Integrative Zoology 2010; 5: 378-389 doi: 10.1111/j.1749-4877.2010.00216.x

REVIEW

Review of research methodologies for tigers: Telemetry

Clayton S. MILLER,[1,2] Mark HEBBLEWHITE,[2] John M. GOODRICH[1] and Dale G. MIQUELLE[1]

[1]Wildlife Conservation Society, Bronx, NY, USA and [2]Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, Montana, USA

Abstract

Over the past half century, wildlife research has relied on technological advances to gain additional insight into the secretive lives of animals. This revolution started in the 1960s with the development of radio telemetry and continues today with the use of Global Positioning System (GPS)-based research techniques. In the present paper we review the history of radio telemetry from its origins with grizzly bears in Yellowstone to its early applications in tiger research and conservation in Asia. We address the different types of data that are available using radio telemetry as opposed to using other research techniques, such as behavioral observations, camera trapping, DNA analysis and scat analysis. In the late 1990s, the rapid development of GPS collar technology revolutionized wildlife research. This new technology has enabled researchers to dramatically improve their ability to gather data on animal movements and ecology. Despite the ecological and conservation benefits of radio telemetry, there have been few telemetry studies of tigers in the wild, and most have been on the Bengal or Amur subspecies. We close with an assessment of the current tiger conservation efforts using GPS technology and discuss how this new information can help to preserve tigers for future generations.

Key words: Global Positioning System technology, *Panthera tigris*, radio telemetry, research methodologies, tiger.

INTRODUCTION

Tigers (*Panthera tigris* Linnaeus, 1758) have been studied by researchers and conservationists for nearly 100 years. Despite the difficulties of collecting data on secretive animals without modern technology, early scientists pioneered research on tigers and provided a baseline for our understanding of tiger ecology. In the early 1900s, Frederick W. Champion recognized that it was possible to tell individual tigers apart by their unique striping patterns and pioneered camera trapping in India (Champion 1927). Observational data from India supplied researchers with detailed information on social organization, communication and feeding behavior (Schaller 1967). Early tiger researchers in the Russian Far East relied on intensively snow tracking a few individuals for long periods of time (Baikov 1925; Kaplanov 1948; Matyushkin *et al.* 1980; Pikunov 1983; Yudakov & Nikolaev 1987). These pioneering scientists used their natural history skills to provide a strong foundation for future scientists. However, there were limitations to the amount and type of data that could be collected and, hence, there were limitations to our understanding of tiger ecology.

Wildlife research was revolutionized in the early 1960s when the Craighead brothers developed a new method of gathering data on wildlife from a distance without visual contact with the animals being studied. By placing radio

Correspondence: Clayton S. Miller, Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA.
Email: cmiller1@wcs.org

collars on free-ranging grizzly bears (*Ursus arctos* Linnaeus, 1758), they greatly increased the quantity and quality of data collected, and followed animal movements through the densest of forests and mountains (Craighead 1979). From 1961 through 1968, the Craigheads used this innovative approach in Yellowstone National Park, USA to efficiently locate, follow and observe 23 grizzlies (Craighead *et al.* 1995). Published data from this groundbreaking study addressed home ranges, movement patterns, reproduction, social hierarchy, mortality patterns and food habits, and was used to develop management recommendations for the Yellowstone grizzly bear population (Craighead *et al.* 1995).

During the 50 years since radio telemetry was first applied to wildlife research, a wide variety of research questions have been addressed that could not have been answered using alternate methods (Table 1). This technological approach to wildlife research has provided an amazing array of opportunities to examine detailed ecological and conservation questions related to movement, home range, habitat use, survival, productivity, population estimation and behavior, as well as other related questions (Samuel & Fuller 1994). Studies examining animal movement patterns have been large scale (e.g. focusing on migration or dispersal) (Nathan *et al.* 2003) and smaller scale, focusing on spatial and temporal travel corridors (Sawyer *et al.* 2009). Behavioral studies using radio telemetry have focused on the daily or seasonal activity patterns of individual animals (Green & Bear 1990). Studies examining the home ranges of individual animals provide quantitative estimates of area used in time and space (Harris *et al.* 1990). Using radio telemetry to examine habitat use and selection has helped researchers to identify and manage important habitat (Mace *et al.* 1999). Applying radio telemetry methods to survival studies has enabled researchers to better differentiate between emigration and mortality, something that has been difficult to accomplish using other research techniques such as camera trapping and genetic analyses (Karanth *et al.* 2006) (Table 1). Radio telemetry has been used effectively to estimate reproductive parameters such as litter size, interbirth interval, adult survival and cub survival, and causes of mortality (Mace & Waller 1998). Population estimation studies using mark–recapture methods have enabled researchers to better estimate population size (White & Garrott 1990).

Since the 1990s, a second revolution in wildlife research has been underway with the advent of Global Positioning System (GPS) collar technology (Cagnacci *et al.* 2010; Tomkiewicz *et al.* 2010). GPS collar technology has provided many rapid advances to the same techniques developed above, especially in the fields of habitat selection and movement modeling, but are also providing ecological insights that were not possible using traditional very high frequency (VHF) technology (Cagnacci *et al.* 2010; Hebblewhite & Haydon 2010). For example, new insights possible through use of GPS collars include the ability to estimate kill rates in summer for the first time, and detailed information on movement paths and dispersal patterns. Regardless of whether using VHF or GPS methods, many of these questions have been addressed by researchers with either technology and could not have been answered using other research techniques, such as tracking, camera trapping, scat analysis or DNA analysis (Table 1).

