaluable, particularly for detecting large and immediate impacts of tagging. However, a more thorough evaluation of potential impacts requires at least as much effort as needed to assess the impacts of any other factor on behaviour or demography, assuming there is any feasible way of getting appropriate data for animals without radiotags in order to compare animals with and without such tags (White & Garrott, 1990). Conclusive evaluations should be prioritised as one component of an overall research framework, a component in addition to or integrated into other individual studies of the species.

Inference about the target population (of individuals and in space and time) depends on proper selection of individuals for inclusion in the study and a careful plan for how data are collected from these individuals (White & Garrott, 1990; Garton et al., 2001). Direct probability sampling from the target population of individuals rarely will be possible, but potential sampling biases need to be minimised—e.g., by distributing trapping efforts throughout the relevant study area when catching animals to be equipped with radiotags. Depending on the type of study, the default survey design most frequently will attempt to have relatively equal probability sampling of individuals from the target population and approximately equal numbers of locations obtained per animal. In choosing the timing and frequency of collecting locations from animals, generally a systematic sample covering the temporal window of interest is recommended (Otis & White, 1999). This coverage should be planned at multiple scales; for example, if the focus is on foraging habitat selection by a nocturnal carnivore, the sample should systematically cover all months of interest as well as all times of night when the animal may be foraging.

However, in some cases it may be more efficient or simply necessary to have unequal probability sampling (of animals, times of day, etc.). If the probability of successfully obtaining a usable telemetry location varies among habitats, this forms a source of measurement bias that needs to be assessed through pilot studies (Garton et al., 2001) and that might be accounted for by differential weighting of locations during analysis (Horne et al., 2007a). Unequal sampling of individuals and over-representation of some portions of the temporal window of interest (e.g., twice as many locations planned for collection during day vs. night) may be appropriate, but such decisions should be carefully planned a priori (Fieberg, 2007b). In some situations, unequal monitoring of individuals may be purposely planned to meet multiple objectives. For example, if both home-range size and survival are of equal importance, the study might combine an extensive sample of individuals monitored periodically for survival estimation, with locations collected much more frequently from a subset of these individuals for quantifying their space use.

***How much effort, and what allocation of effort, is needed to provide sufficiently precise information*?** — The objectives define what quality of information is needed for the study to be useful, relevant to the underling purpose. Quantitative study design—making design decisions that will provide the precision desired by the study while minimising costs—helps ensure that study resources are allocated appropriately and helps one avoid pursuing a study that has little chance of providing useful information (White & Garrott, 1990; Reynolds, 2012).

Typically the biologist must address trade-offs among the number of animals to be tagged, the number and frequency of observations to be collected per animal, and the accuracy needed per location. For example, if a primary study objective is to estimate average home-range size across a population that may include dozens of animals, using GPS tags to obtain locations every 15 minutes from a sample of five animals likely will not provide meaningful information relative to the objective (Otis & White, 1999). As another example, perhaps you have sufficient field help to obtain a total of 1000 telemetry locations across all study animals each season using VHF transmitters (see next section), and your focus again is on average home-range size each season. Garton et al. (2001) suggested that typically 50–200 locations per season from each of at least 20 animals may be a useful expectation of the minimum effort needed to obtain relatively accurate estimates. Collecting 100 locations from each of 10 animals may allow relatively accurate estimation of each individual's home-range size (e.g., Seaman et al., 1999; Belant & Follmann, 2002) but not adequately account for among-individual variability. Collecting 10 locations each from 100 animals would have the opposite problem. Balancing these trade-offs requires careful examination of expected study performance in light of among-individual variation and average measurement uncertainty. When considering the number of locations needed per animal, the investigator should integrate realistic estimates of rates of equipment failure and failure to obtain usable locations when planned (Fuller & Fuller, 2012; e.g., Belant, 2009; Frair et al., 2010). Similarly, the degree of accuracy needed per location fix depends on study objectives and other sources of variability (Withey et al., 2001). Even limited field trials are invaluable for assessing expected accuracy in a study area (e.g., Grassman et al., 2005c; Simcharoen et al., 2008).

Evaluating design alternatives is most straightforward when designing survival studies and other investigations for which there are analytical equations relating sample size to precision or statistical power (Samuel & Fuller, 1994). For planning studies which use the individual animal as the independent "experimental" unit, biologists need estimates of among-animal variability in the biological parameter of interest. They need an approach for characterising how measurement precision changes as a function of sampling intensity (e.g., average uncertainty in estimating each individual's home-range size vs. the number of locations per animal), and they need cost information (e.g., average costs of capturing and tagging each study animal and of obtaining each location for a tagged animal). With many space-use analytical methods, however, there are no simple functions to quantify how within-animal measurement error changes as a function of the number of locations collected per animal. Many techniques, such as most widely used home-range estimation methods, provide an individual-level parameter estimate (e.g., home-range size) but do not easily provide an estimate of the uncertainty in the parameter estimate. Therefore, published empirical studies typically do not partition among-animal (or other ecological variability) from measurement variability, making it difficult to use the reported information to address design trade-offs.

