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Radio-telemetry equipment and applications for carnivores

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Radio-telemetry was not included in the first comprehensive manual of wildlife research techniques (Mosby 1960) because the first published papers were about physiological wildlife telemetry (LeMunyan *et al.* 1959) and because research using telemetry in field ecology was just being initiated (Marshall *et al.* 1962; Cochran and Lord 1963). Among the first uses of telemetry to study wildlife, however, was a study of carnivores (Craighead *et al.* 1963), and telemetry has become a common method for studying numerous topics of carnivore biology. Our goals for this chapter are to provide basic information about radio-telemetry equipment and procedures. Although we provide many references to studies using telemetry equipment and methods, we recommend Kenward's (2001) comprehensive book, *A manual of wildlife radio tagging* for persons who are unfamiliar with radio-telemetry, Fuller *et al.* (2005), and Tomkiewicz *et al.* (2010). Compendia of uses of radio-telemetry in animal research appear regularly as chapters in manuals (Cochran 1980; Samuel and Fuller 1994), in books about equipment, field procedures, study design, and applications (Amlaner and Macdonald 1980; Anderka 1987; Amlaner 1989; White and Garrott 1990; Priede and Swift 1992; Kenward 2001; Millspaugh and Marzluff 2001; Mech and Barber 2002), and in reviews highlighting new developments (Cooke *et al.* 2004; Rutz and Hays 2009; Cagnacci *et al.* 2010). Some animal telemetry products and techniques have remained almost unchanged for years, but new technologies and approaches emerge and replace previously available equipment at an increasing pace. Here, we emphasize recent studies for which telemetry was used with carnivores.

7.1 General background

We use "radio-telemetry" to refer to the process of obtaining information from a remote animal by use of radio waves. Most commonly, biologists use radio waves that are categorized in the spectral bands of Very High Frequency (VHF = 30–300 MHz) or Ultra High Frequency (UHF = 300–3000 MHz [3 GHz]). In their respective countries, governments authorize the specific frequencies that can be used for wildlife studies. The term band or bandwidth is used to describe a specific range of frequencies (e.g. a 2-MHz band of 164–166 MHz). The signal transmitted to, or from, the animal can be used to estimate its location or to carry data about the animal's motion, condition (e.g. heart rate, body temperature), or its environment (e.g. temperature, atmospheric pressure). Radio-telemetry can be used to gather information that is neither practical nor possible to obtain with other methods from rapid-moving, wide-ranging, and secretive carnivores. Biologists have used radio-tracking to find animals for subsequent observation and to document local movements and estimate space use (e.g. home range, Chapter 9), to map dispersal and migration, and to study resource use and selection by carnivores (Chapters 10 and 11). Estimates of population abundance, survival, and fecundity, and information about causes of mortality, can be obtained using data from radio-marked animals (Chapter 5). Radio-telemetry can be applied to research of intraspecific (e.g. social behavior) and interspecific (predator prey) relationships (Chapter 11).

If radio-telemetry seems like a potential technique for addressing objectives, careful study planning is necessary and one must consider several factors relative to alternative techniques (e.g. Long *et al.* 2008a). The first consideration for using radio-telemetry is its potential effects on marked animals (Murray and Fuller 2000; Withey *et al.* 2001; Table 7.1). Researchers must use an appropriate transmitter design and attachment. A study can fail or produce biased results if radio-marking causes aberrant behavior or physiological stress, increases mortality, or reduces reproduction. Animals require capture and restraint, and perhaps sedation or anesthesia (Cattet *et al.* 2008a), while being radio-marked (Mulcahy and Garner 1999; Agren *et al.* 2000; Arnemo *et al.* 2006), potentially compounding the effects of the telemetry package (Tuyttens *et al.* 2002). Biologists must investigate options for packaging and attaching the package when they discuss equipment with manufacturers.

The expense of using radio-telemetry includes costs of equipment (transmitters, antennas, and receivers), salaries, transportation for field personnel to capture and radio-tag animals, and other labor and transportation (e.g. vehicles, aircraft) costs to locate animals in the field. If data are to be obtained via cell phone or satellite, costs include charges for reception, management, and distribution of data. In addition, effort and new procedures might be required to manage the magnitude of the data accumulated from telemetry (Cagnacci and Urbano 2008; Urbano *et al.* 2010). Pilot studies might be necessary for testing the performance and usefulness of equipment and methods, and to learn about variability in telemetry data