During the past 50 years, however, many drawbacks of radio telemetry-based wildlife research have become apparent (White & Garrott 1990; Winterstein *et al.* 2001; Hebblewhite & Haydon 2010). Telemetry-based research can be logistically and financially challenging and is not always the best option for answering many research questions. First, telemetry studies are invasive to the study animals, involve the challenges and dangers associated with capture (Arnemo *et al.* 2006), and capturing and radio-collaring animals is often controversial among segments of the public. Conducting a radio telemetry study requires a high level of field expertise to obtain accurate ground or aerial locations and provides an excellent opportunity to train and educate local biologists in research and conservation techniques. Costs associated with a radio telemetry study include the initial investment of purchasing equipment and training personnel, the extensive labor costs for field staff capturing animals and obtaining ground locations and the aerial telemetry costs to find missing or dispersing study animals. Statistically adequate sample sizes can be especially difficult to obtain from elusive animals that are difficult to capture, occur at very low densities and inhabit remote areas, such as tigers. This problem is made more acute by the high costs of GPS collar systems (Lindberg & Walker 2007; Hebblewhite & Haydon 2010). When considering the additional costs associated with field personnel salaries, travel expenses during monitoring, technical equipment and radio telemetry training, GPS collars might not necessarily be more expensive than traditional VHF collars. Clearly defining research objectives is an important step while determining whether a radio telemetry study is the best method of efficiently gathering the desired information and should be evaluated during the study design process. At the same time, telemetry studies need to be flexible and opportunistic. Some early objectives might prove to be unachievable, whereas other important conservation issues might be addressed using the data gathered for the original questions (Goodrich & Miquelle 2010).

In the present paper on tiger research methodologies, we address the application of telemetry to tiger research and conservation. We start with a technical description of how radio telemetry works, and the following paragraphs describe its' technical aspects. We then review the various research projects that have used radio telemetry to study wild tiger populations and the different re-

Table 1 Advantages of using VHF-based or GPS-based telemetry compared to other wildlife research methods for addressing different tiger ecology and conservation issues

Ecological/ conservation question	VHF-based or GPS-based data	Other methods	Citations
Demographic studies (e.g. survival and reproduction)	Increased precision about timing of mortality and reproduction based on localized movements of study animals. Main method to reliably estimate survival rates of adult tigers.	Localized movements during reproduction might reduce the effectiveness of camera trapping, observational and snow tracking data. Camera trapping yields apparent survival, which can include emigration. Mortalities might never be found, limiting the value of survival studies.	Kenney *et al.* (1995), Kerley *et al.* (2003), Karanth *et al.* (2006) and Goodrich *et al.* (2008)
Dispersal	Ability to locate animals using aerial telemetry or satellites far beyond study area borders enables researchers to differentiate between emigration and mortality.	Difficulty differentiating between emigration and mortality using camera trapping. Snow tracking (where even possible) has limited value during long-distance dispersal.	Smith & McDougal (1991), Smith (1993), Kerley *et al.* (2003) and Karanth *et al.* (2006)
Food habits	Telemetry gives researchers the ability to find areas the tiger has localized its movements and safely investigate for kills after the tiger has left the area.	Snow tracking or opportunistic sampling to gather data on tiger kills. Scat analysis is challenging because scat is often difficult to locate in thick forests or grasslands or sampling is restricted to roads.	Schaller (1967), Miquelle *et al.* (1996), Chundawat *et al.* (1999), Andheria *et al.* (2007), Kerley & Salkina (2007) and Wang & MacDonald (2009)
Home range	Ability to systematically study tigers throughout the year and gather location data in remote or difficult to access areas (especially true for Global Positioning System collars).	Large gaps in area between sample sites during camera trapping efforts. Snow tracking only offers information on winter use.	Schaller (1967), Sunquist (1981), Yudakov & Nikolaev (1987), Chundawat *et al.* (1999), Franklin *et al.* (1999) and Goodrich *et al.* (2010)
Human–wildlife conflict	Telemetry allows managers to track tiger movements during all times of the day to quickly respond to a threat and reduce the potential for human–tiger conflict.	Efforts are usually reactionary and focused on gathering data after a conflict has occurred instead of responding to threats to prevent conflict from occurring.	Nikolaev & Yudin (1993), Goodrich & Miquelle (2005), Miquelle *et al.* (2005), Johnson *et al.* (2006) and Sangay & Vernes (2008)
Population dynamics	Detailed information allows managers to investigate social structure, cohort-specific survival rates, movements and spacing patterns. Difficult to monitor population trend itself except indirectly through vital rates.	Observational or snow tracking data offers detailed information during short intervals. Camera trapping better for monitoring population trends, although often with large confidence intervals.	Sunquist (1981), Smith & McDougal (1991), Smirnov & Miquelle (1999), Karanth *et al.* (2006), Barlow *et al.* (2009) and Goodrich *et al.* (2010)

search questions addressed in previous studies. Similar to the wildlife research revolution experienced as a result of radio telemetry research techniques in the 1960s, GPS technology is presenting another revolution for wildlife biologists. Although examples of GPS-based research on tigers are lacking, studies of other species demonstrate what we can expect from tiger research in the future. We conclude the paper by reviewing 4 current projects that are applying GPS technology to research and conservation of wild tigers.

REVIEW OF RADIO TELEMETRY METHODOLOGIES

Radio telemetry involves following radio signals emitted from a transmitter on a study animal. VHF radio transmitters are attached to leather and fitted to the study animals. The Craighead brothers originally distinguished study animals by their unique pulse rate on a single radio frequency (Craighead & Craighead 1965). Radio transmitters used in wildlife work now usually transmit similar pulse rates, but each transmitter emits a unique frequency. Signals are transmitted "line-of-sight" from the transmitter to the receiver and, as such, vegetation and topography might interfere with and block reception of radio signals (Cochran 1980). The most critical ingredient for successful ground telemetry is establishing line-of-sight between the observer and the transmitter. The best way to do this is by gaining elevation to obtain that line-of-sight between observer and transmitter (Anderka 1987).

