Factors affecting the quantity and quality of Argos telemetry locations for wolverines in the northern Cascade Range in Washington

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Abstract

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Satellite telemetry systems provide wildlife researchers with a valuable tool for tracking species that range over large distances or inhabit remote or inaccessible terrain, such as wolverines (*Gulo gulo*) in the northern Cascade Range in Washington. The Argos system is 1 of 2 satellite telemetry systems that are currently available, and is being used by the USDA Forest Service's Pacific Northwest Research Station's North Cascades Wolverine Study (NCWS) to track study animals. In order to use Argos location data, an understanding of how environmental characteristics and animal behavior may affect location quality and quantity is necessary. However, the only quantitative evaluations of system performance in North America pre-date one or both major upgrades made to the system in 2005 and 2011. Moreover, there have been no published tests of the potential effects of animal behavior on Argos system performance. I conducted a series of static and dynamic tests, the latter using a collared dog, to evaluate the

potential effects of environmental factors and animal behavior on the quantity and quality of Argos telemetry locations in the NCWS study area. My static test results indicated that Argos location data is largely robust to the effects of the vegetative and topographic variables included in the analyses, suggesting that extensive static tests may not be necessary in similar study areas. I report a much higher proportion of high quality locations as well as much smaller location errors for one class of locations (A) than reported from previous tests. However, the dynamic tests I conducted revealed a large decline in both location quality and quantity compared to concurrent static tests. This effect was observed both when the dog wearing the dynamic collar was moving and at rest, so I could not attribute the decrease in location quality to animal movement alone. Test results indicate that researchers should not expect the results of static tests to be representative of location quality in a study area, and that recent upgrades to the Argos system have resulted in improved performance that may allow researchers to use location data at a finer spatial scale than previous tests indicated.

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Chapter 1 – Introduction

History of Wildlife Telemetry Systems

Many wildlife studies rely on the researcher's ability to relocate captured study animals. Studies of home range, habitat use, foraging behavior, activity patterns, dispersal and migration depend on such relocation data. Prior to the development of radio-telemetry tracking systems, relocation data were often impossible to collect in large enough quantities to answer many research questions for free-ranging wildlife (LeMunyan et al. 1959, Ellis et al. 1967).

In 1959, the first radio-telemetry tracking system was designed to relocate captured woodchucks (*Marmota monax*) in their burrows (LeMunyan et al. 1959). The system consisted of an implanted transmitter and an Army Surplus BC 453 Command Receiver and had a range of only 23 m. Cochran et al. (1963) deemed this system unsuitable for cottontail rabbits (*Sylvilagus floridanus*) and other species, and improved upon the system, designing a new transmitter, receiver, and 2 different receiver antennas. Cochran et al. (1963) used this improved system to successfully track cottontail rabbits, striped skunks (*Mephitis mephitis*), and raccoons (*Procyon lotor*). These prototype radio-telemetry devices gave rise to the present-day very high frequency (VHF) telemetry systems.

Wildlife researchers in the 1960's used VHF telemetry systems to study simple concepts such as spatial use by wild turkeys (*Meleagris gallopavo*) in Missouri (Ellis et al. 1967), dispersal by ruffed grouse (*Bonasa umbellus*) in Québec, Canada (Godfrey et al. 1969), nest-site selection and nest success of greater prairie chickens (*Tympanuchus cupido*) in Kansas (Robel et al. 1970), and to locate predated snowshoe hares (*Lepus americanus*) in Minnesota (Mech 1967). Since the 1960's, wildlife professionals have increasingly used VHF telemetry systems to answer their research questions. A search of the *Journal of Wildlife Management* archives on JSTOR demonstrates this trend, yielding an increasing number of articles containing the term radio-telemetry from the period prior to 1971 through the 1990's (Table 1).

Many improvements have been made to the original VHF telemetry system components (Mech and Barber 2002). Advances in transmitter and battery technology have allowed for smaller, lighter, and more powerful transmitters with increased transmitter life and range (Rodgers 2001). The development of microprocessors that allow researchers to program duty cycles (i.e., time of day and duration of data collection) have also increased transmitter life. Concurrent improvements in receiver and antenna design have increased the distance at which signals can be heard, as well as the ease with which signal direction can be determined. While wildlife researchers continue to take advantage of the simpler applications of VHF telemetry, better equipment and increased sample sizes, as well as advances in computational power, have allowed for more complex applications of VHF location data. Kolowski et al. (2002) used VHF telemetry to study microhabitat use of a population of bobcats (*Lynx rufus*) in Illinois that was vulnerable to human disturbance and habitat modification; Gosselink et al. (2003) studied temporal habitat partitioning of sympatric coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in Illinois, where increases in the coyote population were accompanied by decreases in red fox numbers; and Theuerkauf et al. (2003) studied spatiotemporal segregation of wolves (*Canis lupus*) and humans in Poland to predict areas suitable for wolf re-colonization.

The development of the first satellite telemetry systems in the 1970's allowed researchers to obtain location information remotely from target individuals anywhere on the globe. The first successful application of a satellite system for wildlife tracking occurred in April 1970, when

Table 1. Number of telemetry-related articles in the Journal of Wildlife Management archives in JSTOR.

	Search term			
Period	Radio-telemetry	GPS-telemetry	Argos	Total[a]
< 1971	31	0	0	31
1971-1980	42	0	0	42
1981-1990	136	0	0	136
1991-2000	151	5	14	170
2001-2010	91	48	21	160

[a] Total reflects the number of articles found for each term. An article containing multiple search terms was counted once for each term.

Craighead et al. (1972) deployed a transmitter on a female elk (*Cervus elaphus*) near Jackson Hole, Wyoming. The attachment collar plus transmitter weighed 11.3 kg and transmitted data for 29 days. Between 1977 and 1979, transmitters designed by Handar, Inc. were deployed on polar bears (*Ursus maritumus*) off the coast of Alaska (Lentfer et al. 1982, Taylor 1982), the Northwest Territories (Schweinsburg et al. 1982), and Greenland (Larsen et al. 1983). The Handar transmitter-collar combinations were much lighter at 5.6 kg, and transmitted data for up to 9 months. To calculate the location of the transmitter, all of these applications used pre-existing instrumentation onboard the National Aeronautic and Space Administration's (NASA) Nimbus meteorological satellites. These satellites were originally designed to locate and receive meteorological or geophysical data from remote recording stations, and then retransmit the data to an earth-based station (National Aeronautic and Space Administration 2012). Researchers continued to make use of instrumentation onboard the Nimbus satellites through the early 1980's to track wide-ranging species (Fancy et al. 1988).

The next generation of satellite telemetry technology was introduced in 1978 when NASA launched the Television Infrared Observation Satellite Program-N (TIROS-N) weather satellite. This satellite, and all subsequent TIROS-N/National Oceanic and Atmospheric Association (NOAA) satellites, carried Argos instrumentation. The current Argos manual describes the system as "a global satellite-based location and data collection system dedicated to studying and protecting our planet's environment (CLS-America 2011)." The system is a cooperative project between the French operator of the system Collecte Localisation Satellites (CLS), the French space agency Centre National d'Études Spatiales (CNES), the American agency NOAA with support from NASA, and the European meteorological organization

Eumetsat. Transmitters that make use of the Argos system to relay data are called platform terminal transmitters (PTTs) and are designed and produced by various companies.

The first Argos-compatible PTTs were placed at stations on land and floating ice as well as onboard ocean buoys. These PTTs delivered a variety of meteorologic, hydrologic, and oceanographic data. Fancy et al. (1988) provide an extensive list of early deployments on animals in the 1980's, including the first deployment on a humpback whale (*Megaptera novaeangliae*) off the coast of Newfoundland in 1983. Other species on the list include wide-ranging terrestrial species, such as caribou (*Rangifer tarandus*) in Alaska and the Arctic, muskox (*Ovibos moschatus*) in Alaska, grizzly bears (*Ursus arctos*) and polar bears; marine mammals such as sperm whales (*Physeter macrocephalus*), West Indian manatees (*Trichechus manatus*), gray seals (*Halichoerus grypus*), and crabeater seals (*Lobodon carcinophagus*); and birds such as bald eagles (*Haliaeetus leucocephalus*) and Antarctic giant-petrels (*Macronectes giganteus*). Some of these first PTTs were experimental units that provided no or very few locations before failing. Subsequent applications of Argos technology were often focused on recording long-range movements of marine species, including an examination of foraging strategies of wandering albatrosses (*Diomedea exulans*) in the Indian Ocean (Weimerskirch et al. 1993), migration routes of Adelie penguins (*Pygoscelis adeliae*) in the Ross Sea off Antarctica (Davis et al. 2001), and tracking a subset of species in the Tagging of Pacific Pelagics (TOPP) program to study pelagic habitat use throughout the Pacific ocean, including salmon sharks (*Lamna ditropis*) and leatherback turtles (*Dermochelys coriacea*; Block et al. 2002).

The Argos system has undergone several upgrades since its inception. In 1983 there were only 2 earth-orbiting satellites carrying Argos instrumentation; today there are 6 (CLS-America 2011). Argos has upgraded the algorithm they use to calculate locations several times, with the most recent upgrade in 2011 when they transitioned from the least squares to the Kalman filtering algorithm. The least-squares algorithm used information from only 1 satellite pass to calculate a location, whereas the new Kalman filtering algorithm uses a random walk model to predict the next location based on information from the previous one. Testing by Argos indicates that use of the new algorithm will increase the overall number of locations, as well as the quantity of high-quality (low-error) locations (Bernard et al. n.d., Lopez et al. 2011). As with VHF systems, advances in battery and transmitter technology have enabled ever lighter and more powerful transmitter packages, allowing researchers to place PTTs on smaller animals and obtain locations for longer periods of time. For avian applications, solar panels may be used to power transmitters or charge batteries, reducing or eliminating battery weight and extending transmitter life (Microwave Telemetry 2013). Programmable duty cycles allow researchers to tailor data collection to the objectives of their study. While PTTs continue to be used to provide location data, they increasingly include additional sensors to collect data about an animal's physiological state or local environmental conditions, which are then transmitted via the PTT. Shillinger et al. (2011) studied vertical and horizontal habitat preferences of post-nesting leatherback turtles in the South Pacific using PTTs in conjunction with a pressure sensor to record dive depth and duration. Charrassin et al. (2002) used PTTs in conjunction with temperature and depth sensors on king penguins (*Aptenodytes patagonicus*) to map ocean-temperature at depth in a poorly sampled but productive area off the Kerguelen Islands in the Southern Ocean.

A second satellite-based telemetry system was introduced in 1994 when Lotek Engineering, Inc. produced the GPS_1000, a receiver that took advantage of the United States Department of Defense Global Positioning System (GPS) to calculate an animal's location (Mech and Barber 2002). These first GPS receivers were tested for and deployed on large ungulates such as moose (*Alces alces*; Rodgers et al. 1996, Moen et al. 1997), caribou (Johnson et al. 2002), and European red deer (*Cervus elaphus*; Pepin et al. 2004), but were too heavy for smaller mammals such as deer, bears, wolves, or large cats. By 2002, technological advances had led to lighter receivers, with minimum weights of 120 g for a collar plus receiver package and 70 g for a backpack plus receiver package (Mech and Barber 2002).

Improvements to GPS telemetry systems have been similar to those for VHF and Argos systems – decreased weight, longer battery life, and incorporation of solar panels for avian applications. Systems have also been designed that use GPS technology to record an animal's location in conjunction with a transmitter that uses either Argos or Iridium satellites or a cellular telephone network to transmit location data to researchers. Finally, in 2002, Wildtrack Telemetry Systems developed Fastloc® GPS technology, which greatly reduces the time and power necessary to record a location and is ideal for marine species that only surface for short periods of time (Wildtrack Telemetry Systems 2010). Some recent applications of GPS telemetry systems include defining patterns of habitat use and selection by female grizzly bears in northern British Columbia (Milakovic et al. 2012), locating cougar (*Puma concolor*) predation events to study kill rates and prey composition in Alberta, Canada (Knopff et al. 2010), and monitoring spatial use by feral swine (*Sus scrofa*) in Texas in response to aerial gunning as a population control method (Campbell et al. 2010).

