Biologists have been attaching transmitters to wild mammals for nearly 40 years. Frank and John Craighead first used the radiotransmitter collar and a tuned directional receiver and antenna (Craighead and Craighead 1963, Craighead et al. 1963) in 1961 to follow 2 grizzly bears to their winter dens. Since that time, we have witnessed numerous improvements, innovations, and technological advancements in animal tracking systems. Today, the most common technologies employ conventional VHF systems (Samuel and Fuller 1996), although satellite tracking systems, including Argos (Fancy et al. 1988, Harris et al. 1990) and the global positioning system (Rodgers et al. 1996), are becoming more commonplace.

Each tracking system has advantages and problems. Conventional VHF transmitters are relatively inexpensive (US $200–300 [1997]/collar) but have limited range. Obtaining locational data (fixes) can be problematic for species that occupy vast areas, travel great distances, or live in rugged or remote areas. Locating animals on ground or via aircraft is constrained by personnel, logistics, economics, weather, and often daylight. Data collection biased by weather or time of day can produce incorrect estimates of range use or resource selection (White and Garrott 1990, Arthur and Schwartz This Volume).

Satellite-based systems were developed in the late-1970s to overcome some of the limitations associated with VHF transmitters (Fancy et al. 1988). The most common system is the Argos Data Collection and Location System (Fancy et al. 1988, Harris et al. 1990), hereafter referred to as Argos, developed to collect environmental data. Polar-orbiting Trios-N satellites receive signals from platform transmitter terminals (PTTs) during 6-28 overpasses/day, depending upon latitude. A network of satellite tracking stations and communication links transfers satellite data to processing centers for distribution to users (Argos 1984). A transmitter’s location is estimated from the Doppler shift in its carrier frequency at successive intervals during an orbital pass.

Argos satellite tracking provides a means to monitor movements of large wilderness species that travel great distances (Harris et al. 1990), including polar bears (Ursus maritimus), caribou (Rangifer tarandus), Pacific walrus (Odobenus rosmarus), and gray wolf (Canis lupus). This system is more expensive than conventional VHF telemetry (US $2,000–3,000 [1997]/collar), but has been cost effective for some wildlife applications (Craighead and Craighead 1987). The system eliminates the need for ground and aircraft tracking and transmits the data to a fixed base station (Fancy et al. 1988, Harris et al. 1990). The units have a high power demand (about

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**Key words:** animal tracking, Argos, brown bears, global positioning system, GPS, radiotelemetry, Ursus arctos

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**Abstract:** We tested 30 prototype global positioning system (GPS) radiocollars on brown bears (Ursus arctos) over a 3-year period on the Kenai Peninsula, Alaska. Collars were of 2 design types: GPS units with an Argos (Argos Data collection and Location System) satellite uplink (n = 19) and GPS units where the data were stored on board (n = 10) for retrieval at a later date. All units also contained a conventional VHF (very high frequency) transmitter and weighed 1.7 kg. GPS-Argos units obtained 10–82% of expected GPS fixes, and fix rate declined significantly (P < 0.05) with time after deployment. Argos uplink success (proportion of successful transmissions of stored data) was linearly related to GPS fix rate (r = 0.91, P < 0.001). Store-on-board units obtained significantly more successful fixes when compared with the GPS-Argos units (t = -4.009, P < 0.001). Fix success rate for deployed store-on-board collars ranged from 13–96%; because of the increased number of attempted fixes per day, these collars obtained fixes on 97% of days deployed. Accuracy of the GPS units was less than predicted by the NAVSTAR GPS technology using the course acquisition code. Reduced accuracy was likely a result of the proportion of 2-dimensional versus 3-dimensional fixes obtained, although we could not determine this statistic from recorded data. Increased overstory closure was the only variable measured that partially explained the reduced likelihood of a successful fix. Stem density, stem diameter, and overstory height measured within 3 m of the collar did not affect fix success. GPS fix success rates for collars attached to bears varied more and were lower than fix rates for stationary collars placed in various vegetation types, suggesting that the bear, terrain, and movement all influence both fix and uplink success rate. Application of this new technology to grizzly and brown bear research and comparisons to studies with moose (Alces alces) are discussed.