The primary methods for locating the transmitters are homing in on the signal, aerial telemetry and triangulation. Homing might be of use to find a dead study animal, a slipped collar, dens, nests, or kills, to locate evidence of feeding, or to locate an animal when triangulation works poorly or animals can be observed without being disturbed (i.e. species that roost during the day). Most radio collars also include a mortality sensor whereby the pulse rate (beats per minute) changes after the collar has remained inactive for a specified time period (usually 4–6 h), often signaling the death of the study animal. Aerial telemetry is useful when animals travel into areas too distant or difficult (i.e. topography) for ground crews to access, when animals exhibit wide ranging movements, or during dispersal or migration movements. In many study areas, aerial telemetry is the only feasible option and a significant portion of the operating budget must be dedicated to flight time. Triangulation is the most common method of locating an animal from the ground, where 2 or more bearings (preferably 3) are taken at different locations to create an intersection of bearings, and these intersections estimate the tiger's location. In many study areas, a well trained field staff can quickly and accurately locate an animal from the ground, often making triangulation the most common method of obtaining locations. There is some debate regarding whether it is better to obtain 2 or 3 bearings in rapid succession for triangulation (White & Garrott 1990; Winterstein *et al.* 2001). Regardless, we believe the most critical element to accurate ground or aerial telemetry is development of a consistent protocol, practical field experience and development of a test-collar program for training, validation and determination of location error (White & Garrott 1990). Regardless of the method or species, it is common practice to use test collars to obtain study-specific location error rates, and for large-mammal telemetry, ground or aerial telemetry location error is often in the 2–400 m range (White & Garrott 1990).

Capture is obviously the most important and first step in any telemetry study and involves a great deal of risk. Capturing animals to fit them with radio transmitters is a traumatic experience and can be dangerous for animals (Arnemo *et al.* 2006), researchers and the public. Minimizing the risk to both the study animals and the researchers is critical, and is best accomplished by following accepted capture and handling protocols for species (Gannon *et al.* 2007) and working with experienced wildlife veterinarians to establish protocols and, ideally, lead capture and handling operations. Most developed-nation wildlife management agencies and universities now require an approved animal use and capture protocol. A capture-related mortality can result in a suspension of research permits and negative public perception, especially for critically endangered species such as tigers. Noninvasive studies are free from the need to handle wild animals and are often preferred by the public. However, there are limitations to the data available to non-telemetry based studies and the benefits of telemetry can outweigh the risks. While an animal is anesthetized, every effort should be put into gathering as much data as possible, including blood and hair samples for disease and genetic analysis, weight and body measurements, and photographs. With proper equipment and trained personnel present, it is possible to give a complete physical examination, to collect sperm, to perform ultrasounds on females to determine pregnancy and body condition, and to collect a variety of other data.

When reviewing the published ecological literature for benefits and costs of using radio telemetry to address different kinds of ecological and conservation questions, several trends emerge (Table 1). Where information on individual tiger behavior, movements, habitat selection, predator–prey dynamics, home range or dispersal is warranted, radio telemetry seems to be the best methodology for gaining detailed information (Table 1). Furthermore, radio telemetry provides detailed demographic data, such as reproductive rates, survival and even dispersal rates that can eventually be combined in demographic models to estimate population growth rates and trends. Additional strengths include the valuable information obtained regarding human–wildlife conflicts and cause-specific mortality rates, which are really only obtained through radio telemetry in any rigorous fashion. The downside of radio telemetry studies usually lies in the very small sample sizes obtained in most tiger telemetry studies (Table 2), which leads to marginal statistical rigor and strength of inferences. Furthermore, radio telemetry studies are poor at providing rigorous population estimates, except when using gross extrapolation approaches based on average home range size. In contrast, noninvasive studies such as camera-trapping mark–recapture studies (Karanth *et al.* 2006), DNA mark–recapture (Mondol *et al.* 2009) or snow tracking surveys (Yudakov & Nikolaev 1987) can often provide better statistical rigor for estimating population-level parameters such as population size, trend and broad distribution (Table 1). Unfortunately, these noninvasive methods provide coarser resolution for individual-level questions. Obviously, the best methodological approach would be to combine radio telemetry methods in areas at the same time as noninvasive population-level studies, where both methods would provide checks on each other's assumptions (e.g. Apps *et al.* 2004).

Table 2 Summary of published scientific papers that used radio-collared tigers, showing study area, duration, subspecies, the number of collared tigers and the general ecological questions addressed. No published papers have used Global Positioning System collars to date

Study area	Duration	Tiger subspecies	Number of collared tigers	Ecological questions	Citation
India	January 1990 to February 1992	Bengal	4 (3 M, 1 F)	Behavioral correlates of predation	Karanth & Sunquist (2000)
Nepal	December 1973 to April 1974	Bengal	1 (F)	Interspecific competition	Seidensticker (1976)
Nepal	December 1974 to September 1976	Bengal	7 (3 M, 4 F)	Social organization	Sunquist (1981)
Nepal	1972 to 1989	Bengal	31	Reproduction	Smith & McDougal (1991)
Nepal	January 1977 to June 1987	Bengal	26	Dispersal	Smith (1993)
Russia	January 1992 to November 1994	Amur	11	Food habits	Miquelle *et al.* (1996)
Russia	1992 to 2000	Amur	19 (4 adult M, 8 adult F, 7 cubs)	Effects of roads and human disturbance	Kerley *et al.* (2002)
Russia	January 1992 to December 2000	Amur	9 F	Reproductive parameters	Kerley *et al.* (2003)
Russia	2001 to 2003	Amur	4 (2 M, 2 F)	Translocation	Goodrich & Miquelle (2005)
Russia	February 1992 to January 2005	Amur	42	Survival rates and mortality	Goodrich *et al.* (2008)
Russia	February 1992 to December 2006	Amur	19 (5 M, 14 F)	Spatial structure	Goodrich *et al.* (2010)

F, female; M, male.

RADIO TELEMETRY IN TIGER RESEARCH

Radio telemetry research techniques were first applied to tigers on the Smithsonian-Nepal Tiger Ecology Project in Royal Chitwan National Park, Nepal in 1973 to provide a comprehensive understanding of the tiger in its natural habitat (Seidensticker *et al.* 1974). This groundbreaking research project provided some of the most detailed information on tiger ecology to date (Seidensticker 1976; Sunquist 1981; Smith & McDougal 1991; Smith 1993; Smith *et al.* 1998). This team developed the first protocols to safely capture and immobilize free-ranging tigers (Seidensticker *et al.* 1974; Smith *et al.* 1983) and began radio-tagging tigers and other large mammals in Royal Chitwan. Once collared, the team was able to study the life history, movements and activity of these secretive, solitary animals in much more detail than had been possible with traditional methods (Schaller 1967; Table 1). By closely monitoring the tigers of Royal Chitwan, researchers were able to better understand tiger ecology and to develop conservation recommendations necessary to maintain tigers in the habitat fragments where tigers still live in Nepal (Seidensticker 1976).