Differences in Location Acquisition Methods for Telemetry Systems

Each of the 3 telemetry systems discussed here uses a different method to generate location data, each of which results in specific advantages and drawbacks. The oldest system, VHF, consists of a transmitter deployed on a study animal and a receiver that can be tuned to the frequency specific to that animal's transmitter. Although stationary automated telemetry stations have been developed that record the direction to a signal, the range of the receiver limits their use. Non-automated applications of VHF telemetry require an observer on the ground or in an aircraft in close proximity to an animal to acquire accurate locations. A ground-based observer determines an animal's location by homing in on the VHF signal or by triangulating to the signal from multiple locations. An animal's location may be estimated from an aircraft by homing in on the area from which the signal is emanating.

One advantage of a VHF system is that an observer can visually verify an animal's location using the homing method, and a skilled observer familiar with a study area may be able to triangulate an animal's position fairly accurately. VHF telemetry systems also require a lower initial investment than either Argos or GPS systems. However, except in the case of automated telemetry stations, an observer is required to record each location. In cases where the study species is wide-ranging, inhabits rugged or remote terrain, is nocturnal, or moves quickly, an observer may not be able to reliably or consistently locate the target animal. The use of airplanes or helicopters to obtain VHF telemetry locations may mitigate these limitations, but aerial telemetry is often prohibitively expensive. The cost of a VHF telemetry system increases for each location obtained, and increases in greater increments when an animal is difficult to locate (Thomas et al. 2011). In addition, homing in on an animal can be invasive and may change its behavior.

In contrast to a VHF system, neither satellite telemetry system requires an observer to calculate an animal's location. Both Argos and GPS systems can calculate a tagged animal's location anywhere on the globe, 24 hours a day. Both satellite systems require a greater initial investment for the GPS receiver or Argos-compatible PTT, but the cost per location decreases with each acquired location (Rodgers 1997, Thomas et al. 2011). The 2 systems employ different methods to calculate locations, and each method results in advantages and disadvantages that are primarily associated with location quality and data retrieval.

For Argos telemetry systems, an animal-mounted PTT emits a signal at a user-defined, factory-programmed interval (the repetition rate) on a stable frequency (401.650 MHz ± 30 kHz), which may be received by Argos instrumentation aboard any of 6 polar-orbiting satellites (CLS-America 2011). The signal's transmission frequency is Doppler-shifted based on the velocity at which the satellite is moving toward or away from the PTT. The receiving satellite records the time-tag and Doppler shift of the transmission and then relays that information, along with the location of the satellite at the time of signal reception, to a ground-based processing center where a location is calculated based on the signal(s) received by that satellite only. In the case that more than 1 satellite receives a signal from a given PTT, the data are not combined, and each satellite receiving a signal will provide 1 PTT location. All PTT locations are assigned a location class (LC) based on the number of signals received and the probable error of that location (Table 2). Independent tests of the Argos system have demonstrated variable error depending on the assigned LC (Table 3; Britten et al. 1999, Keating et al. 1991, Nicholls et al. 2007, Soutullo et al. 2007, Sauder et al. 2012).

In contrast to Argos systems, GPS telemetry systems use a constellation of satellites (at least 24) in medium Earth orbit. These satellites are arranged into 6 equally spaced orbital planes, ensuring that at least 4 satellites are visible to a GPS receiver at all times from almost anywhere on the globe (GPS.gov 2012). Each satellite continuously transmits its position and the current time. An animal-mounted GPS receiver that receives concurrent signals from 3 satellites can use that information to triangulate a 2-dimensional location; 4 or more satellites are needed to calculate a higher quality 3-dimensional location. Recent evaluations of GPS receiver

Table 2. Description of Argos location classes (LC), from lowest to highest quality. Estimated error is defined by Argos as 1 standard deviation of the estimated location error for that LC (CLS-America 2011).

LC	Number of messages required	Estimated error (m)
Z	1	Invalid location
B	1	NA
A	3	NA
0	4	> 1500
1	4	500 – 1500
2	4	250 – 500
3	4	< 250

Table 3. Results reported in previous terrestrial evaluations of the Argos system. A location class (LC) is assigned by Argos based on the likely accuracy of the associated location as Z, B, A, 0, 1, 2, 3 in order of increasing accuracy.

				% locations in LCs 1-3 by test		68th percentile location errors by LC (km)				
Study location	Year(s) of data collection	Physiographic conditions	Transmitter designed for:	Static	Dynamic	A	1	2	3	Source
Montana, USA	1989	Mountaintops to deep valleys	Medium-sized mammals	NA	NA	NA	1.2	0.9	0.4	Keating et al. 1991
SW United States	1993-1995	Open suburban backyard	Peregrine falcons (*Falco peregrinus*)	9.4	NA	6.8	NA	NA	NA	Britten et al. 1999
Across southern hemisphere	1994-2001	Variable	Various species	24	16	24[b]	3.8[b]	2.3[b]	0.8[b]	Nicholls et al. 2007
Spain and Portugal	2004-2005	Variable	Raptors	NA	7.3	20	4	NA	NA	Soutullo et al. 2007
Idaho, USA	2007	Forested mountains	Fishers (*Martes pennant*)	77.2	NA	NA	1	0.5	0.2	Sauder et al. 2012

[a] NA = not applicable (results were not reported by the authors)

[b] Nicholls et al. summarized data from both static and dynamic tests together.

performance have reported 95% circular error probabilities (CEP; i.e., the radius of a circle within which 95% of acquired locations fall) ranging from 18 to 144 m, varying by unit configuration and test site characteristics (Table 4; Cargnelutti et al. 2007, Sager-Fradkin et al. 2007, Jiang et al. 2007, Wells et al. 2011).

The method that each satellite system uses to calculate locations also influences location retrieval. Argos locations are available for download via the Internet within 24 hours of a satellite receiving a signal from a PTT. In contrast, the simplest GPS receivers (store-on-board) store locations until a researcher can retrieve the unit. Other options to retrieve archived GPS locations require additional instrumentation and include remote download and integration with a satellite (Argos or Iridium) or cellular transmitter. Remote download requires a researcher to be within a certain distance of the unit with instrumentation to trigger and receive the location data. A GPS receiver in combination with a satellite or cellular transmitter results in locations being transmitted to a satellite at a pre-defined interval; such locations are available to the researcher in a manner similar to Argos locations.

While GPS telemetry systems provide the most accurate locations, there are situations in which Argos systems have a distinct advantage. In remote or hazardous terrain or when the study species covers large distances, a researcher may not be able to locate or retrieve a store-on-board unit or get close to a remotely downloadable GPS receiver. In such cases, no location data are obtained and the investment in the unit and its deployment is completely lost. Combination GPS/satellite units solve the problem of data retrieval, but they are expensive and their size and weight makes them an option only for larger animals.

In conclusion, VHF telemetry systems are ideal for species that can be relocated consistently and in situations where there is sufficient staff and equipment to track study animals.

Table 4. Results reported in previous terrestrial evaluations of GPS telemetry systems. The 95% circular error probability (CEP) is defined as the radius of a circle within which 95% of all locations fell. 3D fixes are those that require signals from at least 4 satellites; 2D at least 3 satellites.

				95% CEP (m)			
Study location	Year(s) of data collection	Vegetation type	Receiver designed for:	3D	3D + 2D	2D	Source
Washington, USA	2002-2003	Montane forest	Black bears (*Ursus americanus*)	17.7		264.6	Sager-Fradkin et al. 2007
Mount Fuji, Japan	2002-2003	Montane to subalpine zones, developed foothills	Not stated (Lotek GPS-3300)	25.6		86.7	Jiang et al. 2008
Southwest France	2003-2004	Forest/agricultural mosaic	Medium mammals		144/208[a]		Cargnelutti et al. 2007
Washington, USA	2004-2005	Montane to subalpine zones	Mountain goats (*Oreamnos americanus*)		83.6[b]		Wells et al. 2011

[a] Static/dynamic results.

[b] The value for 95% CEP ranged from 77.5 – 83.6 depending on the data screening technique.

In situations where this is not the case and there are sufficient funds for a larger initial investment, the choice between satellite systems must be made based on desired location accuracy, opportunities for data retrieval, maximum allowable tag (i.e., PTT, GPS receiver, or combination unit) weight based on the study species weight, and cost per tag.

Wolverines in the North Cascades

The wolverine (*Gulo gulo*), the largest terrestrial member of the Mustelidae, is a primarily carnivorous scavenger that exists at low densities throughout its range. In North America, wolverines are found in the boreal forests, tundra, and alpine areas of the northern United States and throughout Canada and Alaska (Banci 1994, Aubry et al. 2007). Historically, wolverine populations in the western contiguous United States occurred in the central and southern Sierra Nevada in California, the Cascade Range of Washington from Mt. Rainier north to the Canadian border, and throughout the Rocky Mountains as far south as New Mexico (Aubry et al 2007). In the southern portions of their North American range, wolverines typically inhabit rugged subalpine and alpine areas distant from human development, and individuals regularly cover large distances over short time periods (Hornocker et al. 1983, Copeland et al. 2007, Krebs et al. 2007). Home range sizes in North America have been reported to vary from 105-405 km^2 for females and 422-1366 km^2 for males (Hornocker and Hash 1981, Whitman et al. 1986, Krebs et al. 2007).

Persistent spring snow cover is believed to be a limiting factor for wolverines. Using telemetry and den site location data, Copeland et al. (2010) found that the geographic distribution of wolverines throughout their circumpolar range was limited to areas where snow cover persists until the end of the reproductive denning period in mid-May. Using satellite imagery, Copeland et al. (2010) showed that all documented wolverine reproductive dens in North America and

Fennoscandia occurred in areas with persistent spring snow cover, and all reproductive dens found by Magoun and Copeland (1998) in both Alaska and Idaho were covered by at least 1 m of snow. In 2010, the U.S. Fish and Wildlife Service (USFWS) designated the wolverine as a candidate for listing under the Endangered Species Act of 1973 (16 U.S.C. 1531-1544, 87 Stat. 884), with the primary threat being loss of habitat and range due to climate warming (U.S. Fish and Wildlife Service 2010), and in February 2013 the USFWS proposed to list the North American wolverine in the contiguous United States as a threatened species (78 F.R. 7864-7890).

Argos-compatible PTTs have been used by several wildlife researchers to study wolverines (Squires et al. 2007, Dawson et al. 2010). In Washington, the USDA Forest Service's Pacific Northwest Research Station initiated the North Cascades Wolverine Study (NCWS) in the winter of 2005-2006. This study tracks wolverine movements using Argos-compatible PTTs, with the goal of estimating wolverine home range sizes, broad-scale habitat use patterns, and reproduction in the northern Cascade Range of Washington (Aubry et al. 2012). The study area contains portions of the Okanogan-Wenatchee National Forest and North Cascades National Park, and much of the study area is located within the Pasayten, Lake Chelan-Sawtooth, and Stephen Mather Wilderness Areas. This landscape is characterized by rugged terrain, with elevations ranging from 600 to 2700 m. Deep snowpack and lack of roads for snowmobile access render large portions of the study area inaccessible for up to 6 months of the year. Due to the study area's limited accessibility and certain aspects of wolverine biology (e.g., large home range, ability to cover large distances over short periods of time), NCWS researchers chose to use Argos-compatible Kiwisat 101 PTTs manufactured by Sirtrack (Havelock North, New Zealand) to track their study animals.