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(Ursus 11:261–274)
2,000 times that of a VHF transmitter, Fancy et al. 1988),
which can be reduced by a programmed duty cycle. Argos
fixes can have poor accuracy (0.5–1.5 km, Harris et al.
1990) because of the inherent manner in which animal
locations are calculated (White and Garrott 1990).
Corrections in the Service Argos’ algorithms for calculating
locations and assigning fix accuracy have improved data
quality in some cases (±150 m, Keating et al. 1991,
Keating 1994). Most wildlife studies that use satellite
telemetry are concerned with large-scale animal move-
ment patterns, and error of this magnitude is inconse-
quential (Craighead and Craighead 1987). Selection
criteria can be used to remove questionable fixes (Keating
The NAVSTAR Global Positioning System, which was
initiated in 1973 (Wells 1986) and became operational
in 1993 (Rodgers et al. 1996), reverses the role of satel-
lite and receiver. Whereas locations are calculated on
board the satellite in the Argos system, the receiver on
the ground calculates positional fixes in the GPS system.
The U.S. Department of Defense controls the accuracy
of the signals transmitted from satellites in the GPS con-
stellation. For purposes of national security, it introduces
an intentional error, called selective availability (SA), in
the transmitted signal. With SA, GPS technology offers
positional accuracy within 100 m 95% of the time, and
to 300 meters 99% of the time (Wells 1986, Hurn 1989).
However, there are 2 ways to correct for SA. The mili-
tary uses receivers fitted with a coded module that pro-
vides accuracy to 3- to 9- meters. The civilian GPS
community, using the course acquisition (C/A) code, has
developed a differential correction system to overcome
SA. Differential correction is accomplished by using a
base station sited on a known point that continually anal-
yzes the satellite signals and computes an error factor.
This factor is used to correct a GPS receiver’s location
information. Accuracy to 4 m can be achieved with dif-
ferential correction (Moen et al. 1997, Rempel and
Rodgers 1997).
Rodgers et al. (1996) listed 3 possible data storage and
retrieval options for GPS systems: (1) store data within
the collar with retrieval after recapture; (2) store data
and transmit for retrieval by secondary satellite; and (3)
store data and retrieve via a local communication link
(i.e., UHF [ultra high frequency] radio modem). Rempel
et al. (1995), Moen et al. (1996, 1997), Rodgers et al.
(1996), and Rempel and Rodgers (1997) tested a GPS
1000 (Lotek Engineering, Inc., Newmarket, Ontario,
Canada) system that used a command unit and computer
to communicate locally with GPS-equipped collars that
stored data in a non-volatile memory chip. Here, we
discuss the testing and reliability of the 2 others: GPS
collars that transmit data through an Argos satellite and
GPS collars that store data on board and must be re-
trieved to obtain information.

STUDY AREA
The study was conducted on the 23,310-km² Kenai Pen-
insula in south central Alaska between 59–61° N and
148–152° W. It is bounded on the west by Cook Inlet,
east by Prince William Sound, and south by the Gulf of
Alaska. A narrow (17.8 km wide) isthmus of land and
ice connects it to mainland Alaska. The rugged, heavily
glaciated Kenai Mountain Range, which rises to 2,000
m, occupies the eastern two-thirds of the peninsula. The
Kenai lowlands dominate the western third, a glaciated
plain with a relief of 15–100 m that is dotted with nu-
umerous lakes (Spencer and Hakala 1964, Peterson et al.