Mel Sunquist and James L. David Smith continued the tiger research in Royal Chitwan with an examination of tiger movements and social–spatial behavior (Sunquist 1981), dispersal of tigers (Smith 1993), and potential effects of poaching (Kenney *et al.* 1995; Table 2). Radio telemetry methods were used to address daily and seasonal movement patterns in relation to foraging, reproductive activity and territoriality (Sunquist 1981; Smith & McDougal 1991; Smith 1993). By comparing telemetry locations of different sex and age classes, tiger social interactions were examined by calculating the distance between animals radio tracked on the same day (Sunquist 1981). Feeding habits of tigers were also examined and incorporated into the first assessment of the impact of tigers on prey populations (Sunquist 1981). Using radio telemetry techniques, the research team examined several questions related to tiger dispersal behavior and estimated the population structure of the Chitwan and surrounding populations (Smith 1993; Smith *et al.* 1998). These early studies in the Nepal/India area in the Terai arc set the foundation and, to this day, the bulk of radio-collared tiger research has come from these areas.

Radio telemetry has been used in the tropical dry forests of the Panna Tiger Reserve, India (Chundawat *et al.* 1999) and in the tropical forests of Nagarahole National Park, India (Karanth & Sunquist 2000) to examine tiger ecology and interspecific competition (Table 2). Panna Tiger Reserve represents an important habitat type for tigers in India and differs from the tropical moist forests and alluvial grassland/subtropical moist deciduous forest types found in other tiger reserves in the Indian subcontinent (Seidensticker & McDougal 1993; Karanth & Nichols 1998; Chundawat *et al.* 1999). This once extensive habitat type has been severely fragmented and degraded by human disturbance and heavy cattle grazing (Chundawat *et al.* 1999). Research in Panna focused on tiger prey requirements, habitat suitability, movements and activity patterns in an effort to identify critical ecological needs of tigers living in the tropical dry forests of India (Chundawat *et al.* 1999). Karanth and Sunquist (2000) used telemetry to examine the role of competition between different predators for space use, movement and activity patterns, hunting techniques and social structure.

Tiger research in the Russian Far East was historically limited to winter when snow tracking allowed researchers to glimpse into the secret lives of tigers. Snow tracking tigers can provide valuable information on movement patterns, food habits, home ranges and marking behavior (Yudakov & Nikolaev 1987). In 1992, the Hornocker Wildlife Institute and the Sikhote-Alin Reserve began radio telemetry-based research on Amur tiger ecology under the Siberian Tiger Project (Miquelle *et al.* 1996). Today, the Wildlife Conservation Society and the Sikhote-Alin Reserve continue this effort as the longest running telemetry research and conservation effort conducted on wild tigers (Table 2). The Siberian Tiger Project has used radio tracking to study social structure (Goodrich *et al.* 2010), food habits (Miquelle *et al.* 1996), reproduction (Kerley *et al.* 2003), mortality (Goodrich *et al.* 2008), impact of humans and roads (Kerley *et al.* 2002), translocation of tigers to alleviate tiger–human conflicts (Goodrich & Miquelle 2005) and improvement of capture and anesthetic protocols (Goodrich *et al.* 2001). The advancement in our knowledge of tiger ecology and behavior that this research project has accomplished has guided and greatly enhanced conservation projects in the Russian Far East and north-east China.

To understand some of the differences in the use of tiger telemetry in tiger research, we reviewed the published scientific studies on tigers that used radio telemetry (Table 2). We did not include unpublished reports or theses because of the difficulty in locating them in an unbiased manner. We summarized, by tiger subspecies, the study area, the duration of the study, the number of tigers' radio collared and the main ecological questions addressed, with the goal of synthesizing tiger telemetry studies across their range (Table 2). On average, published tiger radio telemetry studies lasted 7.2 years, and used 15.7 tigers during each study, with an average of 2. 2 radio collared tigers/year (Table 2). No published studies have used GPS collars yet, although we note that a recent PhD thesis (Barlow 2009) used 2 GPS collars. The main ecological questions have related to predation patterns, interspecific competition, survival and reproduction, spatial structure and social organization (Table 2). From this brief review, several important features of previous tiger telemetry studies are apparent: (i) tiger studies have relied on very small sample sizes from a classic experimental design viewpoint to address important ecological questions; (ii) long-term studies are needed to acquire enough data to gain reliable ecological insights because, for example, tigers are long-lived and ecological dynamics take time (Goodrich & Miquelle 2010). This review highlights the challenges of applying radio telemetry to the study of tiger populations, and emphasizes that in the future, tiger radio-collaring projects should strive to capture and radio collar as many individuals as possible, and commit to long-term monitoring to understand tiger ecology.

GLOBAL POSITIONING SYSTEM COLLAR TECHNOLOGY AND THE FUTURE OF TIGER TELEMETRY

In the years since the Craigheads developed radio telemetry, technological advances have consistently improved the systems while reducing the overall size of the transmitters and batteries, enabling researchers to place longer lasting transmitters on increasingly smaller species (Winterstein *et al.* 2001). Recently, researchers have joined telemetry with GPS systems to revolutionize the amount and type of data that can be gathered (Tomkiewicz *et al.* 2010). We can now collect data from great distances, 24 h a day, during bad weather, and without disturbing the research animals, reducing the potential to affect animal behavior. GPS telemetry was originally used on large mammals such as elephants (Douglas-Hamilton 1998), moose (Rodgers *et al.* 1996) and bears (Schwartz & Arthur 1999) because only large species could carry the large units. As the technology continues to develop, smaller units are available for smaller species and larger units are equipped with longer lasting batteries. GPS collars can also come with remote data retrieval systems, such as UHF data uploads in the field (usually from aircraft), the bidirectional Global System for Mobile Communication (GSM) network, or satellite-borne data uploads through the ARGOS platform (which requires user fees) or newer Iridium technology (Tomkiewicz *et al.* 2010). Furthermore, many collar manufacturers provide remote release mechanisms that are designed to facilitate recovery of the GPS collar without requiring recapture of the animal in the field. This new technology enables researchers to collect a large number of high quality data within a short time period compared to traditional VHF telemetry (Cagnacci *et al.* 2010; Hebblewhite & Haydon 2010).