To date, the NCWS has captured wolverines 26 times (13 individuals), and deployed 25 Argos-compatible collars (Aubry et al. 2012; K. Aubry, U.S. Forest Service, unpublished data). These collar deployments have resulted in over 5000 wolverine telemetry locations during the period 2008-2011. Before using these location data to investigate the spatial-use patterns of wolverines in the North Cascades, it is necessary to first identify the scale at which it is appropriate to use the location data and to determine if the environmental characteristics of the study area or animal movements may bias location quantity and quality within the study area. All previously published evaluations of the Argos system were conducted when Argos was calculating locations using the least-squares algorithm, and only 3 of those studies were conducted in a terrestrial ecosystem in North America (Keating et al. 1991, Britten et al. 1999, Sauder et al. 2012). This project was initiated to fill that knowledge gap.

Chapter 2 – Factors Affecting Argos Location Quantity and Quality in a Mountainous Landscape

Abstract

Argos satellite telemetry systems provide an important tool for wildlife researchers, allowing location data to be consistently collected at regular spatial and temporal intervals. However, previous evaluations of the Argos system have reported a lack of high quality locations and correspondingly large (>10 km) and variable location errors. I used stationary Argos-compatible platform terminal transmitters (PTTs) designed for deployment on wolverines (*Gulo gulo*) to conduct static and dynamic tests of the Argos system in the northern Cascade Range of Washington, USA. With the static tests, I examined the error distribution of Argos locations, as well as the effects of continuous topographical and vegetative variables on location quality (i.e., accuracy and quantity). Furthermore, to explore the effects of animal behavior, I tested the effect of antenna orientation and burial under snow on location quality, and conducted dynamic tests using PTTs deployed on a domestic dog. The results of my static tests indicated a marked improvement in the proportion of highly quality locations, as well as the magnitude of location errors, over several previous evaluations of the Argos system. Neither the error radius nor ellipse data provided with each Argos location were reliable indicators of actual PTT location, though the error radius was a good predictor of the magnitude of location error. Although the vegetative and topographic variables that I tested had little effect on Argos location quality, slope, aspect, elevation, terrain variability, and canopy closure did affect location error. Tree basal area, amount of sky obstructed by topography, elevation error, and slope influenced location acquisition rates. Because Argos location quality was largely robust to the environmental

characteristics tested, variability in those characteristics should not lead to large differences in location quality in other areas. Burial under snow at a depth of 244 cm significantly degraded location quality, but antenna orientation under optimal conditions did not. The PTTs deployed on the dog exhibited lower location quality than nearby concurrently operating static PTTs, though the reasons for this disparity are not clear. In conclusion, I observed an improvement in Argos location quality compared to that previously reported in the literature. Argos-compatible PTTs in my study area appear to be robust to the effects of vegetation and topography, however some aspects of animal behavior appear to degrade location quality when compared to static tests.

Introduction

Wildlife researchers have been using the Argos satellite telemetry system since the 1980s to track free-ranging marine and terrestrial wildlife (Fancy et al. 1988). The Argos system allows researchers to obtain location data via the Internet for study animals located anywhere on the globe 24 hours a day, and is often used for species that are wide-ranging, inhabit remote or inaccessible areas, or have other behaviors that make alternative telemetry systems ineffective or too expensive (Thomas et al. 2011, Fancy et al 1988). Argos technology has allowed wildlife researchers to collect location data for previously unstudied species or populations (Buho et al. 2011, Lindsell et al. 2009) and map previously unknown migration routes (Davis et al. 2001). Effective use of location data requires knowledge of how local conditions may differentially affect location quality (i.e., quantity and accuracy), including animal behaviors and environmental factors such as topography and vegetation. Furthermore, in addition to geographic coordinates, each Argos location includes: a location class (LC) that may have associated error estimates (Table 2, p. 10), an error radius and ellipse, and a measure of the geometric dilution of precision (GDOP) of the location. However, neither the influence of environmental factors and animal behaviors nor the utility of the information associated with Argos location coordinates have been thoroughly evaluated.

Early research programs using Argos-compatible platform terminal transmitters (PTT) in mountainous terrain noted that they received fewer locations from valleys than other areas (Craighead and Craighead 1987). Moreover, Keating et al. (1991) demonstrated that location acquisition rates were lower at a valley site than at a mountaintop site, and Sauder et al. (2012) demonstrated that, for a subset of location classes (1-3), topographic obstruction and canopy cover affect both location error and acquisition rates. However, none of these tests examined the effect of topography and vegetation for all location classes, nor did they test for the effect of a wide range of environmental variables. Because Argos location acquisition is similar to global positioning system (GPS) location acquisition in its dependence on communication between a ground-based unit and instrumentation onboard an earth-orbiting satellite, it is possible that those factors that affect GPS location quality similarly affect Argos location quality. Recent evaluations of GPS telemetry location quality have found that fix rates are negatively affected by canopy and topographic obstruction (Hansen and Riggs 2008); canopy, topographic obstruction, and decreased elevation (Sager-Fradkin et al. 2007); and vegetative cover and tree basal area or vegetative cover and slope (Wells et al. 2011). Similarly, location precision was found to be negatively affected by canopy cover, topographic obstruction, and tree height (Hansen and Riggs 2008). In addition, studies evaluating the impact of animal species and individual behavior on GPS telemetry location quality have shown variable effects. Bowman et al. (2000) found that white-tailed deer (*Odocoileus hemionus*) activity levels affected location acquisition: fix rates for resting deer were lower than for active deer. Mattison et al. (2010) observed a similar reduction in fix rate for resting animals and also found that fix rate is affected by species, with the fix rate for collars deployed on Eurasian lynx (*Lynx lynx*) almost double that of the same collars deployed on wolverines (*Gulo gulo*). Finally, Sager-Fradkin et al. (2007) observed that collars placed at simulated bear-bedding sites at the base of trees had a 16% lower fix rate than nearby collars.

In addition to understanding how a wide range of environmental factors and animal behaviors might affect Argos location quality, evaluating the utility of the information associated with each Argos location will be useful to researchers for determining the appropriate scales for conducting spatial analyses. The Argos user’s manual states that the error radius associated with each location corresponds to 1 standard deviation of the estimated error for that location (CLS-America 2011). For all locations calculated using 4 or more signals (i.e., LC 0-3), the location class is assigned based on the magnitude of the error radius. Published tests of Argos-compatible PTTs in terrestrial systems conducted prior to 2005 observed large overall location error, a low proportion of locations in the most accurate location classes (LC 1-3), and 68th percentile errors exceeding those provided by Argos for LCs 1-3 (Table 3, p. 11). For all these tests, Argos required researchers to specify a single elevation for their PTTs, and Keating et al. (1991) demonstrated that the resulting vertical error led to increased location (horizontal) error. In 2005, Argos removed the requirement to specify elevation by incorporating data from a 30-arcsecond digital elevation model (DEM) into their location calculations to reduce elevation-induced location error. The results of the tests conducted by Sauder et al. (2012) in 2009 showed improvements in both location accuracy and the proportion of high quality locations. After Sauder et al. (2012) conducted their tests, Argos transitioned from the least-squares algorithm to the Kalman filtering algorithm for calculating locations in 2011. Argos publications state that implementation of the Kalman algorithm will result in an overall increase in the number of locations obtained, as well as an increase in the quantity of high-quality (low-error) locations (Bernard et al. n.d., Lopez et al. 2011), however this has not been independently confirmed.

Due to the lack of published tests of Argos location error for all location classes, many researchers continue to run spatial analyses using only LCs 1-3 (Tarroux et al. 2010, Hoenner et al. 2012) because error for the other location classes is either classified as too large (Argos classifies LC 0 error as >1500 m) or unquantifiable (LCs B and A). However, omission of location classes leads to an increase in the time interval between locations, reduced sample sizes, and may result in systematic bias if certain location classes are associated with certain behaviors or environmental conditions, all of which have important consequences for subsequent spatial analyses. For example, Lonergan et al. (2009) used GPS and simulated Argos location data to demonstrate that increasing the intervals between locations results in an increase in linear interpolation errors. Burdett et al. (2007) calculated lynx home ranges using full and reduced datasets, demonstrating significant variation in home range size calculations as more locations were omitted for highly mobile individuals. Determining the scale of error for LCs B, A, and 0 will provide researchers with an empirical basis for determining whether they can use additional location classes in spatial analyses of location data, thus reducing errors and bias in their final results.

My primary objectives were to evaluate the reliability of Argos location information and determine the effects of environmental factors and animal behavior on the accuracy of Argos location data using collars that are currently being deployed on wolverines in the northern Cascade Range of Washington (Aubry et al. 2012). I used location data from stationary collars to examine the distribution of location errors in all Argos location classes, as well as the reliability of the error information associated with each location. I also modeled the effects of environmental variables on stationary collar location accuracy and acquisition rate. The highly variable topography and vegetative cover in my study area allowed me to test Argos system performance under a wide range of environmental conditions, thus the test results I present should be applicable in areas where any combination of those conditions exists. Because previous tests have demonstrated decreased location quality when collars are deployed on animals in an enclosure (Keating et al. 1991), I hypothesized that some aspect of animal behavior may affect collar performance. To examine the effects of animal movement on location accuracy and acquisition rates, I compared these metrics for stationary collars and a collar worn concurrently by a domestic dog. I also examined location accuracy and acquisition rate for collars buried under the snow and with antennas at varying angles to account for other aspects of wolverine behavior that might influence system performance.

Study Area

The study area (~9000 km^2) was located on the east side of the Cascade Crest in Washington, USA immediately south of the Canadian border (Fig. 1). Sampling sites were located on federal land, primarily the Methow Valley Ranger District of the Okanogan-Wenatchee National Forest with additional sites in North Cascades National Park. About 40% of the study area was federally designated wilderness. Topography is characterized by rugged terrain with elevations ranging from 600 to 2700 m. The study area was in the rain shadow of the Cascade Range, with the majority of precipitation falling as snow and average precipitation ranging from >200 cm along the Cascade crest to <30 cm at the eastern boundary of the National Forest. Due to variable precipitation, a steep elevation gradient, and local disturbance regimes, vegetative cover was highly variable at both small and large spatial scales. Vegetation consisted predominately of shrubs and grasses at the lower elevations; xeric forest dominated by Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasciocarpa*), and ponderosa pine (*Pinus ponderosa*) at mid to high elevations with subalpine larch (*Larix lyallii*) and whitebark pine (*Pinus albicaulus*) near timberline (Lillybridge et al. 1995); and alpine meadows, exposed rock, and small glaciers at the highest elevations. for