Because of this challenge, biologists typically rely on rules of thumb obtained from general simulations and empirical case studies (see Garton et al., 2001). Such general rules may help investigators avoid over-optimistic planning, but are only a starting point for developing a sampling design tailored to study-specific objectives, costs, and variance structures. This is an issue that requires further attention. At a minimum, as biologists build radiotelemetry data sets with a carnivore species or species assemblage, we strongly urge these investigators to explore sample size and precision relationships for use in designing subsequent studies.

One form of temporal autocorrelation in radiotelemetry studies is the degree to which a location or behaviour at time "B" is a function of where the animal was or what it was doing at time "A" rather than an independent behavioural decision. Biologists traditionally viewed temporal autocorrelation as a major problem to be avoided or eliminated at all costs. Our field has moved beyond such simplistic conceptual frameworks (e.g., Otis & White, 1999; Fieberg, 2007a). The temporal dimension of radiotelemetry data provides information that should be utilised, not discarded. For example, if you are able to take sequential locations frequently enough such that autocorrelation is a concern, then you likely have valuable information about movements which may be used even if your focus is on general home-range estimation. If you are not going to use the temporal component, at a minimum you should not view autocorrelation as a major problem in most situations if you have an appropriate sampling design (Otis & White, 1999). For example, when estimating home-range size, a set of 100 locations with moderate autocorrelation between sequential locations, spaced systematically across the temporal window of interest, typically will lead to much more accurate estimates compared to a reduced subsample of 40 uncorrelated locations. Unfortunately, with no justification other than "to avoid autocorrelation", biologists still often essentially discard many of their sample locations during analysis by subsampling from the collected locations. Do not do this unless you have a very well-justified rationale!

RADIOTELEMETRY AND RADIO-TRACKING EQUIPMENT

Good technology cannot save a poorly designed study. Conversely, an otherwise well-designed study may fail if equipment is not selected carefully or does not perform as expected. Moreover, there will continue to be some objectives which cannot be addressed with radiotelemetry due to technological limitations (e.g., estimating annual home ranges for a species too small to support transmitters with a battery life of more than a few weeks). Still, such limitations continue to be overcome; readers should keep in mind that technology changes rapidly. Biologists should discuss current options with manufacturers before finalising a study design. Conversely, even for standard equipment applied to species on which similar equipment has been used in the past (e.g., similar transmitters from a different manufacturer), we urge biologists to plan for a thorough testing phase before deployment. This phase will be more extensive for relatively unstudied species in challenging environments—i.e., for many tropical carnivores.

Attaching and powering radiotransmitters. — Every radiotelemetry study uses a radiotag that must be attached to study animals and that is powered by a battery or solar cells. Tropical carnivores are most often fitted with radio collars placed around the neck (e.g., Rabinowitz & Walker, 1991; Simcharoen et al., 2008). In these cases, the collars are individually fitted to the animal, with some space provided between the collar and animal to allow for normal growth and movement but not so much space such that the collar can slip off over the head. Fortunately, the latter risk generally is low because the maximum head circumference of most tropical carnivores (with the possible exception of sun bears; Fig. 2) is considerably larger than their respective neck circumferences.

Implanted transmitters require surgery, but have been used successfully for some species for which neck collars are not preferable or possible (e.g., otters and other mustelids; Reid et al., 1986; Stevens et al., 1997; Goodrich & Buskirk, 1998; Ralls et al., 2006). Although implants with internal antennas provide reduced signal strength, they also have lower risk of adverse effects on behaviour and movements. In contrast, implants with external antennas have signal strength similar to radio collars but there is a higher risk of bacterial infections at the incision site. This is a significant risk in

Fig. 2. Anesthetized Malayan sun bear (*Helarctos malayanus*), with radiotransmitter attached using a neck collar (biologist in photograph: Siew Te Wong).

warm, humid tropical environments, where we discourage use of implants with external antennas. Regardless of the antenna type, surgical implantation requires specialised skills and equipment (e.g., a portable anesthesia machine for field use). Implantation should be performed only by a veterinarian or at least an individual with appropriate specific training under the direction of a veterinarian (Mulcahy, 2006; Small et al., 2006). Appropriate follow-up monitoring and evaluation is critical. Readers considering implanted transmitters should plan for thorough preliminary testing, building on numerous other evaluations of implants in carnivores (e.g., Biggins et al., 2006; Zschille et al., 2008; Quinn et al., 2010; Léchenne et al., 2012).

Transmitter mass is a major consideration when developing any radiotelemetry project. Traditional rules-of-thumb regarding acceptable transmitter mass are only a starting point for consideration. The acceptable transmitter: body mass ratio will depend partly on how the transmitter is attached, attachment characteristics (e.g., collar material), and on observed behavioural response to the transmitter. Our general advice is to choose the smallest unit (including the transmitter and any associated sensors) that will meet study objectives and that is < 5–10% of body mass (Sikes et al., 2011).