The Kenai Peninsula lowlands support typical northern
conglomerate forest. The mature forest vegetation on
dry upland sites is a combination of white spruce (Picea
glaucum), paper birch (Betula papyrifera), and quaking
aspen (Populus tremuloides). Black spruce (P. mariana)
dominates poorly drained sites (Lutz 1956, Spencer and
Hakala 1964), and Sitka spruce (Picea sitchensis) oc-
curs in coastal areas. Deciduous tree species represent
successional stages of revegetation after fire. The Kenai
Mountains also support coniferous and mixed hardwood
forest with the altitudinal limit of trees at approximately
500 m (Peterson et al. 1984). Mountain hemlock (Tsuga
tortensiana), mountain alder (Alnus crispa), willow
(Salix spp.), and bluejoint grass (Calamagrostis
canadensis) dominate the transition zone between forest
and alpine tundra. Alpine communities are lichen tun-
dra, dwarf shrub tundra, or some combination of both.
Lichen tundra occurs on bare ridges and mountaintops,
whereas the dwarf shrub tundra occurs below the lichen
zone. The Harding Icefield, a complex of numerous gla-
ciers and snowfields with bare rock and scree slopes,
dominates the Kenai Mountains and represents about
20% of the total land mass of the peninsula.

MATERIALS AND METHODS
Capture and Handling
We located bears initially from fixed-wing aircraft in
areas bears were expected to occur. We immobilized bears
from Bell Jet Ranger, Hughes 500, or Robinson R44 heli-
ocpters using Cap-Chur® darts (Palmer Chemical Equip-
ment Co., Douglasville, Georgia, USA) loaded with a
combination of telellamite and zolazepam (Telazol®, Fort
Dodge Laboratories, Inc., Fort Dodge, Iowa, USA) to deliver a mean dose of 6.5 mg/kg body weight in spring and 9.8 mg/kg during fall. We monitored bears’ vital signs (body temperature, respiration, heart rate), collected morphometric measurements and weight, blood, and a tooth for aging, and ear-tagged each bear following the protocol described by Schwartz and Franzmann (1991). Bears for this study were fitted with a GPS-Argos or GPS store-on-board collar.

Telemetry System

Transmitters tested were first generation GPS-Argos and GPS store-on-board units (Telonics Inc, Mesa, Arizona, USA). As described by Tomkiewicz (1996), the GPS-Argos electronics employed a ST-14 Argos PTT transmitter. Units contained a 6-channel continuous tracking course acquisition code Trimble GPS receiver powered by 3 C-cell batteries. The C/A code has an approximate horizontal positional accuracy of 100 m (95% of fixes within 100 m of true position) for differentially uncorrected data (U.S. Department of Defense 1984). The filter parameters we used were the recommended default settings for the Trimble receivers. Location coordinates were determined using the World Geodetic System 84.

The units also contained a VHF transmitter with an independent power supply. All components were hermetically sealed in a brass canister (10.9 x 6.9 x 5.8 cm) surrounded by a urethane shock buffer and fixed to a collar made from 65-mm wide machine belting. Both the Argos and VHF antennas were completely contained within the collar, but the GPS antenna, encased in transparent, waterproof housing, was on the top of the collar (dorsal surface of the bear) to increase the probability of a clear view of the GPS satellite constellations. The adjustable collar was designed so the GPS antenna was directly above the canister when fit to a bear with a neck circumference of approximately 74 cm. Each unit weighed 1.7 kg.

The GPS-Argos system (Fig. 1) obtains a position location (fix) when the GPS receiver pinpoints its location based on signals from 3 or more satellites. The GPS receiver attempts to obtain a fix at programmed intervals over a 3-minute period. The unit shuts off after receiving a successful fix, or after 3 minutes if unsuccessful, and attempts another fix at the next programmed time. Data are stored on the collar in a non-volatile storage unit. GPS data are transmitted to a low earth-orbiting relay satellite constellation, the NOAA (National
Oceanic and Atmospheric Administration)/Polar Orbiting Satellites carrying the Argos Data Collection System, at programmed intervals. Fixes are incorporated into the Argos data stream and transmitted from the PTT within the collar to the satellite. In this fashion, Argos serves as a data transfer system rather than as a positioning system, though Argos positioning can serve as a backup. A control unit within the collar turns the PTT on or off according to duty cycles programmed to optimize transmission times relative to satellite overpasses and predicted angle of satellites above the horizon (Fancy et al. 1988). When transmitting, the PTT sends 12–32 bytes of data in approximately 540–920-millisecond bursts once every 90 seconds. Signals acquired by the satellite (hereafter referred to as an “uplink”) are processed and stored on board and later transmitted to ground stations (Fancy et al. 1988). Because the PTT transmits data during the entire “on” portion of the duty cycle, it is possible to obtain multiple uplinks of the same information. Researchers obtain data from the Argos Data Processing Center in Landover, Maryland, via computer modem.