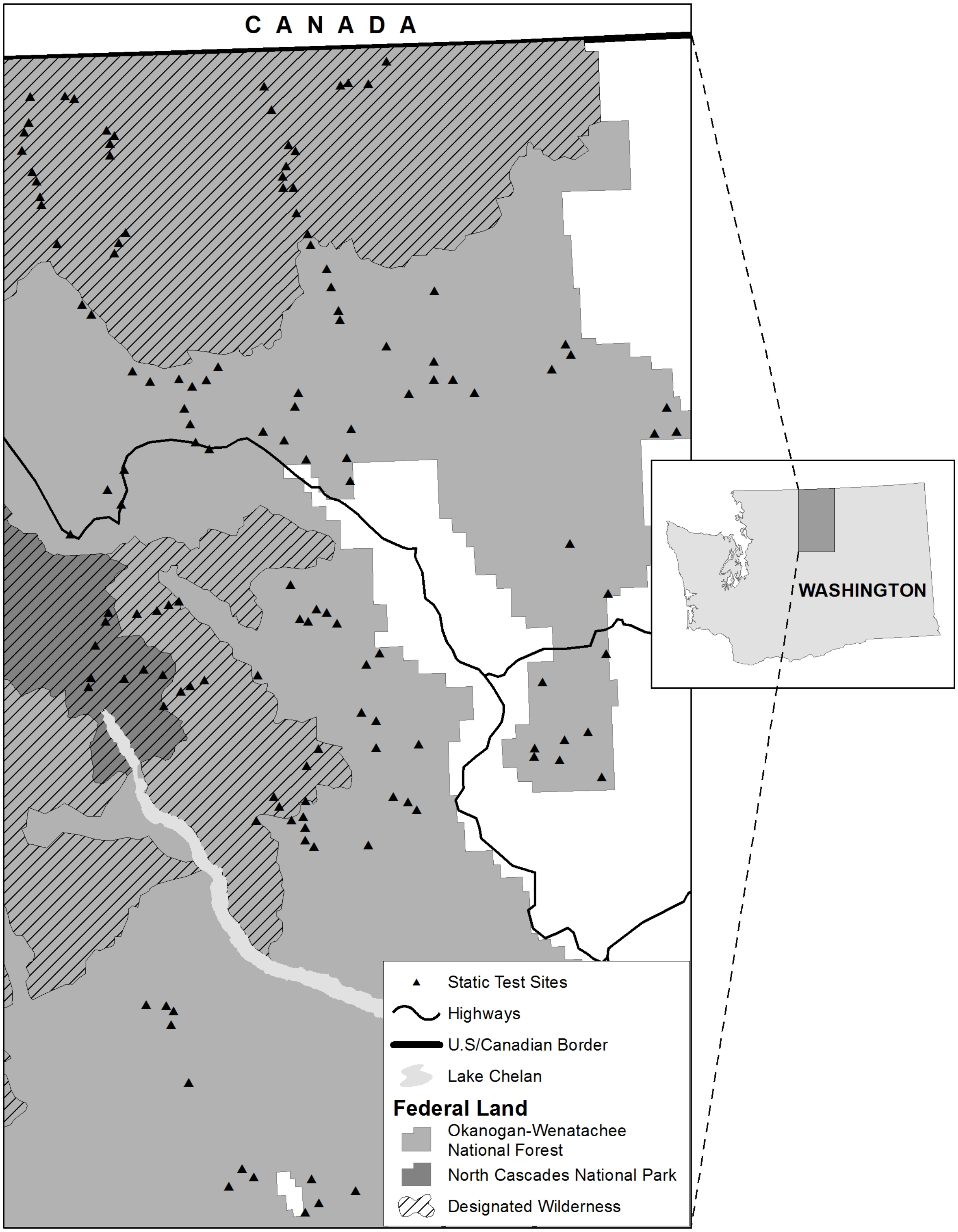

Figure 1. Map of the study area. Sampling sites were located exclusively on federal land.

Methods

Static Field Tests

Prior to selecting test sites, I used ArcGIS 9.3 (Esri, Redlands, CA, USA) to create a grid of potential sites at 100-m intervals across the study area. I chose an interval of 100 m to allow sampling flexibility if a selected site proved inaccessible. I attributed each potential site using vegetative information developed by the Landscape Ecology, Modeling, Mapping & Analysis team (http://www.fsl.orst.edu/lemma), and topographic variables derived from the 2009 update of the 10-m National Elevation Dataset (NED) digital elevation model (DEM) and the 30-arcsecond DEM used by Argos in location calculations (Table 5). To select test sites, I used a stratified random scheme based on the categorical variable site aspect (ASPT_R) and the continuous variables elevation error (ELVERR_R) and visible sky (SKY_R) stratified by septiles. To increase the power of the subsequent regression analysis, I chose to concentrate sampling at sites with values in the upper, middle, and lower septiles of each of the 2 continuous variables. Due to the rugged terrain present in the study area, I maximized sampling efficiency by only selecting sites within 500 m of a road or 250 m of a trail while maintaining the desired concentration of sites per septile.

From July to September 2011, I randomly selected and deployed 1 of 5 PTTs for at least 120 minutes (range: 122–1548 minutes) at each selected static test site (*n*=144). All PTTs were identical to those being deployed on wolverines within the study area (Sirtrack KiwiSat 101 PTT with a 0.5 watt transmitter and 3NC antenna, plus a VHF transmitter with internal brass loop antenna mounted on a 20-mm wide Zilco collar) and were programmed to transmit a signal every 60 seconds (Aubry et al. 2012). I established each test site within 50 m of the pre-determined coordinates, suspending the PTT from a small tree, shrub, or stick at a height of 50-100 cm

Table 5. Descriptions of all variables included in static test model building. Those with an asterisk were also used to stratify the test points prior to selection. Variables followed by an R (e.g. ASPT_R) were derived from remotely sensed data, and those by an F (e.g. ASPT_F) were measured in the field.

Variable	Full Name	Variable Type	Data Source	Description
ASPT_R*	Site aspect	Categorical	NED 10m DEM[a]	Derived from the DEM using the Aspect tool in ArcGIS 10. Categories: N/S or E/W.
CNPY_R	Canopy	Categorical	LEMMA GNN[b] vegetation data	Cover class value (field name = COVCL). Categories: <10%, 10-40%, 40-70%, >70%.
ELVERR_R*	Elevation error	Continuous	NED 10m DEM[a] and USGS GTOPO30 DEM[c]	Absolute value of the difference between the elevation of a raster cell in the 10m DEM and the USGS GTOPO30 DEM used by Argos. Calculated in ArcGIS 10.
ELEV_R	Elevation	Continuous	NED 10m DEM[a]	Elevation in meters.
SKY_R*	Visible sky	Percent	NED 10m DEM[a]	Percent of the hemisphere of sky not obstructed by topography visible from a raster cell. Calculated in SAGA-GIS using the Visibility module.
SLOP_R	Slope	Continuous	NED 10m DEM[a]	Slope in degrees. Calculated in ArcGIS 10.
STRUC_R	Structural condition	Categorical	LEMMA GNN[b] vegetation data	Structural condition value (field name = STRUCCOND). Categories: Sparse (<10%), open (10-40%), sapling/pole, small/medium tree, large tree.
VRM_R	Vector ruggedness measure	Percent	NED 10m DEM[a]	A measure of topographic variability. Calculated in ArcGIS 10 using the Vector Ruggedness Measure script (Sappington 2007).
VALY_R	Valley aspect	Categorical	NED 10m DEM[a]	A visual determination of the orientation of the major drainage (at 1:24000) in which the point was located. Categories: N/S or E/W.
ASPT_F	Site aspect	Categorical	Compass	Categories: N/S or E/W.
BASL_F	Basal area	Integer	10-factor prism	Raw prism reading at the test point.
CNPY_F	Canopy closure	Percent	Concave spherical densiometer	The average of 4 densiometer readings taken at 0, 90, 180, and 270° with the observer at the test point.
ELEV_F	Elevation	Continuous	Altimeter	If an altimeter reading was missing, the elevation from the Trimble GPS was used.

Table 5 continued

SKY_F	Visible sky	Percent	Clinometer	Percent of the hemisphere of sky not obstructed by topography visible from the test point. The result of a calculation using 8 clinometer measurements of angle to the horizon taken at intervals of 45° (0°, 45°,…,315°, Hansen et al. 2008).

[a] National Elevation Dataset 10m digital elevation model (ned.usgs.gov)

[b] Landscape Ecology, Modeling, Mapping & Analysis gradient nearest neighbor model for the Northwest Forest Plan project area, regions 221 and 222 (http://www.fsl.orst.edu/lemma/main.php?project=nwfp15&id=studyAreas)

[c] United States Geological Survey Global 30 arc-second elevation digital elevation model (http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/GTOPO30)

above the ground with the antenna ≤45° from vertical (straight up). At each test site I recorded the geographic coordinates of the PTT using a Trimble Juno SB GPS unit with an advertised accuracy of 2-5 m (Trimble Navigation Limited, Sunnyvale, California), as well as aspect, basal area, canopy closure, elevation, and visible sky (Table 5, p. 26). For each static test site, I also used remotely-sensed data to derive estimates of aspect, canopy closure, elevation error, elevation, visible sky, slope, structure, vector ruggedness, and valley aspect in ArcGIS 9.3 (ESRI, Redlands, CA). I resampled 17 sites in February and March 2012 to test for seasonal variation in Argos performance. All static test sites were >1 km apart to avoid concurrent sampling under similar environmental conditions.

I also tested the effect of antenna angle on Argos performance under conditions of zero obstruction by hanging PTTs at a location with no slope, 100% visible sky, and no vegetative cover for 12-hour intervals. During the first interval, I deployed all 5 PTTs, with one antenna each oriented at 0°, 45°, 90°, 135°, or 180° from vertical (0° corresponded to the antenna pointing straight up). During 4 subsequent intervals I rotated each PTT antenna through the remaining 4 orientations, so that each interval tested all angles and each PTT was eventually oriented at all angles. Finally, because all known wolverine natal dens have been located in areas with snow cover (Copeland et al. 2010), I evaluated the performance of PTTs under snow by burying 4 collars at 61, 122, 183, and 244 cm (2 foot intervals) with the fifth collar hung 50 cm above the snow for comparison. Snowpack at the time of the tests determined the maximum burial depth.

Dynamic Field Tests

To evaluate the effects of animal movements on Argos system performance, I conducted dynamic tests (n=24) using a 55-pound Labrador retriever (*Canis familiaris*). Although the dog differed in size and behavior from a wolverine, having a collar worn by an agile quadruped capable of moving quickly through all types of terrain and vegetation more closely approximates wolverine movements than would attaching the collar to a human. For each dynamic test, the dog wore a randomly selected PTT and carried a GPS data logger (advertised accuracy=5 m; Columbus V-900 Multifunction GPS Logger, Fuzhou Victory Technology Co., LTD, Fujian, China) that recorded its location every 10 seconds. Because the goal of these tests was to mimic wild animal movements as closely as possible, the dog was off-leash and allowed to wander at will and move at variable speeds. To compare location quality between the dynamic and static tests, I conducted some dynamic tests (n=13) concurrently with at least 1 static test within 10 km. Most of the dog's movements were along established trails in wilderness areas, but some time was spent off-trail on the way to and from static test sites, and there were also periods when the dog was resting. Dynamic field tests using the dog were approved and carried out under University of Washington Institutional Animal Care and Use Committee permit 4226-04.

Data Analysis

I downloaded and projected all Trimble and data logger GPS coordinates and Argos-calculated PTT locations to Zone 10 north Universal Transverse Mercator (UTM10N) coordinates based on the 1983 North American Datum (NAD83). I used the GPS coordinates as the true PTT location for all error calculations. To evaluate Argos location error (i.e., the magnitude of the difference between each Argos location and the true PTT location, Fig. 2a), I calculated the magnitude of longitudinal error (ΔH_x) and latitudinal error (ΔH_y) between the true PTT location and the Argos coordinates as:

$$\Delta H_x = |GPS_x - Argos_x|$$

$$\Delta H_y = |GPS_y - Argos_y|$$

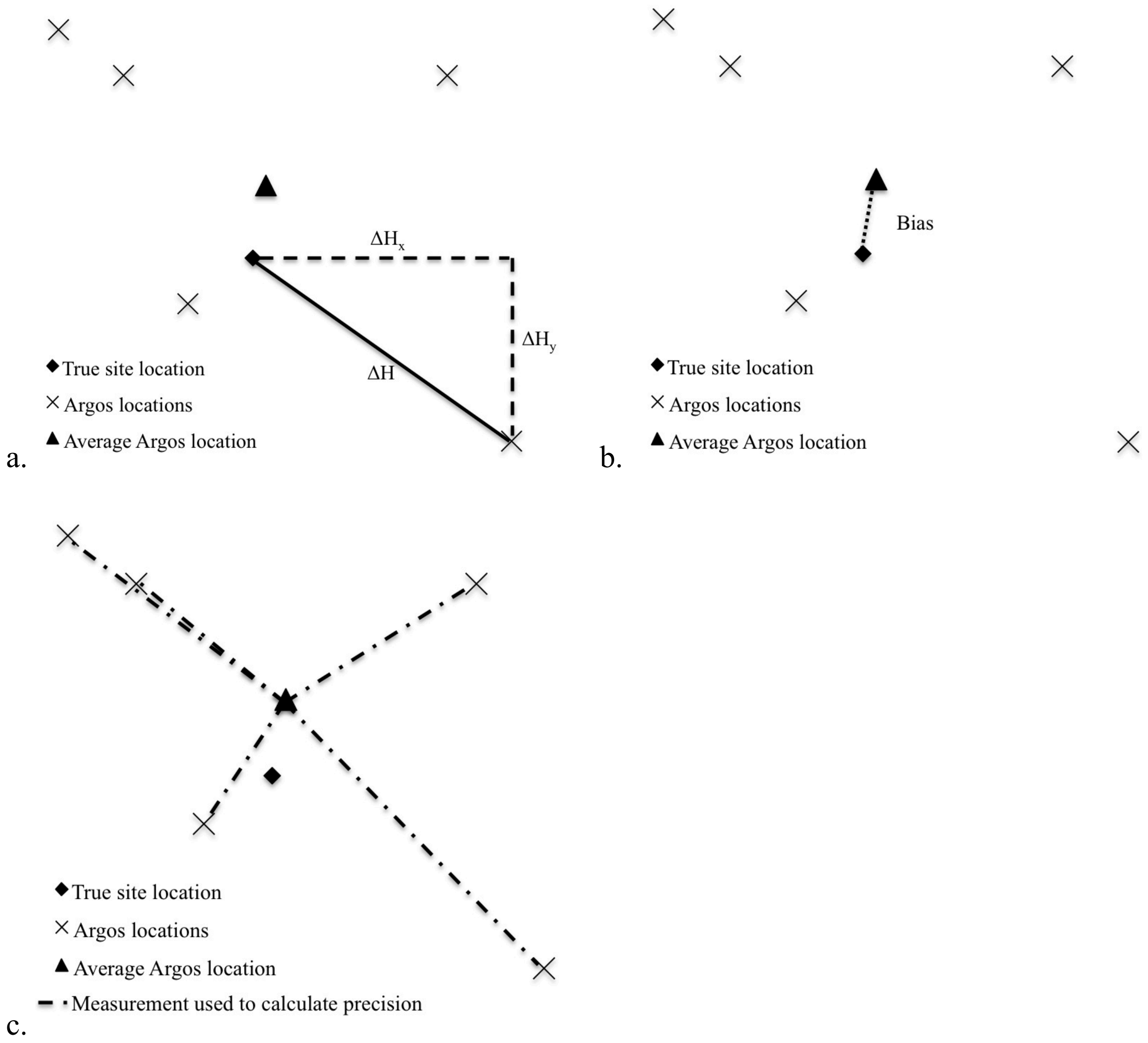

Figure 2. Graphic representation of measurements used to calculate static test site summary metrics, individual location errors and average Argos location (a), test bias (b), and test precision (c).

and the magnitude of total horizontal error (ΔH) as the Euclidean distance from the true PTT location to the Argos coordinates as:

$$\Delta H = \sqrt{\Delta H_x^2 + \Delta H_y^2}$$

I plotted the Argos-reported error ellipses in ArcGIS 9.3 to determine whether they contained the associated GPS coordinate. Because the error radius is an estimate of ΔH, I classified the error radius as accurate if it was ≥ΔH. I also regressed ΔH on the additional information provided with each location (error radius, error ellipse, and GDOP) to determine the predictive power of that information for estimating true location error.

Static Tests

To describe location error for each static test site, I first calculated the average Argos location for that site (Fig. 2a, p. 30). I then calculated 3 different groups of error summary metrics, with each group comprised of one measure each based on the components of location error: ΔH, ΔH_x, and ΔH_y. The first group consisted of simple averages per test of location error. For the second, I calculated test bias as the distance between the true PTT location and the average Argos location (Fig. 2b, p. 30). Finally, I calculated test precision as the average of the distances between each individual Argos location and the average Argos location (Fig. 2c, p. 30). I also calculated the location acquisition rate (number of locations per day) for each static test. Because wildlife studies often use only LC 1-3 locations (Tarroux et al. 2010, Hoenner et al. 2012), and my initial examination of the distribution of LC A location error magnitude was similar to that for 1, I also summarized location errors for each test using only LCs A and 1-3 (LC A123).

I used ANOVA (Zar 2010) to compare all error summary metrics and location acquisition rates between summer and winter for those static test sites that I sampled in both seasons. Because all resulting F values were non-significant ($P >> 0.05$), I used only data from the summer static tests for all subsequent analyses. To model the effects of the topographic and vegetative variables (Table 5, p. 26) on the error summary metrics, I used a forward stepwise regression approach weighted by sample size (number of Argos locations per test), testing quadratic terms and interactions if main effects were significant, until no further terms were significant ($P \leq 0.05$ to include). I log-transformed all error terms to meet assumptions of normality and heteroscedasticity (Zar 2010). For average location error, I first regressed environmental variables on ΔH. Because previous marine and terrestrial tests have demonstrated that latitudinal and longitudinal errors vary independently (Keating et al. 1991, Soutullo et al. 2007, Costa et al. 2010), I also regressed ΔH_x and ΔH_y on those variables that were significant for ΔH. If a variable had both remotely-sensed and empirical estimates (e.g., visible sky), I included both variables during model selection but preferentially selected remotely-sensed over field-measured variables if both were significant to allow for later modeling of error metrics throughout the study area (Sager-Fradkin et al. 2007).

For the antenna angle tests, I used ANOVA and Tukey's HSD (Zar 2010) to test for differences in log-transformed ΔH and location acquisition rates between angle categories (i.e., 0°, 45°, 90°, 135°, and 180°). I fit a generalized linear model (family=poisson, link=log) to test for different proportions of LCs by angle category. To test for the effect of snow burial on location error, I used ANOVA and Tukey's HSD test to determine if ΔH varied by burial depth (depths = 50 cm above snow, burial at 61, 122, 183, and 244 cm).

Comparing Static to Dynamic Tests

To examine the effect of animal movements on Argos location quality, I compared static and dynamic location error distributions, location acquisition by satellite pass, and location class quality by satellite pass. Because the distribution of ΔH was non-normal, I used Wilcoxon's rank sum test (Zar 2010) to compare distribution of ΔH by location class between the static and dynamic tests. To compare static and dynamic location acquisition, I first recorded the times of individual Argos locations by PTT/satellite combination. Because each satellite is visible from a point on the Earth for about 10 minutes (CLS-America, 2011), I assumed that any locations calculated by a single satellite within 10 minutes of each other were from the same satellite pass. For each satellite pass, I assumed that the satellite was visible to all operating PTTs and so locations should be acquired for all operating PTTs. I assigned a 1 to those PTTs that acquired a location and 0 to those that did not. I used the Wilcoxon two-sample signed rank procedure (Zar 2010) for H_0: $\mu=0$ to test for differences in location acquisition between the static and dynamic tests. I used the same procedure to compare location class quality by satellite pass, assigning a 1 to the test with the more accurate location class (accuracy of LC B<A<1<2<3; LCs 0 and Z excluded from analysis), 0 for ties, and excluding those satellite passes where there were multiple static PTTs with location classes both better and worse than the dynamic PTT (n=2).

For all statistical tests, I used R version 2.15.0 (R Development Core Team, 2012) and $\alpha=0.05$ to reject the null hypothesis.

Results

For Argos locations obtained during static tests (n=1298), 75% were in location classes 1-3. Argos defines LC Z locations as invalid, so I removed 1 LC Z location from further analyses. For those locations calculated using ≥4 signals (LC 1-3), 28-90% of location class assignments were accurate (Table 6). That is, ΔH fell within the accuracy estimates for that location class. For locations classes 3, 2, and 1, the upper error estimate for the location class was exceeded by 40, 42, and 19% of locations within that location class, respectively. For those locations calculated using <4 signals, 81% of A and 75% of B locations had ΔH <1500 m. Location errors were concentrated in the latitudinal direction, with the greatest concentration of error to the west-southwest (Fig. 3). Within all Argos location classes, the distribution of ΔH was right-skewed. For LCs 1-3, ΔH at the 68th percentile was no more than 115 m greater than the upper bound for the location class (Table 7), and distribution of ΔH within LC A was similar to that of LC 1. Argos-assigned error radii and error ellipses were spatially unreliable as estimates of the true PTT location, overall and by LC, with the highest reliability for both error radii and ellipses in LC B (62% and 45%, respectively) and the lowest in LC 0 (38% and 0%, respectively). Error radius, both the semi-minor and semi-major ellipse axes, and GDOP were all significant in preliminary univariate analyses, but the best multiple regression model for log-transformed ΔH included only log-transformed error radius ($P<0.001$) with an adjusted R^2 of 0.49 (Fig. 4) and residuals demonstrating good model fit for all values.

Models for ΔH based on environmental conditions varied (Tables 8 and 9). The models of ΔH, ΔH_x, and ΔH_y for all location classes were composed of identical topographic variables (slope and vector ruggedness). For both variables, an increase in the value resulted in decreased predictions of ΔH, ΔH_x, and ΔH_y. The adjusted R^2 values for all models were similar (0.07-0.09). For ΔH for LCs A123 canopy closure and elevation became significant, and vector ruggedness became non-significant. The predicted values of ΔH, ΔH_x, and ΔH_y increased with increasing canopy closure and decreasing elevation and slope (in degrees). The adjusted R^2 values for the LCs A123 models were similar to those for the all location class models.

Table 6. Percentage of Argos-assigned locations classes (LC) by actual LC for static test locations. Actual LC was assigned using calculated location error (ΔH) and the error range Argos assigns to each LC. Because Argos assigns no upper limits for LCs B, A, and 0, any location with error > 1500 m was classified as LC BA0.

	Actual LC				
Argos LC	BA0 (>1500 m)	1 (500-1500 m)	2 (250-500 m)	3 (≤250 m)	n
B	25.2	23.8	24.8	26.2	202
A	18.9	31.1	23.3	26.7	90
0	89.7	10.3	0	0	29
1	18.8	55.1	15.9	10.1	138
2	5.3	36.5	28.2	30.1	266
3	0.3	10.3	29.5	59.8	572

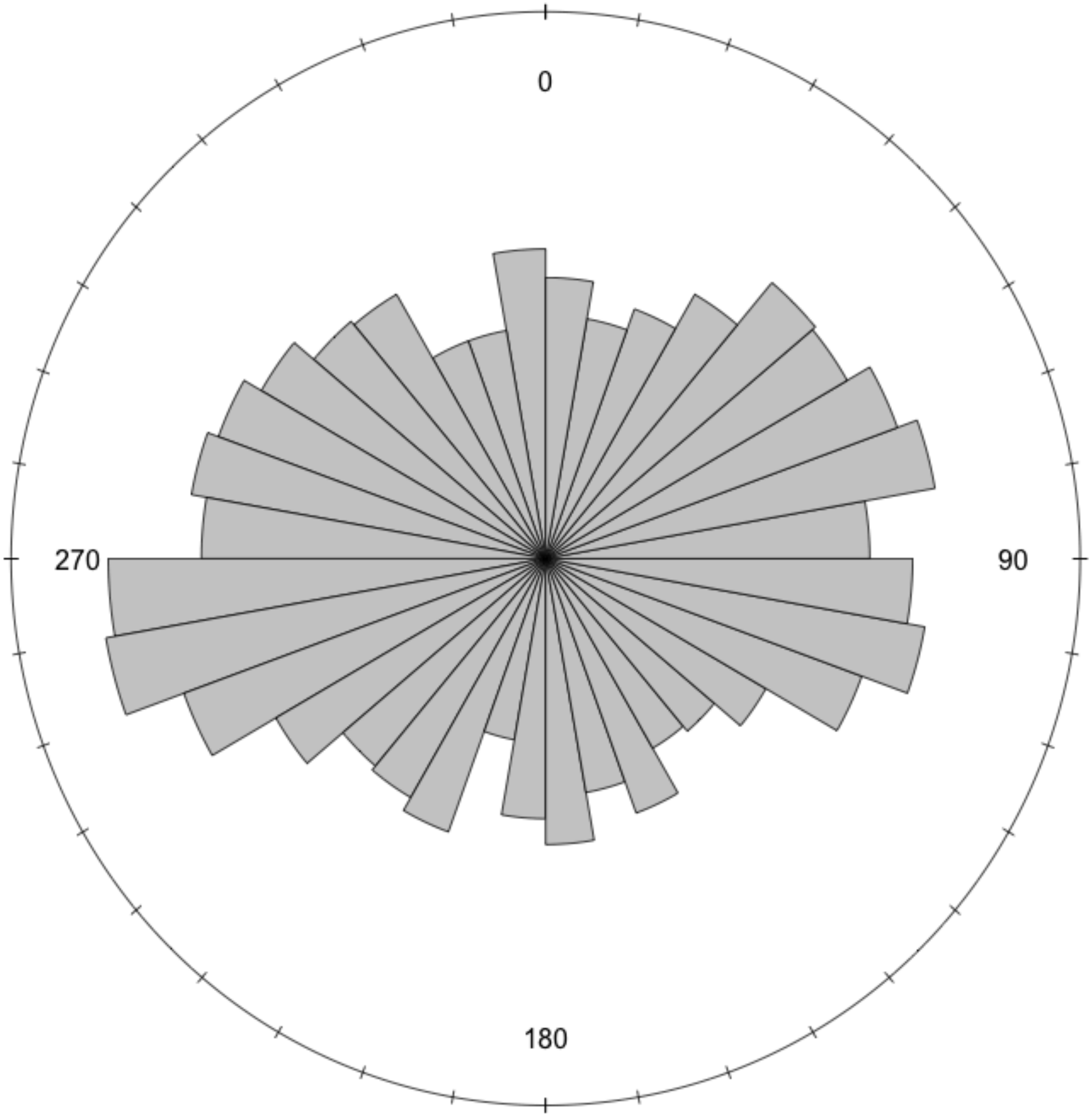

Figure 3. Circular histogram of error azimuth (degrees) for static tests. Location error was concentrated longitudinally, and was more likely to be in a westerly than an easterly direction.