Global Positioning System telemetry has helped researchers to address similar research questions as with VHF with more accuracy and less bias (Table 1), but has also opened new avenues for research in wildlife ecology and conservation. Resource selection studies are now relying on GPS technology to provide fine scale information on the types of resources and habitats selected by research animals (Manly *et al.* 2002). Long distance migration routes can now be accurately mapped using GPS telemetry (Meyburg *et al.* 2003; Littaye *et al.* 2004; Thirgood *et al.* 2004). Home range studies using GPS telemetry have provided an abundance of location data that has led to new analytical methods (Moorcroft & Lewis 2006; Kie *et al.* 2010). Studies focusing on survival and reproduction have benefitted from using GPS collars by finding calving GPS collared caribou (*Rangifer tarandus caribou* Gmelin, 1788) or tracking wide-ranging endangered California condors (*Gymnogyps californianus* Shaw, 1797) (Gustine *et al.* 2006; Woods *et al.* 2007). Research into animal movement patterns has greatly benefitted from the advances in GPS technology (Moen *et al.* 1996; Dagorn *et al.* 2000; Blake *et al.* 2001). Researchers using GPS collars have gained insight into helping mitigate human–wildlife conflicts (Dodd *et al.* 2007; Graham *et al.* 2009). GPS telemetry is also helping researchers better understand the potential consequences of climate change on wildlife populations (Durner *et al.* 2009). As GPS technology continues to develop and become more affordable, more researchers will be able to harness the power of these methods and continue to build on the progress that has been made.

Although the benefits of GPS telemetry might seem obvious, many of the disadvantages are not. The 2 main disadvantages are technical failures and high collar cost. First, all technology fails. When planning a GPS collar study, collar failure and malfunction must be planned for, as almost no study occurs without some level of total collar failure, but typically ranges from 10–50% (Johnson *et al.* 2002; Gau *et al.* 2004; Hebblewhite & Haydon

2010). GPS failure can result in complete loss of the collar, reductions in battery life expectancy, reduced fix-rate (Frair *et al.* 2010), or failure in the collar retrieval (Hebblewhite *et al.* 2007) or 2-way communication system (e.g. ARGOS, Iridium, GSM or UHF). Currently, GPS collars are significantly more expensive than traditional VHF collars. Depending on the features of the collar, costs can reach US$8000 per collar before adding the costs of transferring data via satellites. As with any new technology, costs are already beginning to decline and we expect this trend to continue. As a result of these high costs for collars, budget constraints could potentially force researchers to reduce their sample sizes, sacrificing strong population-level inferences (Hebblewhite & Haydon 2010). Many researchers believe the GPS collar revolution is both a blessing and a curse for biologists. The process of removing biologists from the field, where they tirelessly track their study species in their environment, is creating biologists that only read about natural history and can only relate to points on a computer screen. This might lead to biologists that have no field sense of their study population, or to biologist making false assumptions about their data, or how representative their sample is of the entire population (Hebblewhite & Haydon 2010). Therefore, even with GPS-based studies, accompanying field research should be prioritized to better understand the critical resources (e.g. food, shelter and ungulate prey for tigers) available to GPS collared animals, so as to better understand the mechanisms underlying movements and behavior.

As an example of the benefits of GPS collars to tiger research, in 2005, the Sundarbans Tiger Project began collaring tigers to estimate the density, population size and movement patterns of the Bangladesh Sundarbans tiger population (Barlow 2009). For years, research efforts in the Sundarbans were hampered by the thick vegetation, tidal fluctuations and maze of waterways in this mangrove habitat (Singh 1999). By placing GPS collars on tigers, researchers in the Sundarbans were able to monitor tigers in this difficult terrain and to increase understanding of tiger ecology, population status and human–tiger conflict (Barlow 2009). Despite extensive efforts and expense, researchers were only able to capture and GPS collar 2 tigers over the study (Barlow 2009). Although the first 2 GPS-collared tigers provided critical new insights into tiger ecology, the challenges experienced by Barlow (2009) provide some realistic expectations for GPS-based studies of tigers in the next decade. GPS data collected from this study has been used to mitigate tiger–human conflicts and to help develop a national tiger action plan for Bangladesh in ways that would have been more challenging with only VHF or with no data (Barlow 2009).

The Siberian Tiger Project first attempted to use GPS collars in 2007, but for various reasons these collars did not meet expectations and we continued to use VHF collars for several years. Early GPS collars suffered from the extreme temperatures of the Siberian winter, damage from tigers and general collar failure, similar to early experiences of GPS collars on other large carnivore species (Gau *et al*. 2004; Hebblewhite *et al*. 2007). In 2009, we revisited the use of GPS collars for use in estimating kill rates and monitoring dispersal activities. Because of logistical challenges in locating and approaching radio-collared Amur tigers in the wild, we opted for Iridium upload GPS collars that allow the Siberian Tiger Project to access telemetry locations remotely, a method that might be similarly advantageous for other tiger researchers. A critical component of modern tiger conservation requires an understanding of thresholds of prey availability that can sustain viable tiger populations (e.g. Chapron *et al*. 2008). A critical component of this is the relationship between prey availability and tiger kill rates, the functional response of predators to prey (Nilsen *et al.* 2009; Merrill *et al.* 2010). GPS collars have been used to estimate kill rates in both cougars (*Puma concolor* Linnaeus, 1771) and wolves (*Canis lupus* Linnaeus, 1758) (Sand *et al.* 2008; Knopff *et al.* 2009). As prey populations in the Russian Far East continue to decline (D. G. Miquelle, unpublished data), gaining a better understanding of tiger–prey relationships will benefit conservation initiatives in the area. Understanding dispersal patterns of tigers, particularly female tigers, is important to developing conservation plans for the potential colonization of suitable tiger habitat in China (Li *et al.* 2010).