Table 7.1 *Uses of radio-telemetry to study carnivores—considerations.*

	Topic	Species	References
Attachment	capture collar	wolves	Mech and Gese 1992
	collars	weasels	Gehring and Swihart 2000
		ferrets	Biggins *et al*. 2006
		brown bears	Schwartz and Arthur 1999
	collar release mechanisms	wolves	Merrill *et al*. 1998
		black bears	Garshelis and McLaughlin 1998
	expandable implants	black bear cubs	Vashon *et al*. 2003
		otters	Soto-Azat *et al*. 2008
		badgers	Ågren *et al*. 2000
		fishers	Weir and Corbould 2007
		foxes	Fuglei *et al*. 2002
		wolves	Crawshaw *et al*. 2007
	multiple methods	otters	Neill *et al*. 2008
	subcutaneous	polar bears	Mulcahy and Garner 1999
Effects	of collars	badgers	Tuyttens *et al*. 2002
	of handling	cougars	Fiorello *et al*. 2007
		bears	Cattet *et al*. 2008a
Aerial tracking		cougars	Stoner *et al*. 2008
		lynx	Vashon *et al*. 2008
		wolves	Hebblewhite and Merrill 2008
Triangulation		bobcats, bison	Riley 2006
		pumas	Laundre and Hernandez 2008
		red foxes	Van Etten *et al*. 2007
Auto-tracking system		ocelots	Mares *et al*. 2008
Video and Telemetry System			MacNulty *et al*. 2008
Satellite system performance		brown bears	Graves and Waller 2006
			Heard *et al*.2008
			Walton *et al*. 2001a
GPS performance			Frair *et al*. 2004
			Jozwiak *et al*. 2006
			Johnson *et al*. 2002
			Lewis *et al*. 2007
		lynx	DeCesare *et al*. 2005
			Mattisson *et al*. 2010
		brown bears	Sundell *et al*. 2006
			Gau *et al*. 2004
		cougars	Lindzey *et al*. 2001
			Ruth *et al*. 2010
		maned wolves	Coelho *et al*. 2007

quantity and quality, which affect sample size, study design, and interpretation of results (Girard *et al.* 2002; Lindberg and Walker 2007; Mills *et al.* 2008). Finally, the number of animals that must be radio-marked, the spatial scale over which they must be sampled, the duration of the study, and training of personnel, affect the expense of using radio-telemetry.

After identifying the study objective(s) and reviewing relevant literature, correspondence with telemetry vendors (via http://www.biotelem.org; accessed March 17 2011) and biologists who have done similar research with the equipment and species is a critical step in deciding how technology can best be applied to the research question. Biologists must be able to describe the environment in which a study is to take place and how they expect the equipment to function. Biologists should test the performance of their radio-telemetry "system" (transmitters, receivers, antennas, coaxial cables, data loggers; Mills and Knowlton 1989; Merrill *et al.* 1998; D'Eon and Delparte 2005), including field-testing in the topographic (D'Eon *et al.* 2002; Zweifel-Schielly and Suter 2007) and vegetative conditions of the study area (Dussault et al 1999; Di Orio *et al.* 2003; DeCesare *et al.* 2005). When equipment is used in naturally varying environments, and when animal behavior causes variability, it often does not perform to the specifications obtained by manufacturers from controlled laboratory testing (Gau *et al.* 2004; Coelho *et al.* 2007; Hwang and Garshelis 2007; Mattisson *et al.* 2010). When a minimum sample of radio-marked animals is critical, researchers must estimate average operational life and failure rates from a sample of transmitters acquired for the study. Some transmitters will surely fail before their predicted operation life is achieved. The scheduled reception of data can be interrupted (Graves and Waller 2006) by factors such as atmospheric interference, vegetation, terrain, and buildings, thus reducing sample size (Hebblewhite *et al.* 2007). Observation bias results when the probabilities of obtaining scheduled location estimates are not equal along animals' movement paths or within a period of interest, and when measurement error occurs when the true location of the animal is different from the estimated location. Equipment performance can affect any use of radio-telemetry data (Hupp and Ratti 1983; White and Garrott 1990; Land *et al.* 2008) and the application of relatively accurate, regular, Global Positioning System (GPS) and other satellite technology has renewed focus on these issues (Rempel *et al.* 1995; Hurlbert and French 2001; D'Eon 2003; Cain *et al.* 2005; Hansen and Riggs 2008).

Researchers must understand the performance of the telemetry equipment to correctly use and interpret telemetry data (Belant and Follmann 2002; Theuerkauf and Jedrzejewski 2002; Frair *et al.* 2004; Mills *et al.* 2006; Hebblewhite *et al.* 2007; Horne *et al.* 2007; Andersen *et al.* 2008; Frair *et al.* 2010). If the telemetry unit on an animal fails to function, and each animal is a sample unit, then sample size is reduced. If data are received less often than expected, or if the telemetry does not perform consistently among all study conditions (e.g. weather, terrain, vegetation), then the quantity or regularity of data might be insufficient for an analysis that had been planned. Analyses for telemetry data are included in some books (White and Garrott 1990) and manuals (Fuller *et al.* 2005), and new procedures are developed constantly (Coyne and Godley 2005; Sand *et al.* 2005; Tinker *et al.* 2006; Young and Shivik 2006; Beyer *et al.* 2010; Boyce *et al.* 2010; Kie *et al.* 2010; Smouse *et al.* 2010).