Table 7. Magnitude of location error (ΔH) and reliability of Argos-assigned error ellipse and radius data for all static test locations. Upper LC error bound refers to the maximum estimated error for that LC assigned by Argos.

				ΔH statistics				ΔH percentiles				
LC	n	p(n)	upper LC error bound	range	mean	SD	median	68th	90th	95th	p(error radius≥ ΔH)	p(test site in error ellipse)
B	202	0.16	NA	41 - 61826	3721	10231	488	995	7937	18258	0.62	0.45
A	90	0.07	NA	10 - 12124	1161	2085	500	887	2402	5113	0.53	0.31
0	29	0.02	NA	960 - 28745	5798	6025	3842	6092	10587	12982	0.38	0.00
1	138	0.11	1500	59 - 7576	1184	1232	810	1173	2094	3478	0.45	0.23
2	266	0.21	500	8 - 5701	576	621	385	615	1189	1458	0.40	0.20
3	572	0.44	250	4 - 2217	258	224	198	292	503	642	0.45	0.28

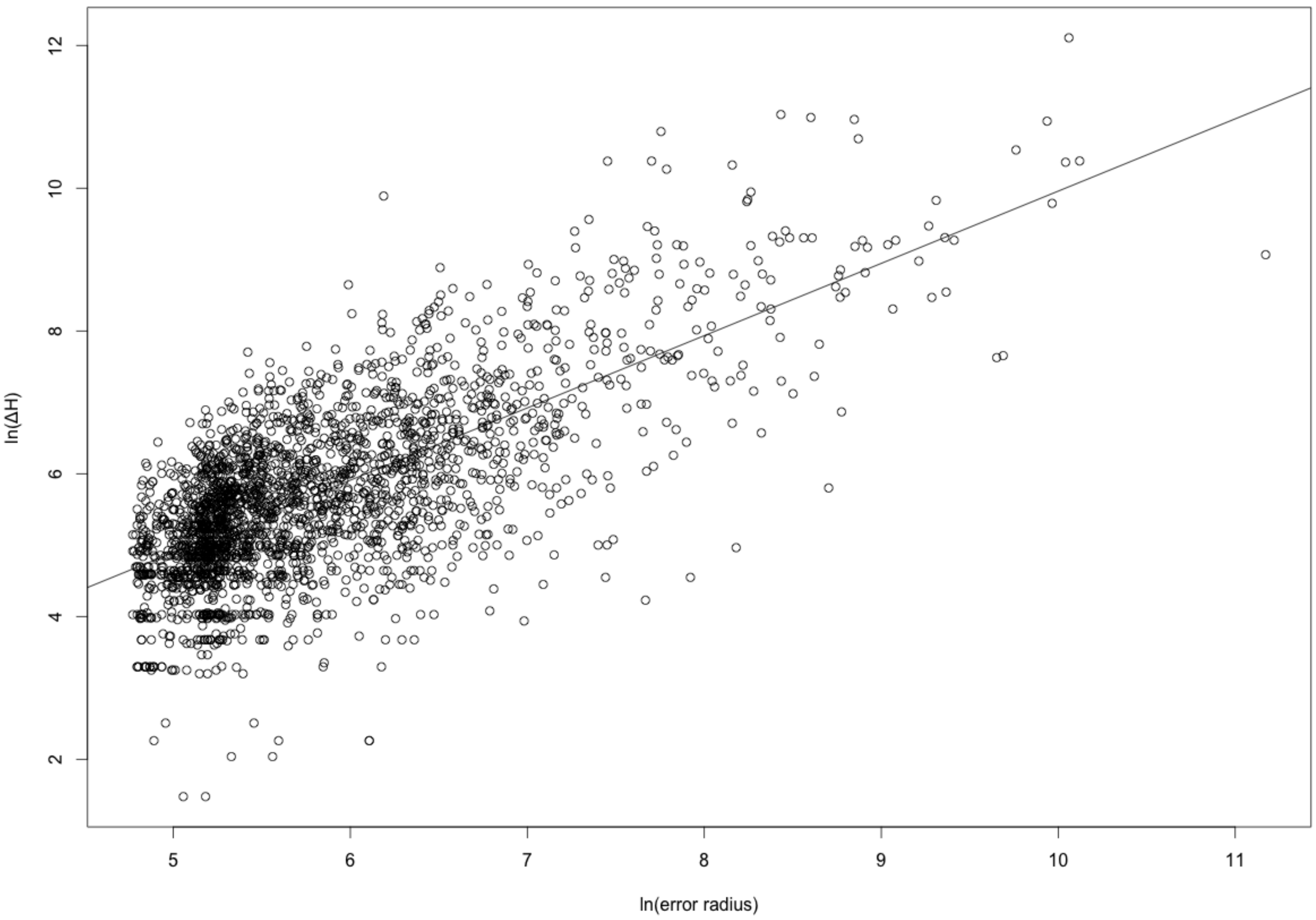

Figure 4. Relationship between log-transformed ΔH and log-transformed error radius. The regression line is in black (ln(ΔH)= -0.17 + 1.01(ln(error radius)), and R^2 for the model was 0.49.

Table 8. Best supported models for each error term for all LCs and LCs A and 1-3 (LC A123). For the categorical aspect variables, the category is indicated by “.E” or “.N” (e.g. ASPT.N). Those variables that were obtained from remote sensing data through GIS analysis are followed by ”_R”, and field-based empirical estimates are followed by “_F”. Sample sizes are smaller for the bias terms because there was 1 test site with only one location (2 for LC A123), so bias could not be calculated.

All LCs	n	model parameters	adjusted R^2
ΔH	140	- SLOP_R - VRM_R	0.09
ΔH_x	140	- SLOP_R - VRM_R	0.08
ΔH_y	140	- SLOP_R - VRM_R	0.07
precision	139	- SLOP_R - VRM_R	0.07
precision_x	139	- SLOP_R - VRM_R	0.06
precision_y	139	- SLOP_R - VRM_R	0.05
bias	139	- SLOP_R - VRM_R - VALY.N_R - ASPT.N_F	0.16
bias_x	139	- SLOP_R - VRM_R - VALY.N_R - ASPT.N_F	0.14
bias_y	139	- SLOP_R - VRM_R	0.15
locations per day	140	- BASL_F + SKY_R + ELVERR_R + SLOP_R	0.20
LC A123			
ΔH	140	+ CNPY_F + SLOP_R – SLOP_R^2 – ELEV_R	0.12
ΔH_x	140	+ CNPY_F + SLOP_R – SLOP_R^2	0.08
ΔH_y	140	+ CNPY_F – SLOP_R – ELEV_R	0.10
precision	138	- SLOP_R - VRM_R	0.08
precision_x	138	- SLOP_R - VRM_R	0.06
precision_y	138	- SLOP_R - VRM_R	0.06
bias	138	- VALY.N_R – SLOP_R – VRM_R	0.12
bias_x	138	- VALY.N_R – SLOP_R	0.15
bias_y	138	– SLOP_R	0.04
locations per day	140	- BASL_F + SKY_R + SLOP_R + ELVERR_R	0.24

Table 9. Coefficients for location error models. Models were constructed for error for all location classes (LC) combined, and location classes A and 1-3 (LC A123).

	ΔH			precision			bias			locations per day
All LCs	overall	x	y	overall	x	y	overall	x	y	
Intercept	9.18	9.03	7.98	9.3343	9.1248	7.9218	11.2923	11.0128	9.5562	-9.2009
ELVDIFF_R										0.0169
SKY_R										0.5138
SLOP_R	-0.04	-0.04	-0.03	-0.0375	-0.0383	-0.0369	-0.0672	-0.0700	-0.0699	0.1918
VRM_R	-2.55	-2.68	-2.08	-2.6526	-2.7431	-1.9267	-4.7278	-4.6114	-4.5189	
VALY_R(N)							-0.7960	-1.0239		
ASPT_F(N)							-0.5159	-0.6426		
BASL_F										-0.3689
LC A123										
Intercept	6.0038	5.3364	5.5813	8.9706	8.6794	7.6049	7.8469	6.3556	4.7582	-31.2885
ELVDIFF_R										0.0180
SKY_R										0.6822
SLOP_R	0.0309	0.0426	-0.0118	-0.0361	-0.0362	-0.0367	-0.0375	-0.0572	-0.0317	0.2653
SLOP_R^2	-0.0010	-0.0013								
VRM_R				-2.4603	-2.4549	-1.7900	-2.1305			
VALY_R(E)							-0.5888	-1.2986		
ELEV_R	-0.0003		-0.0003							
BASL_F										-0.3320
CNPY_F	0.8165	0.6167	0.7998							

The best-supported models for the all location classes precision terms (Tables 8 and 9, pp. 39-40) were identical to those for the corresponding ΔH terms. Increasing slope and vector ruggedness resulted in improved precision (lower predicted values). The adjusted R^2 values were similar between models (0.05-0.07). Unlike the pattern seen for ΔH models for LCs A123, the precision models for LCs A123 were identical to the corresponding precision models for all location classes (and ΔH models for all location classes). The adjusted R^2 values for LCs A123 were similar to those for all location classes.

For the bias terms for all location classes, the best-supported models (Tables 8 and 9, pp. 39-40) included slope and vector ruggedness, but also included an additional adjustment for north valley aspect and north site aspect for both bias and bias_x. All variables impacted bias in the same direction, with a decrease in the model variables resulting in an increase in predicted bias. The adjusted R^2 values (0.14-0.16) for the bias terms were larger than for either the ΔH terms or the precision terms (0.05-0.09). For LCs A123, the direction of the effect for all variables remained the same, but the order of entry into the model changed, aspect became non-significant, and vector ruggedness was significant only for the overall bias model. The adjusted R^2 values were similar for bias and bias_x (0.12 and 0.15), but the adjusted R^2 for bias_y was only 0.04.

The models for acquisition rate (locations per day) for all location classes and LCs A123 contained an identical set of variables, though the order of entry into the model differed. The adjusted R^2 values were similar (0.20 and 0.24, respectively) and higher than those for any of the error term models. These models included only 1 variable that was common to all the error term models (slope), and included 3 new variables, basal area, visible sky, and elevation error, that were not significant in any of the error models. For both location rate models, predicted acquisition rate increased with decreasing basal area and increasing visible sky, elevation error, and slope.