Several projects in Southeast Asia are also beginning to harness the power of GPS collars for tiger research and conservation efforts. The Thailand Tiger Project based at the Khao Nang Rum Wildlife Research Station is working to secure a future for tigers in Thailand and surrounding areas through careful research, responsible management and community outreach (Thailand Tiger Project 2010). This research project is using GPS collars to monitor movement patterns through travel corridors, reproduction and dispersal into new territories (Thailand Tiger Project 2010). As this project continues over the next few years, more information will be gathered to help conserve tigers in Thailand. GPS collars are currently being used on translocated tigers in Sumatra to allow land managers to track tiger movements, to compile data on areas that are of particular importance to tigers in the area and to reduce the potential for human–tiger conflict (J. M. Goodrich, pers. comm.).

CONCLUSIONS

In conclusion, we are excited about the recent advances in GPS-based wildlife research and look forward to applying these new methods to support current conservation initiatives in tiger ranges. We acknowledge that GPS or VHF radio telemetry technology is not the answer for all ecological and conservation questions but are encouraged by the opportunities GPS telemetry offers (Table 1). By combining the advantages offered by GPS telemetry with traditional VHF radio telemetry, and through basic field work, conservationists could make great advances in understanding tiger ecology and this knowledge can be applied to current efforts to preserve the world's remaining wild tigers.

ACKNOWLEDGMENTS

Funding and assistance was provided by the Wildlife Conservation Society, the University of Montana, the Mohamed bin Zayed Species Conservation Fund and Panthera.

REFERENCES

Andheria AP, Karanth KU, Kumar NS (2007). Diet and prey profiles of three symaptric large carnivores in Bandipur Tiger Reserve, India. *Journal of Zoology* **273,** 1–7.

Anderka FW (1987). Radiotelemetry techniques for furbearers. In: Novak M, Baker JA, Obbard ME, Malloch B, eds. *Wild Furbearer Management and Conservation in North America.* Ontario Ministry of Natural Resources, Toronto, pp. 216–27.

Apps CD, Mclellan BN, Woods JG, Proctor MF (2004). Estimating grizzly bear distribution and abundance relative to habitat and human influence. *Journal of Wildlife Management* **68**, 138–52.

Arnemo J, Ahlqvist P, Anderson R *et al.* (2006). Risk of capture-related mortality in large free-ranging mammals: Experiences from Scandinavia. *Wildlife Biology* **12**, 109–13.

Baikov NA (1925). *The Manchurian Tiger*. Obshchestvo Izuchenia Manchurskogo Kraya, Harbin, China (In Russian).

Barlow ACD (2009). The Sundarbans tiger: Adaptation, population status, and conflict management (PhD Dissertation). University of Minnesota, Minneapolis, USA.

Barlow ACD, Mcdougal C, Smith JLD *et al.* (2009). Temporal variation in tiger (*Panthera tigris*) populations and its implications for monitoring. *Journal of Mammalogy* **90**, 472–8.

Blake S, Douglas-Hamilton I, Karesh WB (2001). GPS telemetry of forest elephants in Central Africa: Results of a preliminary study. *African Journal of Ecology* **39**, 178–86.

Cagnacci F, Boitani L, Powell RA, Boyce MS (2010). Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philsophical Transactions of the Royal Society B* **365**, 2157–62.

Champion FW (1927). *With a Camera in Tiger Land.* Chatto & Windus, London.

Chundawat RS, Gogate N, Johnsingh AJT (1999). Tigers in Panna: Preliminary results from an Indian tropical dry forest. In: Seidensticker J, Christie S, Jackson P, eds. *Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes.* Cambridge University Press, Cambridge, UK, pp. 123–9.

Cochran WW (1980). Wildlife telemetry. In: Schemnitz, SD, ed. *Wildlife Management Techniques Manual.* 4th edn. The Wildlife Society, Washington, DC, pp. 507–20.

Craighead FC (1979). *Track of the Grizzly.* Sierra Club Books, San Francisco, CA.

Craighead FC, Craighead JJ (1965). Tracking grizzly bears. *BioScience* **15**, 88–92.

Craighead JJ, Sumner JS, Mitchell JA (1995). *The Grizzly Bears of Yellowstone: Their Ecology in the Yellowstone Ecosystem, 1959–1992.* Island Press, Washington, DC.

Dagorn L, Bach P, Josse E (2000). Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Marine Biology* **136**, 361–71.

Dodd NL, Gagnon JW, Boe S, Schweinsburg, RE (2007). Assessment of elk highway permeability by using global positioning system telemetry. *Journal of Wildlife Management* **71**, 1107–17.

Douglas-Hamilton I (1998). Tracking African elephants with a global positioning system (GPS) radio collar. *Pachyderm* **25**, 81–92.

Durner GM, Douglas DC, Nielson RM *et al.* (2009). Predicting 21st-century polar bear habitat distribution from global climate models. *Ecological Monographs* **79**, 25–

58.

Frair JL, Fieberg J, Hebblewhite M, Cagnacci F, Decesare NJ, Pedrotti L (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**, 2187–200.

Franklin SP, Troyer JL, Terwee JA *et al.* (2007). Frequent transmission of immunodeficiency viruses among bobcats and pumas. *Journal of Virology* **81**, 10961–9.

Gannon WL, Sikes RS, The Animal Care and Use Committee of the American Society of Mammalogists (2007). Guidelines of the American Society of Mammalogists for the Use of Wild Mammals in Research. *Journal of Mammalogy* **88**, 809–23.

Gau RJ, Mulders R, Ciarniello LM *et al.* (2004). Uncontrolled field performance of televilt GPS-simplex™ collars on grizzly bears in western and northern Canada. *Wildlife Society Bulletin* **32**, 693–701.

Goodrich JM, Miquelle DG (2005). Translocation of problem Amur tigers (*Panthera tigris altaica*) to alleviate tiger–human conflicts. *Oryx* **39**, 1–4.