7.2 Basic telemetry system

The majority of wildlife radio-telemetry has been conducted with VHF frequencies (e.g. Rhodes *et al.* 1998), but satellite telemetry, at UHF frequencies, is being used more and more often. Most component categories (e.g. transmitter, power source, microprocessor) are used with VHF and satellite telemetry and have no special considerations for carnivores. Table 7.1 lists, among other topics, papers that emphasize components; other tables (Tables 7.2, 7.3, 7.4, 7.5, 7.6) provide examples of how various combinations of components and field procedures have been applied to the study of carnivores. Many papers do not provide detailed information about components and simply name manufacturers. Correspondence with telemetry vendors is critically important for deciding which equipment is best for the species, the objectives, and the environmental setting of a proposed study.

Selection of a transmitter includes designating the radio frequency, signal repeat (aka pulse) rate, signal strength (radiated power), duration of operation, and configuration and mass of the unit. The VHF transmitter unit comprises electrical circuitry, a power source, transmitting antenna, encapsulation, material for attachment to an animal, and if needed, sensors. A 10-KHz spacing among transmitter frequencies to be used on a study area is necessary because frequency drift, transmitter crystal variation, and tuning deviations (e.g. nominal 164.000 MHz, received at 164.005) of a receiver can otherwise result in more than one transmitter being received simultaneously at the same frequency setting on a receiver.

The power source is the main determining factor for the duration of operation for an animal's telemetry unit. Signal power and operational life are tradeoffs with battery powered telemetry because batteries with greater energy capacity add bulk and mass to units. Thus, the mass of a telemetry unit that a species can carry without adverse effects limits the size of the power source, and in turn, limits signal power and operation life. Many electronics designs use microprocessors and low power clocks to conserve power by turning transmissions on and off at prescribed times (called the duty cycle). Photovoltaic solar cells, an alternative to batteries, can

Table 7.2 *Uses of radio-telemetry to study carnivores—movements.*

Topic	Species	References
Dispersal	cougars	Stoner *et al*. 2008
	wolves	Ciucci *et al*. 2009
		Kojola *et al*. 2009
Dispersal/survival	raccoon dogs	Sutor 2008
	ferrets	Byrom 2002
Home range/habitat	honey badgers	Begg *et al*. 2005
	brown bears	Edwards *et al*. 2009
	jackals, 3 spp.	Fuller *et al*. 1989
	leopards	Simcharoen *et al*. 2008
	lynx	Vashon *et al*. 2008
	ocelots	Mares *et al*. 2008
	polar bears	Parks *et al*. 2006
	southern river otters	Sepulveda *et al*. 2007
Modeling		Christ *et al*. 2008
Movements/activities	polar bears	Amstrup *et al*. 2001
		Parks *et al*. 2006
	snow leopards	McCarthy *et al*. 2005
Range use/ecology	cheetahs	Marnewick and Cilliers 2006
	Malay civets	Jennings *et al*. 2006
	lions	Metsers *et al*. 2010
Response to wildfire		Ballard *et al*. 2000
Response to big game hunting		Ruth *et al*. 2003
Spatial ecology	spatial theory	Young and Shivak 2006
	spotted hyenas	Boydston *et al*. 2005
	Darwin's foxes	Jimenez 2007
	stoats	Hellstedt and Henttonen 2006
	golden jackals	Admasu *et al*. 2004
	bobcats, gray foxes	Riley 2006

be used with a capacitor or rechargeable battery, but they have limited applicability when animal behavior precludes regular exposure to sunlight (e.g. nocturnal, dense vegetation cover).

Material for transmitting antennas should be strong and, for many applications, flexible. Often the antenna is covered with tough, tight plastic coating. Whip antennas are most efficient when of optimal length, a quarter wavelength of the transmission frequency. Whip antennas, however, are often positioned close to the animal's body to reduce the likelihood of the animal damaging it or having it snag on objects. Proximity to the body and a less than optimal length reduce the efficiency of an antenna and affect reception distance and rates. Flexible wire, or brass or copper loop antennas can be incorporated in a collar but the tuned

Table 7.3 *Uses of radio-telemetry to study carnivores—interactions and predation.*

Topic	Species	References
Comparative ecology	mongooses	Ray 1997
	jackals	Loveridge and MacDonald 2002
Depredations	large carnivores	Kolowski and Holekamp 2006
Food habits	jaguars	Cavalcanti and Gese 2010
Interference interactions		Linnell and Strand 2000
Kill-site locations	wolves	Webb *et al.* 2008
	lions	Tambling *et al.* 2010
Predation rates	cougars	Anderson and Lindzey 2003
		Ruth *et al.* 2010
	jaguars	Cavalcanti and Gese 2010
	wolves	Demma *et al.* 2007
		Hebblewhite and Merrill 2008
		Merrill *et al.* 2010
	large carnivores	Laundré 2008
	wolves	Sand *et al.* 2005
Species interactions	mesocarnivores	Kowalczyk *et al.* 2008
Survival/mortality	coyotes, swift foxes	Karki *et al.* 2007