Batteries are typically the heaviest component of battery-powered transmitters. Larger batteries with more capacity have stronger signals and function longer, but are more likely to affect animal behaviour. Therefore, choice of battery will partly determine whether a study can obtain sufficiently accurate data over a suitable time frame from animals whose behaviour and survival are not hindered by excessive transmitter weights. Technological options can extend battery life. For example, microcontrollers in VHF transmitters can allow precise control of the pulse rate and pulse width and allow the user to program ‘duty cycles’ that switch units off and on during portions of the day or year.

A variety of sensors can be integrated into radiotags to provide information about animal behavioural and physiological activity (Millspaugh et al., 2012b). Activity sensors include those that change the transmitted signal depending on whether the animal is motionless or moving, mortality sensors that change pulse after a specified period of inactivity, and accelerometers for capturing fine-scale movements. Physiological sensors include those that measure temperature, heart rate, and other attributes. See Fuller & Fuller (2012) for an overview of applications to carnivores, as well as broader reviews of remote sensors for studying animal ecology (e.g., Cooke et al., 2004; Ropert-Coudert & Wilson, 2005).

Radiotelemetry systems. — Radiotags are one component of an overall radiotelemetry system. For each component in the system, there are various options with advantages and disadvantages that determine the types of studies for which each option is useful. The biologist must consider how each component will integrate with other components in the context of study objectives, cost considerations, and characteristics of the focal species and study area (e.g., accessibility, topography, vegetation structure).

VHF Systems: The most commonly used radiotelemetry system for tropical carnivores uses very high frequency (VHF) wavelengths, cycling at 30–300 MHz (see overviews in Tomkiewicz et al., 2010; Millspaugh et al., 2012b). For example, note that all Asian carnivore studies cited in previous sections used VHF radiotelemetry. Each radio collar transmits a unique frequency that allows individual identification. Using specialised antennae and receivers, study personnel detect transmitter signals and estimate the location of each animal as well as the uncertainty in that estimate. When each location for each animal is collected through labour-intensive field tracking, it may be difficult to obtain more than one location (or a short series of locations) from each study animal every few hours or even few days, depending on the situation. Uncertainty in estimated locations may be significant depending on factors such as equipment, terrain, distance to the animal, and the ability to rapidly take triangulation bearings before the animal has moved.

Choice of appropriate frequencies is one of the many decisions investigators will face when using VHF systems to track tropical carnivores. For example, longer wavelengths (lower frequencies) require larger transmitting and receiving antennas than do higher frequencies. However, lower frequencies transmit better through wet, dense vegetation typical in tropical forests, so the most appropriate choice will depend on study-area characteristics. Under conditions typical of tropical areas, we suggest using transmitter frequencies from 148.000–170.000 MHz. Frequencies of radio transmitters occasionally drift, or change slightly, due to environmental conditions. Consequently, we recommend investigators order transmitters that differ in frequency by > 10 kHz (Mech, 1983; e.g., 164.005, 164.015, etc.), ideally by 25 kHz if possible. Every study area typically has background interference at certain frequency bands. These problematic frequencies should be identified by testing the range of potential frequencies to be used before ordering transmitters (Withey et al., 2001).

Receiving antennas acquire signals from transmitters and relay those signals to VHF receivers. Multiple options are available (Millspaugh et al., 2012b). Omni-directional antennas are useful for detecting a signal, but do not provide directionality. Adcock or ‘H’ antennas are a compact, commonly used directional antenna with 2 elements. Handheld Yagi antennas often have 3 or 4 elements, and mounted units can have more. The increased number of elements improves both power to detect a signal and directional sensitivity. Both Yagi and H antennas provide the strongest signal when pointing directly at the transmitter, and another, slightly weaker, ‘peak’ signal when pointed 180° from the transmitter. Although Yagi antennas in general have more power for detecting signals, the bulkiness of the antennas often hinder ground tracking when moving through thick vegetation. Therefore, researchers working in tropical forests should use the “Rubber-ducky” H antenna which has rubbery flexible elements or flexible 3-element Yagi antennas (Biotrack Ltd., Wareham UK). Although most field studies of tropical carnivores have used portable antennas (and mobile field personnel), antennas also may be mounted on fixed-location towers for detecting animal presence and estimating locations (e.g., Kays et al., 2011).

Receivers acquire a signal through the antenna and process that signal to produce an audio tone. In selecting an appropriate receiver, one consideration is the available bandwidth. Many receivers now come with a bandwidth of 4 MHz or greater; however, some less expensive units are useful in only narrow bandwidths. If transmitters with microcontrollers are used to emit uniquely coded pulses on the same frequency, the user will need an appropriate receiver to decode those pulses. Programmable scanners can store many frequencies and are used to search for many animals concurrently. Most scanners allow for variable scanning speeds, so that speeds can be selected appropriate to the specific application (e.g., using faster speeds if tracking is done aerially to avoid missing a pulse).