Goodrich JM, Miquelle DG (2010). Tiger telemetry. In: Tilson R, Nyhus P, eds. *Tigers of the World: The Science, Politics, and Conservation of* Panthera tigris, 2nd edn. Elsevier, Oxford, UK, pp. 261–73.

Goodrich JM, Kerley LL, Schleyer BO *et al.* (2001). Capture and chemical anesthesia of Amur (Siberian) tigers. *Wildlife Society Bulletin* **29**, 533–42.

Goodrich JM, Kerley LL, Smirnov EN *et al.* (2008). Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. *Journal of Zoology* **276**, 323–9.

Goodrich JM, Miquelle DG, Smirnov EN, Kerley LL, Quigley HB, Hornocker MG (2010). Spatial structure of Amur (Siberian) tigers (*Panthera tigris altaica*) on Sikhote-Alin Biosphere Zapovednik, Russia. *Journal of Mammalogy* **91**, 737–48.

Graham MD, Douglas-Hamilton I, Adams WM, Lee PC (2009). The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation* **12**, 445–55.

Green RA, Bear GD (1990). Seasonal cycles and daily activity patterns of Rocky Mountain elk. *Journal of Wildlife Management* **54**, 272–9.

Gustine DD, Parker KL, Lay RJ, Gillingham MP, Heard DC (2006). Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs* **165**, 1–32.

Harris S, Cresswell WJ, Forde PG, Trewhella WJ, Woollard T, Wray S (1990). Home-range analysis using radio-telemetry data – A review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* **20**, 97–123.

Hebblewhite M, Haydon DT (2010). Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**, 2303–12.

Hebblewhite M, Percy M, Merrill EH (2007). Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the central Canadian Rockies. *Journal of Wildlife Management* **71**, 2026–33.

Johnson A, Vongkhamheng C, Hedemark M, Saithongdam T (2006). Effects of human–carnivore conflict on tiger (*Panthera tigris*) and prey populations in Lao PDR. *Animal Conservation* **9**, 421–30.

Johnson CJ, Heard DC, Parker KL (2002). Expectations and realities of GPS animal location collars: Results of three years in the field. *Wildlife Biology* **8**, 153–9.

Kaplanov LG (1948). Tigers in Sikhote-Alin. In: Ognev, SI, Geptner, VG, eds. *Tigers, Manchurian Elk, and Moose.* Materials on the fauna and flora of the USSR. Organization for the Investigation of Nature, Moscow, Russia, pp. 18–49.

Karanth KU, Nichols JD (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* **79**, 2852–62.

Karanth KU, Sunquist ME (2000). Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. *Journal of Zoology* **250**, 255–65.

Karanth KU, Nichols JD, Kumar NS, Hines JE (2006). Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology* **87**, 2925–37.

Kenney JS, Smith JLD, Starfield AM, McDougal CW (1995). The long-term effects of tiger poaching on population viability. *Conservation Biology* **9**, 1127–33.

Kerley LL, Salkina GP (2007). Using scent-matching dogs to identify individual Amur tigers from scats. *Journal of Wildlife Management* **71**, 8.

Kerley LL, Goodrich JM, Miquelle DG, Smirnov EN, Quigley H, Hornocker MG (2002). Effects of roads and human disturbance on Amur tigers. *Conservation Biology* **16**, 97–108.

Kerley LL, Goodrich JM, Miquelle DG, Smirnov EN, Quigley H, Hornocker MG (2003). Reproductive parameters of wild female Amur (Siberian) tigers (*Panthera tigris altaica*). *Journal of Mammalogy* **84**, 288–98.

Kie JG, Matthiopoulos J, Fieberg J *et al.* (2010). The home-range concept: Are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**, 2221–31.

Knopff KH, Knopff AA, Warren MB, Boyce MS (2009). Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. *Journal of Wildlife Management* **73**, 586–97.

Lindberg MS, Walker J (2007). Satellite telemetry in avian research and management: Sample size considerations. *Journal of Wildlife Management* **71**, 1002–9.

Littaye A, Gannier A, Laran S, Wilson JPF (2004). The relationship between summer aggregation of fin whales and satellite-derived environmental conditions in the northwestern Mediterranean sea. *Remote Sensing of Environment* **90**, 44–52.

Mace RD, Waller JS (1998). Demography and population trend of grizzly bears in the Swan Mountains, Montana. *Conservation Biology* **12**, 1005–16.

Mace RD, Waller JS, Manley TL, Ake K, Wittinger WT (1999). Landscape evaluation of grizzly bear habitat in Western Montana. *Conservation Biology* **13**, 367–77.

Manly BFJ, Mcdonald LL, Thomas DL, Mcdonald TL, Erickson WP, eds (2002). *Resource Selection by Animals: Statistical Analysis and Design for Field Studies*. Kluwer, Boston, MA.

Matyushkin EN, Zhivotchenko VI, Smirnov EN (1980). The Amur tiger in the USSR. Zoological Museum of Moscow University, Moscow.

Merrill E, Sand H, Zimmermann B *et al.* (2010). Building a mechanistic understanding of predation with GPS-based movement data. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**, 2279–88.

Meyburg BU, Paillat P, Meyburg C (2003). Migration routes of Steppe Eagles between Asia and Africa: A study by means of satellite telemetry. *Condor* **105**, 219–27.

Miquelle DG, Smirnov EN, Quigley H, Hornocker MG, Nikolaev IG, Matyushkin EH (1996). Food habits of Amur tigers in Sikhote-Alin Zapovednik and the Russian Far East, and implications for conservation. *Journal of Wildlife Research* **1**, 138–47.

Miquelle DG, Nikolaev IG, Goodrich JM, Litvinov MN, Smirnov EN, Suvorov E (2005). Searching for the coexistence recipe: A case of conflicts between people and tigers in the Russian Far East. In: Woodroffe R, Thirgood S, Rabinowitz A, eds. *People and Wildlife: Conflict or Coexistence?* Cambridge University Press, London, pp. 305–22.