Table 7.4 *Uses of radio-telemetry to study carnivores—resource use and selection.*

Topic	Species	References
Denning ecology	brown bears	McLoughlin *et al.* 2002a
Finding dens	Iberian lynx	Fernández *et al.* 2002
	Canada lynx	Moen *et al.* 2008
Habitat differentiation	3 spp.	May *et al.* 2008b
Habitat selection/use	brown bears	Berland *et al.* 2008
		Christ *et al.* 2008
		Martin *et al.* 2008
	Florida panthers	Land *et al.* 2008
	polar bears	Mauritzen *et al.* 2003b
	sloth bears	Ratnayeke *et al.* 2007
	Arctic foxes	Pamperin *et al.* 2008
	red foxes	Van Etten *et al.* 2007
Habitat suitability modeling	cheetahs	Muntifering *et al.* 2006

loop antenna must retain the size and shape delivered by the manufacturer when placed on an animal (Gehring and Swihart 2000). For mammals that break antennas (Biggins *et al.* 2006), the antenna is often placed between two layers of heavy collar material (Schwartz and Arthur 1999; Loveridge and Macdonald 2002).

Table 7.5 *Uses of radio-telemetry to study carnivores—behavior and physiology.*

Topic	Species	References
Activity	Asiatic black bears	Hwang and Garshelis 2007
	brown bears	Gervasi *et al.* 2006
		Kaczensky *et al.* 2004
		Kowalczyk *et al.* 2003
	mountain lions	Janis *et al.* 1999
	Andean bears	Paisley and Garshelis 2006
	badgers	Tanaka 2005
	fishers	Weir and Corbould 2007
Circadian activity	wolves	Ciucci *et al.* 1997
		Merrill and Mech 2003
Communication	river otters	Ben-David *et al.* 2005
Disease	jackals	Rhodes *et al.* 1998
Group living	coatis	Hass and Valenzuela 2002
Heart rate/temperature	Arctic foxes	Follman *et al.* 1982
	red foxes	Kreeger *et al.* 1989
	dogs	Li *et al.* 2008
	mink	West and Van Vliet. 1986
	wolves	Kreegar *et al.* 1990
Parent/offspring	pumas	Laundré and Hernández 2008
Paternity and mating system	wolverines	Hedmark *et al.* 2007
	black bears	Kovach and Powell 2003
Response to human activity	wolves	Hebblewhite and Merrill 2008
		Merrill and Erickson 2003
	3 species	Ruth *et al.* 2003
		Linnell *et al.* 2000
	brown bears	Waller and Servheen 2005
Sociality	river otters	Blundell *et al.* 2002
	raccoons	Pitt *et al.* 2008
Sociality and disease	badgers	Böhm *et al.* 2008
Steroids	sun bears	Schwarzenberger *et al.* 2004
Territoriality	wolves	Demma and Mech 2009
		Jedrzejewski *et al.* 2001

Encapsulating, or "potting," the electronics and power source protects the unit from shock and moisture, and keeps animals from damaging components. Most radio transmitters are potted in acrylics, epoxy resins, or hermetically sealed canisters, and large, long-lived transmitters for large mammals usually are cast in a form filled with potting. Transmitters to be implanted require special encapsulation to prevent rapid penetration by body fluids and to preclude adverse reaction from body tissues.

Table 7.6 *Uses of radio-telemetry to study carnivores—population biology.*

Topic	Species	References
Demography	cheetahs	Marker *et al.* 2003
	sea otters	Tinker *et al.* 2006
Genetic and spatial structure	swift foxes	Kitchen *et al.* 2005
Litter size	black bears	McDonald and Fuller 2001
	eastern wolves	Mills *et al.* 2008
Mortality and habitat	brown bears	Nielsen at al. 2006
Population delineation	polar bears	Amstrup *et al.* 2004
	brown bears	McLoughlin *et al.* 2002b
Population genetic structure	polar bears	Crompton *et al.* 2008
Survival and mortality	tigers	Goodrich *et al.* 2008
	furbearers	Kamler and Gipson 2004
	gray fox	Farias *et al.* 2005
	wolverines	Krebs *et al.* 2004
	wolves	Mills *et al.* 2008

A variety of sensors and options is available from many manufacturers. Sensors that detect body movement (Garshelis *et al.* 1982; Gervasi *et al.* 2006), that detect temperature or ambient temperature, or that incorporate a diode for visual tracking (Tuyttens *et al.* 2002) are available. Activity, temperature, and atmospheric pressure are often conveyed by modulating pulse interval, by which a change in pulse is calibrated to a change in the sensor. The pulse interval can be interpreted manually or with a data logger. A tilt switch can report whether an animal's body is in a particular posture by triggering a slow or fast pulse (Theuerkauf and Jedrzejewski 2002). The integration of accelerometers in transmitter units allows three-dimensional motion sensing (Kappeler and Erkert 2003; Moll *et al.* 2007). Conduct a pilot study to test special designs, using a surrogate or captive animal, if possible. Remember, however, that field conditions can affect the function of telemetry systems.