Global tracking systems: Our ability to track many wildlife species across large and remote areas has evolved rapidly with the availability of Global Positioning System (GPS) tags and other satellite-based tracking systems (Hebblewhite & Haydon, 2010; Tomkiewicz et al., 2010). These systems provide 24-h coverage, typically high accuracy of relocations, and the potential to locate animals with very short intervals between relocations. Near-continuous relocation data can produce data sets consisting of thousands of locations per animal per month or season, allowing analyses of fine-scale movement decisions. However, these advantages must be weighed against the high unit cost of global-tracking equipment and data retrieval, typically shorter lifespan due to higher current and voltage requirements, and greater unit weight (Tomkiewicz et al., 2010). Instead of simply assuming that GPS-based systems are always preferable when available, investigators must carefully consider the relevant trade-offs in light of the study-design issues discussed earlier (Hebblewhite & Haydon, 2010). In addition, suitable GPS tags currently are unavailable for many small to moderate-sized tropical carnivores.

These GPS units use information transmitted from a constellation of satellites to estimate a geographic location. Compared to other wildlife tracking equipment, GPS tags provide extremely accurate locations, with errors often ranging from < 20–150 m. Although the utility of GPS tags historically has been limited, particularly in rugged terrain and thick vegetation which could block satellite transmissions (Bourgoin et al., 2008), recent technological developments have made the equipment much more robust, at least under modest vegetation cover (Holland et al., 2009; Tobler, 2009). However, researchers working in tropical forest with multiple canopy layers or steep terrain should test the success of obtaining location data from GPS units before investing significant resource in such transmitters.

There are several options for retrieving data from GPS units. Data can be accessed directly from the collar after animal recapture. However, animal recapture can be challenging, thus, GPS units for larger species (e.g., sun bear, clouded leopard) can come equipped with remote drop-off mechanisms. For smaller species, leather or cotton spacers that deteriorate can be inserted in the collar to allow the unit to be retrieved once off the animal (Garshelis & McLoughlin, 1988; Hellgren et al., 1988). Other options for data retrieval include remote download through a signal transmitted from the tag or integrating the GPS unit with a communication network such as Argos platform terminal transmitter (PTT) or GSM telephone networks. For animals that move over large areas or live in remote, topographically complex areas, such satellite-based receiving equipment may be the only practical way of obtaining transmitter signals (Jouventin & Weimerskirch, 1990). However, integrated PTT / GPS units remain unfeasibly heavy for smaller carnivores, while stand-alone PTT transmitters, useful mainly for examining very large-scale movements (Millspaugh et al., 2010b), will have little utility for most tropical carnivores.

ANALYSIS OF RADIOTELEMETRY DATA

In any radiotelemetry investigation, biologists need to choose among an ever-expanding and often bewildering variety of analytical approaches. This makes it essential to start thinking about data analysis options early during study development. Once the objectives have been specified, one should identify which analysis approach or alternative approaches will provide the desired parameter estimates, and then determine which sampling design and equipment will provide the data needed as input (Reynolds, 2012). This ensures that all aspects of the study are integrated effectively.

Behavioural questions. — It is convenient to categorise the types of behavioural questions generally addressed with radiotelemetry into a few major groups, as we do in this section. However, such categorisation should not mislead readers into neglecting the interrelated nature of these questions. Overall patterns of animal space use (e.g., home-range characteristics) are the result of individual movement decisions and reflect the simultaneous effects of resource and environmental characteristics, interactions with humans and other animals, and the animal's previous experience. More broadly, radiotelemetry data can form a foundation for questions across physiological, behavioural, and demographic scales. Increasingly, ecologists are emphasising conceptual frameworks and analytical approaches for integrating these different scales and types of questions (Nathan et al., 2008; Schick et al., 2008; Struve et al., 2010). Any investigator using radiotelemetry to study tropical carnivores should understand and build on these developments. Readers also need to be aware that much of the recent literature focuses on methodologies for analysing massive data sets with very high temporal resolution, typical of GPS-telemetry studies. Yet, radiotelemetry studies of many tropical carnivores will continue to rely on VHF systems and usually obtain modest numbers of locations per animal.

General movement characteristics: Radiotelemetry analyses may focus on quantifying simple aspects of movements ranging from fine-scale decisions (e.g., hourly movements) to large-scale movements (e.g., dispersal). Simply describing basic metrics such as the distance, direction, and rate of movement (e.g., Wong et al., 2004; Austin et al., 2007; Jennings et al., 2010a; see Kernohan et al., 2001, for an overview) may improve our understanding of a species' natural history, may have direct management relevance, or may form the basis for comparisons among groups or habitats to make inference about underlying processes. Descriptive models of movements and movement patterns (random walk models, first passage time analyses, multi-behavioural models, fractals, and Lévy flights) have been reviewed thoroughly in other literature (Turchin, 1998; Hagen et al., 2001; Börger et al., 2008; Schick et al., 2008). Beyond describing movements and modeling simple movement rules, studies may link movement decisions directly to factors affecting movements to produce more mechanistic insights. Such factors may be external to the animal, such as habitat patterns, as well as intrinsic, such as physiological state and the scale at which animals perceive their environment (With, 1994; Nams, 2005). There has been rapid development and applications of powerful quantitative methodologies for modeling movement behaviour (Morales et al., 2004; Forester et al., 2007; Eckert et al., 2008; Patterson et al., 2008; Schick et al., 2008).