Neither of the tests for the influence of antenna angle on location quality showed a significant effect (Table 10). Antenna angle had no influence on ΔH, and the best model for interaction between antenna angle and location class count was total independence (no interaction). The ANOVA to test for differences in ΔH by depth for the snow-burial test yielded a significant F-statistic. The subsequent Tukey's HSD test indicated that ΔH for collars buried up to 183 cm was not significantly different from that of the collar above the snow (average=309 m), but that the observed ΔH for the collar buried at 244 cm (average=925 m) was statistically greater.

Overall, PTTs in static tests outperformed PTTs in dynamic tests (Tables 10 and 11). For concurrent location acquisition, a Wilcoxon two-sample signed-rank test yielded a significant V-statistic, indicating that there were significantly more successful locations for the static tests (94%) than for the dynamic tests (45%). Similarly, a Wilcoxon two-sample signed-rank test for concurrent location quality yielded a significant V-statistic, indicating that static locations were assigned a higher quality location class more frequently than concurrent dynamic locations. Of 96 concurrent location pairs, the dynamic location class was of higher quality in 7 cases, the static in 85, and they were equal in 4 cases. Wilcoxon's rank sum test for equivalent distributions of ΔH by location class indicated that distributions were the same for both tests for all location classes except B, though it should be noted that the W-statistic was almost significant for LC 2 (*P*=0.056). For both LCs B and 2, the sample mean of the dynamic tests was greater than that for the static tests. Results for LCs 0 and 3 were based on very few locations for the dynamic tests (*n*=5 and 2 respectively).

Table 10. Summary of results for angle, snow-burial, and static/dynamic comparison tests. For all tests, α-level was 0.05.

Variable	Test statistic	*p*	Conclusion
Antenna angle			
on ΔH	$F_{4,16}$=0.70	0.60	No effect of antenna angle on ΔH.
interaction with PTT on location class count	G_{136}= 133.98	0.53	Location class count independent of PTT and antenna angle.
Snow-burial depth category			
on ΔH	$F_{4,557}$= 5.44	0.0003	Some difference in ΔH by category.
on ΔH by depth	Tukey's HSD	NA	Group ΔH for burial at 0, 61, 122, and 183 cm; ΔH for burial at 244 cm is statistically different.
Concurrent static/dynamic comparison			
location acquisition	2-sided Wilcoxon's V=180	~0	More successful locations in static tests.
location quality	2-sided Wilcoxon's V=329	~0	Higher quality locations in static tests.
distribution of ΔH by location class	2-sided Wilcoxon's W by LC		Distributions of ΔH by LC not significantly different between static and dynamic tests for LCs A and 0-3; significantly different for LC B.
	LC B: 7434	~0	
	LC A: 719	0.69	
	LC 0: 18	0.43	
	LC 1: 826	0.63	
	LC 2: 2273	0.06	
	LC 3: 1835	0.28	

Table 11. Percent locations by location class (LC) for all static and dynamic tests.

LC	static (n=1297)	dynamic (n=97)
B	16	55
A	7	15
0	2	2
1	11	9
2	21	13
3	44	5

Discussion

Effective use of Argos location data for wildlife research applications depends on a comprehensive understanding of the utility of the information Argos provides with each location (i.e., location class, error radius, and error ellipse) and how factors such as season, topography, vegetation, and animal behavior may degrade or bias location quality. My evaluation of the Argos system in mountainous terrain shows an improvement over several previously published tests in both the proportion of locations in the better location classes (1, 2, and 3) and location accuracy in those same location classes. While my results suggest that the error radius provided by Argos for each location may be a useful predictor of the magnitude of location error, neither the error radius nor the error ellipse were accurate spatial predictors of the true PTT location. In this study area, season had no effect on location quality. However, local environmental conditions did influence location quality, with topography having more influence than vegetation. Finally, while the effect of antenna angle on location quality was non-significant, both burial under snow at a depth of 244 cm and deployment on an animal significantly degraded location quality.

The results of my static testing confirm the improvement in Argos location quality demonstrated by Sauder et al. (2012) over previously published evaluations of the system. These are also the first results of static testing under the Kalman filtering algorithm implemented in 2011. Of the 1298 Argos locations I acquired during static tests, 75% were in LCs 1-3, similar to the 77% observed by Sauder et al. (2012), and more than a 3-fold increase over the maximum previously reported for terrestrial tests (24%; Nicholls et al. 2007). The 68th percentile location errors for my static tests were larger than those reported by Sauder et al. (2012) for LCs 1-3, but much smaller than those previously reported by Nicholls et al. (2007) and Keating et al. (1991), especially for LCs 2 and 3. My 68th percentile errors were also close to Argos' location class accuracy estimates for LCs 1-3. For example, the 68th percentile location error for LC 3 was 292 m, a difference of 52 m from Argos' upper accuracy estimate of 250 m. Argos provides no location error estimates for LC B or A, but previous terrestrial evaluations of the Argos system have reported 68th percentile location errors ranging from 6.8-24 km (Britten et al. 1999, Nicholls et al. 2007, Soutullo et al. 2007). In contrast, my static tests resulted in a distribution of location error for LC A similar to that of LC 1. LC A had a smaller mean, median, and 68th percentile location error than that of LC 1, though overall location error variability for LC A was greater and the distribution more heavily right-skewed, suggesting that LC A locations might be used for any spatial analyses for which LC 1 locations are considered appropriate. For Argos locations obtained for wolverines in this study area for 2008-2011 by the North Cascades Wolverine Study (Aubry et al. 2012), including LC A locations in spatial analyses could result in an 83% increase in the number of usable locations versus using only LCs 1-3 locations (C. Raley, U.S. Forest Service, personal communication). Applications of PTT location data, such as movement and home range analyses, may be sensitive to location error (Hays et al. 2001, Jerde and Visscher 2005, Bradshaw et al. 2007). In these cases, using the 90th or 95th percentile location errors, instead of Argos's location class accuracy estimates, may be more representative of actual variability in location error. For LCs 1-3, my location data had 90th percentile errors that were 40%, 137%, and 101% greater, respectively, than Argos's upper location class error estimates.

This study is the first to report on the utility of the error radius and error ellipse information Argos provides for each location. Because the error radius and error ellipse provide a discrete description of the estimated accuracy of each location, they could be extremely valuable when analyzing animal location data. However, my static tests revealed that the error radius and error ellipse did not serve as a reliable estimate of the true PTT location - only 47% of error radii and 28% of error ellipses contained the true PTT location. Although the raw error radius did not prove a reliable estimate of location error, I did find a strong relationship between error radius and overall ΔH (R^2=0.49). For those locations assigned to LCs with no accuracy estimates (0, A, and B), using the error radius as a filter to remove those locations predicted to have large errors could greatly increase the number of locations used in spatial analyses.

Keating et al. (1991) reported that PTTs deployed on a mountaintop out-performed those deployed in a valley in terms of location acquisition and accuracy, and Sauder et al. (2012) tested for the effect of canopy cover and topographic obstruction and found both affected location quality. However, there have been no published studies on how a wide range of continuous environmental variables may affect Argos system performance. There have, however, been multiple tests of GPS collars in highly variable terrain, and I expected the environmental variables that affect GPS location quality to similarly affect location quality for my static tests. Hansen and Riggs (2008) reported an R^2 value of 0.68 for GPS location error modeled on canopy cover. The R^2 values (0.07-0.12) associated with the Sauder et al. (2012) models (0.06) and my models for the effects of environmental variables on ΔH (Tables 8 and 9, pp. 39-40) are much lower than those reported by Hansen and Riggs (2008), suggesting that PTT location accuracy is more robust to the influences of vegetative and topographical variation than GPS collars in a similar environment. For location acquisition rates, the R^2 values (0.20 and 0.24) for models in this study are similar to Wells et al.'s (2011) R^2 of 0.20 for their model of GPS location acquisition based on aspect and vegetative cover, but much higher than those reported by Sauder et al. (2012; R^2=0.01).

With the notable exception of the model of ΔH for LCs A123, all models of location error (ΔH, bias, and precision) were either completely or primarily composed of topographical variables. Due to the steep elevation gradient in the study area, I had expected elevation error, visible sky, and aspect to be a component of all of the models. However, topographic variability (as vector ruggedness) and slope were the primary components of almost all the models, with an increase in either corresponding to a decrease in the predicted value of the error term, and thus more accurate locations. For the bias and bias_x models, a north-facing site or valley aspect also decreased the predicted value of the error term. The exclusion of visible sky and elevation error, 2 of the variables I expected to be included in the models, may be due to vector ruggedness more completely capturing terrain variability. I found it counterintuitive that increasing slope and vector ruggedness actually decreased the predicted values for all error terms, but this effect was also observed by Sauder et al. (2012). Thus, it may be that those PTTs situated in highly variable, steep terrain had a limited view of the sky, thus limiting the opportunity for poor quality locations that might be obtained from satellites low on the horizon.

The models of ΔH for LCs A123 differed from all the others, with canopy closure (which was not included in any of the other models) being the most significant variable. The finding that canopy closure appears to increase error for situations where at least 3 signals can be transmitted to a satellite suggests that canopy closure degrades signal quality but does not block signal transmission entirely. Perhaps for the all LCs models, terrain variability (as vector ruggedness) influenced ΔH by blocking PTT signals, resulting in an increase in the proportion of LC B locations (that only require 1 signal) and, thus, more variable location error.

Vegetation (as tree basal area) and visible sky were the primary descriptors of location acquisition rates, with elevation difference and slope also contributing. Although Sauder et al.

(2012) tested for the effect of canopy closure on location acquisition, they did not test for the effect of basal area, which may be one reason that the R^2 value for my models of location acquisition (0.20 and 0.24) are higher than the value they reported (0.01). Both tree basal area and the percent of visible sky represent measures of physical obstructions that may block signal transmission between a PTT and a satellite, and the coefficients for both bear this out, with increasing basal area negatively impacting and increasing visible sky positively impacting location acquisition. Because basal area was the most significant variable in the model, it is likely that the presence of obstructions such as tree trunks or boulders in close proximity to the PTT may block signal transmission more than distant topographical features. If this is true, it could lead to bias in Argos location acquisition rates for species that spend part of their time in dense forest containing large trees or rocky terrain.

Though my models did explain a portion of the variation for each measure of location quality, the associated adjusted-R^2 values (all <0.25) suggest additional sources of variation not included in the modeling process. Specifically, because Argos locations are calculated using signal data received by a single satellite, it may be that satellite position relative to the PTT is responsible for a portion of the variation in location quality. For example, a satellite low on the horizon is only in sight of the PTT for a limited time, resulting in very few signals being available for location calculation, resulting in reduced location quality.

Although the results of the static tests are informative, Argos PTTs used for wildlife research are deployed on animals whose behavior may have additional impacts on location quality. For the static tests, I did not vary collar height or antenna orientation, did not place collars in dense vegetation or right under large trees, and each collar stayed in the same location throughout the test. In contrast, a collared animal will move at variable speeds, may climb a tree or rest under a rock, will vary antenna orientation while moving, foraging, resting, etc., and may permanently alter antenna orientation through damage or if the collar rotates around the animal's neck.

Argos location quality in my tests was robust to changes in antenna orientation under conditions of zero topographic or vegetative obstruction. These results are different from those observed in similar tests using GPS collars, which have demonstrated that antenna angles >90° from vertical result in significant decreases in collar performance (D'Eon et al. 2005), though for some collars this effect was only observable under a forest canopy (Jiang et al. 2007). Therefore, PTT performance may be more robust than GPS performance to certain effects of animal behavior, such as a collared animal's head position while feeding or sleeping. My tests did not account for other conditions associated with a non-vertical antenna angle that could result in reduced location quality, such as an animal lying on the antenna or feeding in dense vegetation.