"Activity" can be interpreted from changes in radio signal strength and consistency (Weir and Corbould 2007) that occurs when an animal moves. Motion can also be conveyed from sensors that change pulse rate when an animal has moved within a short period. Such motion sensors can indicate possible mortality of a marked animal that has not moved for a long period (Hass and Valenzuela 2002; Kamler and Gipson 2004; Mills *et al.* 2008). The sensor can reset the pulse rate if the transmitter moves or can be programmed to remain in "mortality" mode for a long period (e.g. to prevent scavengers or other sources of movement from resetting the mortality signal). Mortality also can be indicated with a body temperature sensor that changes the pulse rate when the temperature drops below a prescribed level. Using temperature and motion sensor data together can provide further evidence of mortality or that the transmitter has become detached from the animal (Bates *et al.* 2003). More than one type of data (e.g. motion and temperature) can be sent from a single transmitter of certain manufacturers.

Data storage options allow information to be logged in the telemetry unit for later downloading to a receiver system via radio transmissions to ground-, air-, or satellite-based receivers, or from a transmitter that has dropped from the animal or recovered by recapture or from a dead animal. This option is very useful when the radio signal is beyond reception range or reception is limited by environmental factors (e.g. water, topography), or when numerous locations are obtained from GPS receivers (see below). Temperature, motion, or pressure data can be time stamped and logged for retrieval. These and many other animal and environmental data are gathered by data logging or biologging (Ropert-Coudert and Wilson 2005). Rutz and Hays (2009) summarized engineering and research activity in equipment development and application, data management, and analyses, and the many questions and topics to which biologging is now being applied.

The materials and methods used to attach the telemetry unit to the animal are very important for ensuring the well-being of the animal and for ensuring the unit remains in place for the study period (e.g. Biggins *et al.* 2006). A collar around the neck is a common attachment method for radio-tagging carnivores. The telemetry unit and collar should be able to withstand attention from the animal (D. Garshelis and P. Ciucci, pers.com.) or from conspecifics during social interaction, should fit the animal's neck contours, distribute the package mass evenly, accommodate swallowing, accommodate seasonal changes in neck size, and minimize interference with the animal's natural movements.

A variety of materials are available for collars, depending upon the size of the animal, desired mass, configuration, durability, and attachment method. For small mammals, a collar can be made of steel cable, elastic, or braided fishing line covered by flexible, hollow plastic tubing. Each telemetry unit should be adjusted to fit the individual. For medium or large mammals (Loveridge and Macdonald 2002), the collar is typically constructed of leather, machine belting, braided nylon, or synthetic dog collar material and secured with adjustable bolts, rivets, or buckles to custom fit each individual. Some collars accommodate growth of young animals or temporary neck expansion by incorporating foam rubber inserts or sewn pleats (Garcelon 1977; Strathearn *et al.* 1984; Jackson *et al.* 1985). Telemetry units can be retrieved for reuse, to obtain data loggers, and to relieve animals of the burden. Mechanisms can be integrated in some collars to anesthetize animals using a remote transmitter (Mech and Gese 1992), or to detach the collar at a preprogrammed time (Sawyer *et al.* 2006). Further development continues to overcome performance deficiencies of automatic release collars (Garshelis and McLaughlin 1998; Kochanny *et al.* 2009) and to adapt mechanisms to the variety of species and collar types (Müller *et al.* 2005).

Radio transmitters can be surgically implanted in body cavities or implanted subcutaneously. Abdominal implants often are used in mammals whose body configuration precludes collar attachment (river otters, Melquist and Hornocker 1979; mink, Eagle *et al.* 1984; sea otters, Ralls *et al.* 1989), or to obtain physiological data (Fuglei *et al.* 2002). Implantation of the entire radio transmitter and antenna in the abdominal cavity can reduce reception range of VHF radios by $\geq$ 50% (Melquist and Hornocker 1979). Subcutaneous implants have been used to radio-track polar bears (*Ursus maritimus*) (Mulcahy and Garner 1999). When a smaller transmitter is adequate (e.g. short duration or low transmission power) or other attachment methods are precluded, radio transmitters can be affixed to ear tags, which typically are used for marking livestock (Servheen *et al.* 1981).

Receiving systems for VHF wildlife telemetry comprise radio receivers, antennas, cables to connect the antenna to the receiver, accessories (e.g. head phones, chargers), counters and decoders, and recording devices. The receiver components can process and convert the transmitter's signal to an audio tone, and can produce signals for processing by demodulators, decoders, or pulse counters.