Resource utilisation and selection: Although similar principles are involved regardless of which type of resource a study is examining (e.g., prey, habitat type), in most of this section our discussion will focus on studies of habitat ecology, as this context illustrates the confusing suite of analytical options and issues relevant to resource utilisation and selection studies. However, we note that radiotelemetry often is highly useful in assessing prey utilisation and feeding rates by carnivores, facilitating quantification of fundamental predator-prey relationships (Mech, 1983; Miller et al., 2010).

Radiotelemetry has been an essential tool for quantifying habitat relationships, and such studies involve numerous widely used terms and concepts (Table 1). Biologists typically view resource and habitat use as having a fundamentally hierarchical nature, in which choices at each of several scales constrain and otherwise interact with choices possible at other scales (Johnson, 1980). The order of selection that is the focus of the study must be considered explicitly because it identifies the population of interest, the appropriate observational (experimental) units, and the context for considering management implications (Thomas & Taylor, 1990). It is important to recognise that this organisational hierarchy is a useful framework but should not constrain the biologist's conceptual thinking about how complex behavioural decisions actually occur. For example, the home range may partly be an emergent outcome of all finer-scale choices and interactions, not simply a higher-order decision that constrains finer-scale choices.

A related but messier issue is that when trying to quantify selection rather than just absolute use of various resources, our inference becomes dependent on what alternatives we think the animal could have considered. The concept of selection order is a useful starting point, but even at any specific order, conclusions may be sensitive to how availability has been defined at that scale. There are various pitfalls and strategies for addressing these potential problems (Johnson, 1980; Porter & Church, 1987; Arthur et al., 1996; Cooper & Millspaugh, 1999; Buskirk & Millspaugh, 2006; Beyer et al., 2010). Some approaches may have stronger justification than others in any given situation. However, there is the unavoidable issue that regardless of how availability is defined, we do not know whether it adequately corresponds to what the animal perceives to be available (Marzluff et al., 2001). For example, an individual's behavioural decisions will be influenced not just by habitat but also factors more difficult to measure (e.g., social hierarchies and predation; Otis, 1997, 1998; Mysterud & Ims, 1998). The animal likely is integrating information of various types across multiple scales simultaneously, probably in light of past experience.

Therefore, our insights into habitat-selection decisions will continue to be improved by evaluations across scales (e.g., DeCesare et al., 2012) and consideration of functional responses to availability (potential changes in preference as a function of underlying availability; Mysterud & Ims, 1998; Beyer et al., 2010). There is high potential value in integrated mechanistic models that relate individual movement decisions to resource characteristics at multiple scales as well as to other factors hypothesized to affect these decisions (Moorcroft & Lewis, 2006). Further important mechanistic insights likely will be gained by considering the specific behaviours the animal was demonstrating at each location or during each movement (Cooper & Millspaugh, 2001; Marzluff et al., 2001). Ultimately, more powerful and accurate insights will be gained for all wildlife species, including tropical carnivores, if we focus less on simply describing relative use of different habitats, and more on quantifying the demographic outcomes and other consequences of resource-utilisation patterns and resource-selection decisions (e.g., McLoughlin et al., 2006, 2007; Van Daele et al., 2012; Ayers et al., 2013).

The monograph by Manly et al. (2002) as well as recent reviews (Buskirk & Millspaugh, 2006; Beyer et al., 2010) provide essential starting points for planning and implementing resource-selection studies. We expect that as the use of radiotelemetry for tropical carnivores develops, biologists most frequently will use individual radiotelemetry locations for evaluating use by comparing characteristics of these used locations to characteristics of other locations deemed available to the animal. These other locations may be truly unused areas, or they may be locations where use simply was not observed during the limited sampling of the animal's activities (i.e., the sample of available locations may be "contaminated" with used locations; Lancaster & Imbens, 1996; Keating & Cherry, 2004).

There have been dramatic recent advancements and syntheses of models for estimating resource-selection relationships from location data. Johnson et al. (2006), Lele & Keim (2006), Johnson et al. (2008), and Lele (2009) used weighted

Table 1. Some commonly used fundamental terms and concepts relevant to resource selection and space-use studies. See text for additional terms and discussion, as well as Johnson (1980), Manly et al., (2002) and Beyer et al., (2010).