Another aspect of animal behavior that may influence location quality is the use of specific sites and structures for denning. Specifically, all wolverine dens in North America have been found under snowpack (Magoun et al. 1998, Copeland et al. 2010), and the 2 dens that have been located in the North Cascades were both associated with structural elements (logs and boulders; Aubry et al. 2012). The results of my snow-burial tests demonstrated no significant effect of burial under snow up to a depth of 183 cm on ΔH when compared to a control collar above the snow. However, burial at a depth of 244 cm, which corresponds to the minimum recorded depth for wolverine dens in the North Cascades, resulted in a significant increase in ΔH. Although I was unable to include potential den structures in my tests, the results of my static tests suggest that addition of solid objects to the den structure, such as logs and boulders, would degrade acquisition rates and possibly location accuracy. Though a decrease in the number and accuracy of locations is never desirable, for species that den in snow caves or other structures that are known to degrade location quality, any abrupt decrease in location quality for an adult female could be used as an indicator of denning activity.

There have been 2 terrestrial tests of the Argos system using PTTs deployed on animals. Britten et al. (1999) reported location accuracy for PTTs deployed on caged rock doves (*Columba livia*) in a suburban backyard, and Soutullo et al. (2007) reported location accuracy for PTTs equipped with a GPS receiver deployed on golden (*Aquila chrysaetos*) and Bonelli's eagles (*Aquila fasciata*). However, neither compared the dynamic results to static results to determine the efficacy of static testing. In contrast, my dynamic tests (using a free-roaming dog) were conducted concurrently with static tests in the immediate vicinity and provide new insights into how deployment on an animal may affect location quality. In the concurrent tests, static PTTs consistently out-performed dynamic PTTs in terms of location quantity and location-class quality. About half as many locations were acquired for dynamic test PTTs compared to concurrently-operating static PTTs; in addition, concurrent location quality was almost always lower for dynamic PTTs. Thus, results from static tests represent a best-case scenario, and subsequent deployments on study animals should be expected to result in larger location errors and reduced sample sizes.

Prior to data analysis, I suspected that reduction in location quality for dynamic PTTs could be due, in part, to changes in antenna angle as has been demonstrated for GPS collars (D'Eon et al. 2005, Jiang et al. 2007), but this link is unlikely as antenna orientation was non-significant in the angle tests. Another potential cause of the reduction in location quality could be the rate of motion of the dynamic PTT (Nicholls et al. 2007), given that a change in location of the PTT during the interval of signal transmission (up to 10 minutes) could confound location calculation. However, my dynamic tests suggest that there were factors in addition to motion that affected location quality. The locations missed for the dynamic PTT occurred sporadically throughout the concurrent tests. In all but 1 instance, no more than 2 consecutive locations were missed for the dynamic PTT. The only exception occurred when the dog wearing the PTT was asleep for about 3 hr in one location within 200 m of a concurrent static test site. During that time there were 3 consecutive locations for the static PTT, but none for the PTT on the dog. Because the dog was stationary and 3 consecutive locations were missed, it appears that some other factor in addition to movement may contribute to missed locations, such as an animal lying on the antenna and blocking signal transmission.

Dynamic tests provided information beyond that available from the static tests as to how the Kalman algorithm might affect the accuracy of LC B locations. In the static tests, the error distribution for LC B indicated that these locations could be useful for applications at scales where error up to 8 km is acceptable at the 90th percentile. However, visual examination of a small subset of dynamic tracks indicated that LC B locations were often very close to the previous Argos location, regardless of the actual PTT location (Fig. 5). One potential conclusion that could be drawn from observing multiple consecutive LC B locations in a small area is that the PTT may actually be in that area. However, because the Kalman algorithm uses a random walk model to predict the current location based on information from the previous one (CLS-Argos 2011), if the location immediately prior to 1 or more LC B locations was inaccurate, it is likely that those subsequent LC B locations will also be inaccurate and, thus, uninformative. This characteristic of LC B locations under the Kalman algorithm may have also affected static test results if it resulted in a “zeroing-in” effect for a static PTT, reducing location error for LC B locations. Future dynamic tests of the Argos system should be conducted over longer periods

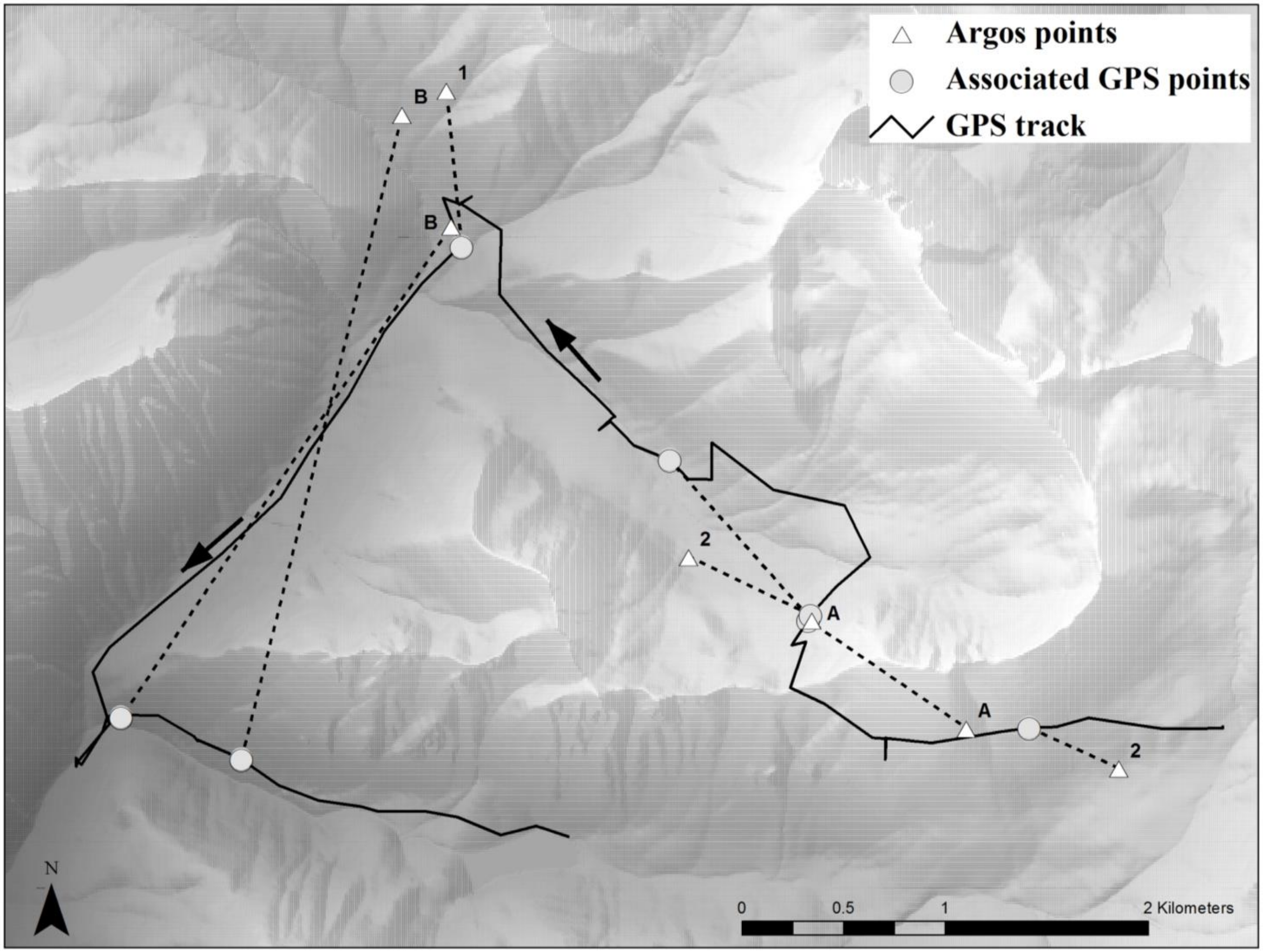

Figure 5. Example of a dynamic test using a domestic dog wearing an Argos-compatible PTT and GPS-data logger. Each Argos point is labeled with its associated location class. The points of particular interest are the B locations at the northern edge of the track. Though the dog continued to move away from the location class 1 location (direction of travel indicated by arrows), both subsequent location class B locations remained near the previous location.

(>>3 hr) to provide more information about how LC B locations correspond to previous locations, and whether 1-signal LC B locations differ from 2-signal locations in their spatial relationship to the previous location.

I was unable to record local environmental conditions at each point where an Argos location was or should have been acquired during the dynamic tests. Yet, my comparisons of concurrent static and dynamic tests conclusively demonstrate that some aspect of the collar being deployed on a free-roaming animal resulted in a decrease in both location acquisition and quality. Furthermore, these results indicate that static tests are not sufficient to determine location acquisition rates in an area, and may be misleading when modeling location quality because static tests underestimate location error and acquisition rates. Additional investigations of the source of the reduction in location quality and quantity for dynamic PTTs would be useful to determine whether certain species or behaviors are less likely to yield reliable location data. Future dynamic tests could benefit from a design similar to mine, using concurrently deployed static collars to determine times of potential location acquisition and a GPS-logger to track PTT locations. Once a dynamic track has been completed and potential location acquisition times determined, the time-stamped coordinates from the GPS-logger could be used to return to the actual PTT location that corresponds to each potential location acquisition time in order to measure the associated environmental conditions. Furthermore, constant monitoring of animal activity during the dynamic test would facilitate a more thorough examination of the potential effects of animal behaviors on location quality (e.g., an animal-mounted digital video camera to continuously record activity and head position that could be reviewed later),

Results of the static tests confirm improvement in location accuracy, as well as an increase in the relative quantity of locations in LCs 1-3, observed by Sauder et al. (2012) over those of tests published prior to 2009. It is possible that study area characteristics may have contributed to this improvement. However, due to the rugged terrain and variable vegetative cover, I believe it is more likely a result of improved PTT technology and implementation of the Kalman filtering algorithm. Wolverine PTT location data collected within my study area from 2008 to 2011 by the North Cascades Wolverine Study (Aubry et al. 2012) demonstrate the improvement resulting from implementation of the Kalman filtering algorithm. Specifically, application of the Kalman filtering algorithm to recalculate location data that were originally processed using the Least Squares algorithm resulted in an increase in the number of locations by 38% for LCs 1-3 and 45% for LC A (C. Raley, U.S. Forest Service, personal communication).

Although environmental characteristics affected both location accuracy and acquisition rates, most of the variability in location quality could not be explained by the measured variables. Accordingly, this study suggests that Argos location quality is largely robust to the environmental characteristics tested; thus, variability in those characteristics should not lead to large differences in location quality in other areas. The improvements in static location quality most likely translate into improvements in dynamic location quality, but additional and more focused dynamic testing will be required to better understand the impacts of environment, animal movement, and species-specific behavior on location quality.

Management Implications

The Argos system enables wildlife researchers to collect large amounts of location data without the need for field personnel (VHF systems) or the need to recapture or get close to the collared animal to download location data (GPS systems). However, given the variable (and sometimes large) error seemingly inherent to the Argos system that I demonstrated in my static tests, research questions must be asked at a spatial scale that is appropriate for the location data.

Because the upper error estimates associated with Argos LCs 1-3 are estimates of 68th percentile error, using a larger error estimate in spatial analyses may be more appropriate. In addition, researchers can increase sample sizes by using locations in LCs A and B for spatial analyses, using the error radius to remove those locations suspected of having large error. Because only a small portion of the variability in location error was explained by environmental characteristics in my static tests, extensive static testing need not be carried out for each new study area, though I would recommend testing of different PTT models before deployment to evaluate variation in location quality due to PTT design. Researchers with the resources to test Argos-compatible PTTs more extensively prior to deployment should focus on dynamic testing, as static tests will be insufficient to adequately characterize location accuracy and rates of location acquisition. Dynamic tests should mimic the suspected movement patterns and behaviors of the study species as closely as possible. Furthermore, dynamic testing should also be used to determine whether LC B locations are too biased by previous and potentially inaccurate locations to be of value, especially for highly mobile species. Argos location accuracy will most likely continue to improve, but conducting static testing every few years should be sufficient to obtain 90th or 95th percentile error for all location classes regardless of geographic location.

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