Simple manual receivers operate within bandwidths of about 50 to 200 KHz, and can be used with about 5 to 20 transmitter frequencies. Receivers are powered by batteries and most have a meter to indicate the supply voltage. Most have a built-in speaker and a jack for connecting earphones. Manual receivers are usually the simplest and smallest receivers used in the field. More complex (and more expensive) receivers can cover from 1 to 45 MHz bandwidths, and include a programmable, automatic frequency scanning capability that can be interrupted when a radio signal is detected. Programmable receivers are useful when many transmitters are in the area of reception, such as when one surveys from an aircraft or when a receiver can be left unattended to record signals automatically.

Recorders, counters, decoders, and data loggers mechanize processing of radiotelemetry signals and data by measuring intervals between pulses, recording changes in signal amplitude, marking the presence or absence of a signal, decoding a signal, or recording data.

Receiving antennas have several basic designs: omni-directional, loop, Adcock or H antenna, Yagi, null-peak system. Biologists should discuss their needs with vendors and clearly describe the environment where the research will take place. Omni-directional ("whip") antennae have a uniform, 360° reception pattern, and have relatively low gain. They are easily adapted for magnetic or bolt-on attachment to vehicles and aircraft, and are used commonly to detect presence of signals over comparatively small areas. Directional receiving antennas have a three-dimensional pattern of power oriented by the element(s) of the antenna. A directional receiving antenna will detect the strongest radio signal when directed toward the signal. Making the antenna more directional generally increases gain, and thus the distance over which a signal can be received.

Elevation of the transmitting and receiving antennas generally increases the reception range. However, "obstacles" (e.g. terrain, moist vegetation, buildings) can block signal transmission and having the receiving antenna close to a person, a vehicle, or even earth's surface can affect reception. Therefore, optimal performance is usually achieved by holding or mounting the receiving antenna high. Hold an antenna above one's head, stand on an elevated place, raise the antenna on a mast above the ground, or receive from an aircraft. Custom VHF telemetry systems can be devised for vehicles (Gilsdorf *et al.* 2008) and for remote data collection (MacNulty *et al.* 2008; Mares *et al.* 2008).

7.3 Radio-tracking field procedures

The performance of equipment can be altered dramatically by animal behavior, topography, vegetation, and climate. Personnel need to be trained, and location accuracy and precision are maximized through careful, consistent procedures, including estimates of location error (White and Garrott 1990; Nams and Boutin 1991; Withey *et al.* 2001). The location of a radio-marked animal can be estimated by triangulation along bearings from two or more receiving sites (O'Donoghue *et al.* 1997). Mech (1983), Samuel and Fuller (1994), and Kenward (2001) detail basic tracking methods.

Homing is a method by which the operator uses antenna directionality and signal strength information to move toward and find a transmitter (or animal). Radio-tracking from aircraft is usually a special case of homing to find animals in a large area. Flying can increase reception range by 10 times or more, and increasing altitude usually increases detection distance. When two directional antennas are mounted facing downward and to opposite sides of the aircraft under the wings or struts, signal strength indicates the side of the aircraft where the animal occurs.

7.4 Satellite telemetry systems

Satellite telemetry allows remote tracking of animals from most places on earth. The Argos system became available in the 1980s (Harris *et al.* 1990a, http://www.argos-system.org/manual/, accessed March 17 2011). This system requires using specialized transmitters, called Platform Transmitter Terminals (PTTs), which weigh $\geq$5 g. Polar-orbiting satellites receive sensor data and calculate animal locations from Doppler measurements of ultra-high frequency (UHF) transmissions from PTTs. Processed data are distributed to researchers in several formats, including Internet access to data received about 4 hours previously. The cost of data acquisition from Argos depends on the quantity of data received and choice of data distribution options.

PTTs can transmit data from up to eight sensors (e.g. temperature, motion, pressure voltage) and can be programmed to transmit at particular times, including only during predicted satellite passes, and during particular periods (e.g. seasons). Transmission strength can be adjusted to conserve battery power, but this can lead to fewer location estimates per duty cycle (Walton *et al.* 2001a). VHF transmitters can be mounted on collars with PTTs to locate animals on the ground (McLoughlin *et al.* 2002b). Finding PTTs (Bates *et al.* 2003) provides valuable information about the status of marked animals and facilitates retrieval of PTTs for reuse.

Location estimates from Argos are assigned to Location Classes (LC) that provide nominal location accuracy. Biologists must consider if regular location accuracy of $\leq$1 km is appropriate for their objectives. A pilot study can be useful to assess how satellite telemetry performs under the conditions of a particular project. In September 2010, Argos implemented a new location and error estimation procedure, which can decrease error.