Moen R, Pastor J, Cohen Y, Schwartz CC (1996). Effects of moose movement and habitat use on GPS collar performance. *Journal of Wildlife Management* **60**, 659–68.

Mondol S, Karanth KU, Kumar NS, Gopalaswamy AM, Andheria A, Ramakrishnan U (2009). Evaluation of non-invasive genetic sampling methods for estimating tiger population size. *Biological Conservation* **142**, 2350–60.

Moorcroft PR, Lewis MA (2006). *Mechanistic Home Range Analysis. Monographs in Population Biology.* Princeton University Press, Princeton, NJ.

Nathan R, Perry G, Cronin JT, Strand AE, Cain ML (2003). Methods for estimating long-distance dispersal. *Oikos* **103**, 261–73.

Nikolaev IG, Yudin VG (1993). Conflicts between man and tiger in the Russian Far East. *Bulletin of the Moscow Society Naturalist* **98**, 23–36.

Nilsen EB, Linnell JDC, Odden J, Andersen R (2009). Climate, season, and social status modulate the functional response of an efficient stalking predator: The Eurasian Lynx. *Journal of Animal Ecology* **78**, 741–51.

Pikunov DG (1983). The Amur tiger and its impact on the wild ungulates in the Primorie. *Redkie vidy mlekopitaiuschikh SSSR i ikh okhrana. Materialy 3 Vsesoiuznogo soveschania. M : IEMEZH i VTO AN SSSR.* 128–9.

Rodgers AR, Rempel RS, Abraham KF (1996). A GPS-based telemetry system. *Wildlife Society Bulletin* **24**, 559–66.

Samuel MD, Fuller MR (1994). Wildlife radiotelemetry. In: Bookhout TA, ed. *Research and Management Techniques for Wildlife and Habitats*, 5th edn. The Wildlife Society, Bethesda, MD, pp. 370–418.

Sand H, Wabakken P, Zimmermann B, Johansson O, Pedersen HC, Liberg O (2008). Summer kill rates and predation pattern in a wolf–moose system: Can we rely on winter estimates? *Oecologia* **156,** 53–64.

Sangay T, Vernes K (2008). Human-wildlife conflict in the Kingdom of Bhutan: Patterns of livestock predation by large mammalian carnivores. *Biological Con-*

servation **141**, 1272–82.

Sawyer H, Kauffman MJ, Nielson RM, Horne JS (2009). Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications* **19**, 2016–25.

Schaller GB (1967). *The Deer and the Tiger.* University of Chicago Press, Chicago.

Schwartz CC, Arthur SM (1999). Radiotracking large wilderness mammals: Integration of GPS and argos technology. *Ursus* **11**, 261–74.

Seidensticker J (1976). Ecological separation between tigers and leopards. *Biotropica* **8**, 225–34.

Seidensticker J, McDougal C (1993). Tiger predatory behaviour, ecology and conservation. *Symposia of the Zoological Society of London* **65**, 105–25.

Seidensticker J, Tamang KM, Gray CW (1974). The use of ci-744 to immobilize free-ranging tigers and leopards. *Journal of Zoo Animal Medicine* **5**, 22–5.

Singh LAK (1999). Tracking tigers. WWF Tiger Conservation Programme, New Delhi, India.

Smirnov EN, Miquelle DG (1999). Population dynamics of the Amur tiger in Sikhote-Alin Zapovednik, Russia. In: Seidensticker J, Christie S, Jackson P, eds. *Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes.* Cambridge University, Cambridge, New Jersey, USA, pp. 61–70.

Smith JLD (1993). The role of dispersal in structuring the Chitwan tiger population. *Behaviour* **124**, 165–95.

Smith JLD, McDougal C (1991). The contribution of variance in lifetime reproduction to effective population size in tigers. *Conservation Biology* **5**, 484–90.

Smith JLD, Sunquist ME, Tamang KM, Rai PB (1983). A technique for capturing and immobilizing tigers. *Journal of Wildlife Management* **47**, 255–9.

Smith JLD, Ahern SC, McDougal C (1998). Landscape analysis of tiger distribution and habitat quality in Nepal. *Conservation Biology* **12**, 1338–46.

Sunquist ME (1981). The social organization of tigers (*Panthera tigris*) in Royal Chitawan National Park, Nepal. *Smithsonian Contributions to Zoology* **336**, 1–98.

Thailand Tiger Project. [Cited July 15 2010.] Available from URL: www.thailandtiger.org

Thirgood S, Mosser A, Tham S *et al.* (2004). Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation* **7**, 113–20.

Tomkiewicz SM, Fuller MR, Kie JG, Bates KK (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**, 2163–76.

Wang SW, Macdonald DW (2009). Feeding habits and niche partitioning in a predator guild composed of tigers, leopards and dholes in a temperate ecosystem in central Bhutan. *Journal of Zoology* **277,** 275–83.

White GC, Garrott RA (1990). *Analysis of Wildlife Radio-tracking Data.* Academic Press, San Diego.

Winterstein SR, Pollock KH, Bunck CM (2001). Analysis of survival data from radiotelemetry studies. In: Millspaugh, JJ, Marzluff, JM, eds. *Radio Tracking and Wildlife Populations.* Academic Press, New York, pp. 351–80.

Woods CP, Heinrich WR, Farry SC, Parish CN, Osborn SAH, Cade TJ (2007). Survival and reproduction of California condors released in Arizona. In: Mee A, Hall LS, Grantham J, eds. *California Condors in the 21st Century.* American Ornithologists Union and Nuttall Ornithological Fund, Washington, DC, pp. 57–78.

Yudakov AG, Nikolaev IG (1987). *The Ecology of the Amur Tiger: Based upon Winter Obersvations at a Field Station in the West Central Sikhote-Alin between 1970–1973.* Nauka, Moscow, Russia.

Li ZX, Zimmermann F, Hebblewhite M *et al.* (2010). Study on the potential tiger habitat in the Changbaishan Area, China. A collaborative work conducted by: WWF, WCS, Northeast Normal University, KORA, University of Montana and with the support of Chinese key stakeholders.