Terms and Concepts	Definitions and Explanations
Use	Proportion or amount of time spent in a habitat; absolute or relative consumption of a food item; or similar measures of the degree to which a resource is utilised.
Availability	Accessibility of a resource to an animal during some time period.
Selection	A behavioural process "in which an animal actually chooses" a resource; use is considered selective "if components are used disproportionately to their availability" (Johnson, 1980:66).
Preference	The likelihood of a habitat or other resource "being chosen if offered on an equal basis with others" (Johnson, 1980:66); assessment generally requires experimentation.
Resource Selection Function (RSF)	A function specifying relative probability of use of alternative resources by an animal.
Resource Selection Probability Function (RSPF)	A function specifying the absolute probability of use of each resource by an animal.
Order of selection	Johnson (1980:69) defined the following orders of selection: First order: selection of the range of a species; second order: selection of an individual's or group's home range; third order: selection of habitats within the home range; fourth order: selection of food items at a specific feeding site.
Resource selection study designs	Thomas & Taylor (1990) defined designs based on the scales at which use and availability are each evaluated; see also Alldredge et al. (1998). Study design I: use and availability data are collected at the population level. Design II: use is recorded per animal, but availability defined at the population scale. Design III: estimates use and availability for each animal. Design IV (Erickson et al., 2001): use is summarised per animal, but availability defined separately for each location of observed use.
Utilisation Distribution (UD)	A summary of the relative frequency or probability of use of areas by an animal (Jennrich & Turner, 1969; Van Winkle, 1975); now usually viewed as a probability density function.
Core areas	An area with disproportionately high use compared to the rest of the home range. Such areas can be defined based on arbitrary contour levels or by using graphical tests and various analytical methods that define thresholds in the intensity of use (or density of locations) of areas within the home range (Samuel et al., 1985; Samuel & Green, 1988; Powell, 2000).

distributions to provide a general framework encompassing a variety of specific models. This framework supports estimation of absolute probability of use, termed a "resource selection probability function", even with a contaminated sample of available locations. The framework can be extended to most situations in which location data are the basis for analysis. A general sample of available locations may be selected randomly without any matching between individual used and available locations, or availability may be defined separately within some local area around each observed location (i.e., as in discrete-choice analysis; Cooper & Millspaugh, 1999, 2001). Intuitively, the latter approach may better capture the choices available to the animal when it makes finer-scale selection decisions. These developments are applicable to all location-focused resource-selection studies, whether VHF- or GPS-based.

When one can obtain only a relatively small number of locations per animal (50–150) over several weeks or a season, one has a very limited sample of the animal's activity. In such cases, there may be intuitive appeal in fitting a flexible model of the animal's home range or (preferably) the underlying Utilisation Distribution (UD: Table 1), and using the model as the basis for examining habitat relationships (Aebischer et al., 1993; Marzluff et al., 2004; Millspaugh et al., 2006; Rittenhouse et al., 2008). Such an approach essentially attempts to use the spatial pattern of locations and the resulting UD model to derive more information from the limited collection of locations—particularly information about intensity of use of local areas. However, the quality of inference will depend on the accuracy of the descriptive UD-estimation model used for each animal. Other location-based approaches simultaneously use the second-order information provided by the spatial pattern of locations along with resource characteristics and other factors in estimating the UD (Matthiopoulos, 2003; Horne et al., 2008). As described earlier, when suitable data are available (e.g., locations every 15–60 mins), one can go beyond simply modeling locations or simple UD models, and examine specific movement decisions as a function of resource characteristic and other factors. Although there is the potential for powerful insights from such mechanistic modeling, this does not mean that fine-scale movement data are automatically necessary or even useful for meeting one's specific objectives (Hebblewhite & Haydon, 2010).

The Utilisation Distribution and home-range analysis: More than with any other type of question addressed with radiotelemetry, there are an enormous number of techniques available for home-range estimation and high variation in the quality of published advice attempting to guide biologists in choosing among alternatives. As a starting point, it is critical to carefully assess what "home range" means in the context of your particular study; biologists studying tropical mammalian carnivores should become familiar with recent discussions in the Aug.2012 special feature of the Journal of Mammalogy. General definitions provide a starting point; Kernohan et al. (2001:126) defined home range as "the extent of area with a defined probability of occurrence of an animal during a specified time period." Thus, home-range size can be seen as one summary of an animal's Utilisation Distribution. For example, the 95% home-range contour is most commonly viewed as the minimum overall area with a 0.95 probability of use during some focal time frame. The choice of probability level and time frame will depend on study objectives.