The Global Positioning Satellite System (GPS) is a US Department of Defense array of satellites that transmit signals to GPS receivers. GPS systems allow three-dimensional and frequent locations with accuracy of <30 m. Currently, GPS receivers estimate locations within seconds of receiving signals from satellites. Animal-borne GPS systems integrate the GPS receiver into a telemetry unit (on a collar, for example) including a micro-power data acquisition/controller (MDAC). The MDAC turns the GPS receiver, sensors, and data-transfer components on and off to manage the energy budget of the system, to acquire positions at programmed sampling times, and to store location estimates. Some packages provide an interface for the user to program parameters and to download stored data (Tomkiewicz *et al.* 2010). The GPS receiver requires considerable power, which can limit the operational life of the unit. Even with recent low-power GPS receiver technology, receiver power management usually is necessary to achieve regular receptions and long operational life. Collar units for some animals can be powered by solar arrays.

Data stored on board (SOB) a GPS telemetry unit can be downloaded when the unit is recovered. Storing data on board is dependable but if the unit is not recovered, the data are lost. Store-on-board systems can store about 35 000 GPS positions per megabyte of memory and some GPS subsystems have >6 megabytes of memory. Incorporating programmable release mechanisms or VHF transmitters into a GPS telemetry package increase the likelihood of recovering data (Sager-Fradkin *et al.* 2008). Some GPS telemetry packages incorporate transponders that transmit data via VHF or UHF from the unit when queried (Cavalcanti and Gese 2010; Chadwick *et al.* 2010). Power source restrictions limit the VHF transmission to a narrow bandwidth and data rate, requiring perhaps 7 s to transfer a single GPS position and 45 min to transfer 180 positions. Most GPS systems with data-transfer technology also retain data on board, so that data can be downloaded if the unit is recovered.

Another approach to data transfer is to configure each GPS transmitter package as a separate link in a network. When tagged animals aggregate (e.g. a pride of lions), the links communicate, storing data from each package on all other packages. Retrieval of data from all marked animals requires querying only one telemetry package (Juang *et al.* 2002; Martonosi 2006).

GPS data can be transferred from radio-marked animals via the Global System for Mobile Communications (GSM) mobile telephone-data services (Gervasi *et al.* 2006; Sundell *et al.* 2006; Tambling *et al.* 2010). Regular contact and data recovery from an area where service is available (widely in Europe) allows transfer of all data stored in the memory of each GPS telemetry package. The system also can be used in a two-way manner, allowing users to change on-board collar parameters (Sundell *et al.* 2006). Unfortunately, many vast areas (e.g. much of North America, sparsely populated Africa) lack GSM services.

Data transfer via low earth orbiting (LEO) satellites offers much more comprehensive coverage. The Argos LEO satellites orbit about 850 km above the earth, thereby accommodating low power transmitters (100 mW to 1W) with omni-directional antennas. While it is a global system, interference from the environment in Europe and Mongolia–Pakistan disrupts data transfer presently on the Argos uplink frequency, limiting its use in those places. Argos can relay 24–48 GPS positions per day from units on medium- to large-sized animals. GPS data can be recovered as frequently as daily, but the limited energy budget of most animal tags limits the number of GPS positions that can be transferred. Recent developments allow the GPS data transfer to be used with on-board Argos orbit prediction programs enabling transmitting only during satellite overpasses. This increases data transfer efficiency of the system.

The Globalstar satellite system includes more than 40 low earth orbit satellites designed for telephone communication and data transfer. GPS-Globalstar animal telemetry collars can transmit every GPS location acquired in real time or log and store location estimates for later retrieval. Retrieving GPS data via Globalstar is expensive but a GPS-Globalstar unit can be programmed to acquire a GPS location eight times per day, but to transmit only one GPS location per day or per week, thus conserving battery and costing less for data delivery via the satellite system. The other stored data must be obtained later from the retrieved unit. Wildlife collars using a GPS receiving antenna and a Globalstar patch transmitting antenna are recently available and being used on many projects, but we are unaware of published results. Names of current users can be obtained from North Star Science and Technology and from Vectronic-Aerospace. The greatest limitation is that areas lack land-based receiving stations, which limits Globalstar geographic coverage.

The Iridium 66 low earth orbit satellite constellation provides worldwide, two-way, near continuous coverage for voice and data communications. Iridium is used in oceanographic applications in dial-up and in short burst modes. Opportunities for use with wildlife are just becoming available. Current technology is suitable for larger terrestrial species (Aastrup 2009). Vectronic-Aerospace has been the manufacturer offering data transfer via Iridium.