Regardless of how a parameter such as "home-range size" is defined, the biologist needs to think strongly about whether it is a concrete and worthwhile parameter to estimate given the underlying purpose of the study (White & Garrott, 1990). One then faces a complicated decision about which estimator is most appropriate. There are numerous alternative general approaches. Moreover, many modern home-range (or more broadly, UD) estimators come with numerous options. The choice of options may have a large impact on the resulting conclusions. For example, when using one of the most commonly implemented methods, kernel density estimation (Worton, 1987, 1989; Seaman & Powell, 1996), a key step is the choice of bandwidth value. Several bandwidth-selection options have been evaluated (e.g., Worton, 1995; Seaman et al., 1999; Gitzen et al., 2006; Horne & Garton, 2006; Steury et al., 2010), and variation in performance of alternative methods may often be as great as the variation between any form of the kernel method and any other available estimator. The appropriate choice of such options for a given method, and the appropriate choice among all available home-range estimation methods, will depend strongly on the pattern of space use in the focal species, the sample size, the study objectives, and the often unpredictable relative performance of alternatives for any particular data set (Gitzen et al., 2006; Downs & Horner, 2008; Lichti & Swihart, 2011; Cumming & Cornélis, 2012). Unfortunately, such details continue to be ignored even in many methodological studies. Readers must critically evaluate published guidance when selecting home-range estimators.

Most traditional estimators are simply descriptive models of space use, using only the observed pattern of locations and movements to produce an estimated home range (or preferably, estimated UD from which a home range estimate is derived; Kernohan et al., 2001). Frequently, the estimated UDs or resulting home ranges will then form the basis for evaluating ecological hypotheses about underlying processes (e.g., demographic differences in UD characteristics; fine-scale resource use, Marzluff et al., 2004; spatial overlap among individuals, Seidel, 1992; Millspaugh et al., 2004; Fieberg & Kochanny, 2005). Mechanistic models directly incorporate information about underlying ecological processes, i.e., about factors hypothesized to affect space use and movements. The most powerful and flexible mechanistic modeling usually will require high-frequency data not obtainable with VHF-telemetry studies and may require significant quantitative expertise to be tailored to a particular situation (see Moorcroft & Lewis, 2006, for an introduction). We expect continued increasing development and application of such estimators that simultaneously integrate observational and underlying ecological processes in hierarchical frameworks, consistent with the overall trend in ecology (e.g., Royle & Dorazio, 2008).

Analytical choices will differ depending on the frequency of data collection, and whether sequential locations offer usable information about specific movement paths and decisions. When a study is collecting coarse-resolution data, such that the animal could have covered a significant portion of its home range in the time between locations, sequential locations likely do not offer useful information about specific movement decisions, and one will largely make use of location-based estimators. Mechanistic location-based estimators should see increasing use (Matthiopoulos, 2003; Horne et al., 2008). The predominant current descriptive estimators include kernel density estimation, local convex hulls (Getz & Wilmers, 2004; Getz et al., 2007), characteristic hulls (Downs & Horner, 2009; Downs et al., 2012), and other linkage / clustering approaches (Kenward et al., 2001). The oldest location-based method, the Minimum Convex Polygon approach (Mohr, 1947; Hayne, 1949) continues to be heavily used. However, in most situations it simply is not a justifiable option compared to alternatives (Seaman et al., 1999; Börger et al., 2006; Laver & Kelly, 2008; Millspaugh et al., 2012a).

Conversely, when one has high-frequency data typical of satellite-based telemetry, home-range estimators such as Brownian Bridge and movement-based kernel density estimators can incorporate movement information to produce more accurate UD estimates (Horne et al., 2007b; Benhamou & Cornélis, 2010; Cumming & Cornélis 2012). We classify these estimators as descriptive because although they model individual movement steps, factors such as resource characteristics and interactions with other animals are not integrated into the model. Mechanistic models based on partial differential equations, to date developed primarily to integrate social behaviour of canids (Moorcroft & Lewis, 2006; Moorcroft et al., 2006) can directly integrate such factors. Alternatively, there may be valuable insights obtainable from applying traditional location-based estimators to subsets of the high-frequency data (e.g., calculating daily or weekly home ranges separately for each subset) and assessing temporal dynamics in these metrics (Keating & Cherry, 2009; Kie et al., 2010).

Finally, there are numerous other study-specific considerations. A primary argument for using polygon-based approximations to a UD rather than standard kernel estimators is that the latter may estimate significant use of unusable areas when there are sharp boundaries separating usable and definitely unavailable portions of the study area (Getz & Wilmers, 2004; Getz et al., 2007). However, kernel estimators can be modified so that they do not estimate any use of unusable areas, at least when the boundaries are known and relatively simple (Benhamou & Cornélis, 2010). Arguably, the general location-based kernel approach—with bandwidth values selected appropriately—remains the default general-purpose choice for modest/small sample sizes of locations (Lichti & Swihart, 2011; Cumming & Cornélis, 2012), but other modern estimators often will be viable alternatives. The appropriate choice should depend partly on a priori justification, but with any particular data set, the initially selected method may fail to produce reasonable estimated UDs. We expect increasing use of relative goodness-of-fit measures for evaluating alternative choices (Cumming & Cornélis, 2012), and we expect that ecologists will more formally incorporate such model uncertainty when making biological inferences.

Demographic estimation. — For tropical carnivores, there are three primary ways of using radio-marked animals in estimating population abundance or density (White & Shenk, 2001; Millspaugh et al., 2012a). First, mark-resight studies may use radiotags as "marks". Second, for species feasibly detectable with visual surveys, radio-marked animals may be used to develop sightability models, which are then used with incomplete visual counts collected during subsequent operational surveys to estimate abundance. Third, radio-marked animals can be used in conjunction with sampling arrays to assess demographic closure and effective area trapped (e.g., Soisalo & Cavalcanti, 2006; Núñez-Pérez, 2011). Thus, radiotelemetry can be a useful tool for assessing abundance, although for some tropical carnivores its best use may be to augment other primary methods (e.g., DNA- or photo-mark-recapture; Miller et al., 2010). An additional heuristic approach to estimating density of territorial carnivores involves dividing the amount of suitable habitat by average territory size. This approach has not been validated for tropical carnivores, and is best seen as an index to density.

By allowing repeated assessment of the fate of individual animals, radiotelemetry is an invaluable technique for estimating survival rates, cause-specific mortality, and factors influencing survival. Comprehensive discussions of the alternative models adapted or developed to estimate survival of radio-marked individuals are provided by White & Garrott (1990), Winterstein et al. (2001), Kenward (2001a), and Murray (2006). As with any other type of radiotelemetry study, key assumptions involved in survival estimation must be considered carefully at the design stage (Tsai et al., 1999; Winterstein et al., 2001; Fuller et al., 2005).

Scaling from movement, space use, and resource selection to demographic outcomes. — Often, studies of space use and resource selection are based on the implicit assumption that there is a strong link between the observed behavioural patterns and higher-level outcomes, particularly demographic outcomes. For example, if animals select habitat type "A", we assume that they need this habitat type and will show adverse effects if we reduce its availability. This may be a safe assumption if there is an absolute dependence by the species on this habitat. More often, this assumption is unverifiable unless we have collected data at both scales (behavioural and demographic). With such data, we can ask more meaningful questions: Is individual survival or reproductive output correlated with the proportion or raw area of habitat type "A" in each individual's home range, or are there alternative habitat-utilisation paths to similar demographic outcomes? Is the relationship between survival and extent of that habitat linear, or does it reach a threshold beyond which there is no measurable benefit of having additional area of habitat "A" available? By more thoroughly examining such links, investigators will be better able to quantify the implications and importance of behavioural information obtained through radiotelemetry (C. Ayers & J. Belant, unpublished manuscript). We are likely to see ever-greater integration across scales, from individual physiological states to behavioural decisions to demographic outcomes to resulting patterns of species occurrence (Struve et al., 2010).

SOFTWARE TOOLS

Effective processing, management, and analysis of radiotelemetry data involve non-trivial decisions about software, and may require significant investments in money and time. In addition to well-designed databases and standard statistical tools, radiotelemetry investigations looking at movements, resource selection, and space use generally depend on Geographic Information Systems (GIS) for some analytical and visualisation steps, and on specialised statistical packages for key analyses. Increasingly, the freely available program R (R Development Core Team, 2012) has become the most flexible and powerful option for implementing many specialised analyses. This is driven by the rapid deployment of new techniques in specialised freely available packages (e.g., the “adehabitat” package by C. Calenge; package “ResourceSelection” by S. Lele et al.), the ability to take advantage of a vast number of other R packages with broad statistical applications, and the availability of software that can integrate the computing power of R into a GIS (e.g., Geospatial Modeling Environment; http://www.spatialecology.com/gme/). Although R is well-suited to demographic analyses, Program MARK (White & Burnham, 1999)—also freely available—generally remains the default choice for demographic estimation based on maximum likelihood approaches. Such accessible software does not free biologists from their responsibility to understand and properly choose among analytical options (regardless of the defaults specified by authors of such software) and to make transparent these choices.

CONCLUSIONS

Radiotelemetry is an important tool for understanding, managing, and conserving wild animals. It can become an invaluable tool for conclusively examining ecological hypotheses about tropical carnivores if biologists build on and contribute to ongoing developments in equipment and relevant methodology throughout the field of animal ecology. These biologists can also benefit from advances in technology such as the development of GPS tags. However, biologists should not be overly enamored with newer technology, as VHF transmitters remain suitable and often the only feasible option for many carnivore studies. Moreover, assuming that suitable technology exists and that radiotelemetry is the right tool for a given situation, the value of the information it can provide will depend most heavily on whether the study is addressing meaningful questions and using a rigorous design and analytical methods. The biological and methodological assumptions appropriate for each analytical technique should be considered and tested before collection, analysis, and interpretation of radio-tracking data. Some of the most exciting recent developments in radiotelemetry include the increasing focus on addressing questions that integrate across physiological, behavioural, demographic, and even biogeographic scales, and the availability of mechanistic/process-based models that directly incorporate hypothesized relationships about factors determining animal movements and space use. Such developments contribute to the high potential of radiotelemetry for dramatically improving our ecological understanding of tropical carnivores.

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