Other data-transfer possibilities (e.g. data recovery using radio modem technology) are available as are innovations with GPS and other technology (Tomkiewicz *et al.* 2010) that will increase the options available to biologists. For example, inertial navigation devices in GPS collars allow estimation of animal locations on a continuous basis between GPS fixes (Hunter *et al.* 2005; Elkaim *et al.* 2006). Inertial navigation systems suffer from deteriorating accuracy as errors compound over time, but GPS fixes at short intervals can be used to reset the accuracy of the estimated track (Hunter 2007). Advances in battery technology, decreases in GPS power requirements, and increases of on-board memory capacity lead to capabilities to track a diversity of species and to know where animals are almost continuously. To ensure having the most appropriate equipment, discuss options with animal telemetry manufacturers and vendors.

7.5 Radio-telemetry applications for carnivores

Many insights into carnivore ecology and behavior have been garnered using radio-telemetry. Animal movements (Table 7.2) are usually studied over time frames of days to years, and often are quantified in terms of distance traveled or total area covered. Ground-based, VHF telemetry has been used extensively to delineate and describe home ranges of animals whose movements are somewhat restricted (e.g. honey badgers, Begg *et al.* 2005), and satellite telemetry has revealed the limitations of ground tracking for some species (e.g. snow leopards, *Uncia uncia*, McCarthy *et al.* 2005). For wide-ranging species, such as wolves, aerial VHF telemetry has long been used to follow resident packs, but packs that depend on migratory prey have been monitored more effectively using satellite telemetry (e.g. in the Arctic, Walton *et al.* 2001a). Similarly, dispersal of smaller carnivore species may be monitored from the ground with VHF transmitters (e.g. ferrets, *Mustela furo*, Byrom 2002) but for large species, GPS telemetry has proved invaluable for studying connectivity among distant populations, specific travel routes, and movements after settling into new territories (e.g. wolves in Finland, Kojola *et al.* 2009).

Investigations of predator interactions with prey and other animals have been enhanced by use of telemetry (Table 7.3), particularly in locating kills and quantifying predation rates (e.g. VHS and GPS telemetry of cougars, *Puma concolor*, Laundré 2008; Knopff *et al.* 2009) and in identifying how interactions affect distribution (GPS and VHF telemetry of wolves and elk, *Cervus Canadensis*, Proffitt *et al.* 2009). Telemetry has provided instantaneous locations and observations and, with new data-retrieval capabilities from satellites, data are very accurate and nearly in real time. Simultaneous VHF telemetry studies of several species also have facilitated in-depth understanding of competition, demographics, space use, and prey use (e.g. jackals, *Canis* spp., Loveridge and Macdonald 2002).

Resource use and selection have been much studied using telemetry because of the volume of locations that can be accumulated (Table 7.4). Many studies have related carnivore distributions to a variety of vegetative or topographic "habitat" variables, sometimes to gain general insights into various habitat requirements and sometimes for specifically targeted insights (e.g. denning of brown bears, McLoughlin *et al.* 2002a). Data have been incorporated into models used to enhance restoration efforts or to minimize conflicts (e.g. VHF telemetry of cheetahs, Muntifering *et al.* 2006).

Behavioral and physiological parameters, otherwise unobtainable, can be monitored via telemetry from wide-ranging animals (Table 7.5). Activity patterns and time budgets have been identified for cryptic, tropical carnivores (e.g. VHF telemetry of Andean bears, *Tremarctoc ornatus*, Paisley and Garshelis 2006), and paternity assignment has been shown to correspond well with overlapping ranges of male and female wolverines (*Gulo gulo*, Hedmark *et al.* 2007) derived from telemetry. Clear identification of social patterns of species not easily observed is possible with telemetry (e.g. river otters, *Lontra canadensis*, Blundell *et al.* 2002), and they can give insights into sociality and disease transmission (e.g. badgers, *Meles meles*, Böhm *et al.* 2008).

Radio-telemetry has contributed to advances in carnivore population biology (Table 7.6). Denning sites and thus litters of young can be found rather quickly using ground-based or GPS telemetry. Unbiased estimates of survival and mortality of individuals leads to better understanding of population status and limiting factors (e.g. ferrets, Byrom 2002; tigers, *Panthera tigris*, Goodrich *et al.* 2008).

Population estimates are more refined because assumptions of population closure can be monitored, and capture–recapture estimates can be assessed in light of having known, marked individuals within the sampling unit (e.g. brown bears, Miller *et al.* 1997).

Research of carnivore biology is fraught with challenges. Radio-telemetry has facilitated gathering much information about many carnivore species that is otherwise not available. Telemetry has been used with carnivores since the earliest application of radio-telemetry to wildlife studies, and many of the techniques from 50 years ago continue to be used with great success today. In the last 20 years, however, advances in electronics and space-age technology have given innovative engineers and manufacturers new material, which they use to provide biologists with new equipment with which new methods are developed. Radio-telemetry equipment is now available with more options from more vendors than ever before, and new capabilities become available at a rapid pace. To know what is available and to apply it best to meet objectives, biologists must have detailed dialogues with manufacturers. Research and conservation of carnivores will surely benefit from continued use of radio-telemetry.