The GPS-Argos collars we used employed the Telonics GPS format (T02) for Argos PTTs (Rios 1996). This format supported transmission of up to 32 bytes of compressed GPS data, allowing 5–7 fixes/Argos message depending upon proximal location of fixes. As a consequence, with each new GPS location, the oldest stored fix was no longer transmitted. T02 used an absolute fix and a variable length field for relative fixes (0–6) to minimize message length. Position resolution was to the 0.0001 degree, with error detection incorporated into the data stream via a 6-bit cyclic redundancy check/fix. The absolute fix was also stamped with a Julian day. Details of the GPS-Argos format can be found in Rios (1996).

Collar Deployment and Testing

We tested a prototype GPS-Argos unit in 1995. For this prototype, GPS fixes were attempted at 6-hour intervals. The Argos duty cycle was 8 hours on 12 hours off. With this frequency of GPS fixes and PTT transmissions, the unit was designed to last approximately 5 weeks. We deployed this collar on an adult female brown bear with 2 cubs-of-the-year on 28 August 1995 but removed it on 9 September due to poor Argos uplink performance. The Argos antenna was redesigned and a second prototype was deployed on an adult female on 4 October. This collar was tested 29 days; we removed the collar on 1 November when the bear showed signs of denning.

We tested 10 GPS-Argos collars in 1996. GPS fixes were attempted once every 23 hours. The first fix after initializing the collar occurred at 2300 GMT (Greenwich mean time) and advanced 1 hour each day thereafter. We adjusted the uplink schedule to transmit data in 540–920-millisecond bursts every 60 sec over a 4-hour interval alternating between 54 and 58 hours. The Argos uplink duty cycle was set at 4 hours on (0100–0500 GMT), 58 hours off, 4 hours on (1500–1900 GMT), 54 hours off. With this frequency of transmissions, each unit was designed to last approximately 6 months. We deployed collars on bears between May and July. Of the 10 bears collared, 1 was found dead on 8 November, 1 shed its collar in mid-August, and 1 entered a den before the collar could be removed. We retrieved 7 collars during September–November and sent them back to the manufacturer for refurbishment. The remaining collar was retrieved after den emergence the following spring.

After refurbishing, we tested 9 of the GPS-Argos collars for a second field season in 1997. The first GPS fix after initializing the collar occurred at 2300 GMT. Subsequent fixes were obtained at intervals of 13 hours. The Argos uplink duty cycle was set at 4 hours on, 32 hours off. Based on the previous year’s performance, collars were anticipated to function for approximately 6 months. Of the 9 bears collared, 1 bear lost its collar in mid-July and we lost contact with a second and consequently could not retrieve the collar. We do not know why we were unable to locate this bear, but we suspect the bear was killed illegally or that the collar failed. Collar failure seems less likely because the GPS-Argos system worked independent of the VHF transmitter, and we were unable to contact either, despite intensive aerial searching. It is unlikely that the bear (a female with cubs-of-the-year) moved off the peninsula beyond the extent of our searches.

For the GPS-Argos units, we monitored 2 parameters: (1) the percent of unique Argos uplinks resulting in successful data transmission, and (2) the percent of total possible GPS fixes that we retrieved via the Argos system (hereafter referenced as a “fix success rate”). This fix success rate was a function of both the GPS technology (successful GPS contact with the satellites) and the Argos uplink transmission success rate. We were unable to directly monitor GPS fix rate success because we could not determine if missed GPS fixes were due to poor performance of the GPS unit (missed GPS fixes) or loss of data associated with the limited transmission capabilities of the Argos system (5–7 GPS fix capacity) coupled with missed uplinks.

We compared GPS fix and Argos uplink rates with those of 3 collars deployed on grizzly bears in Yellowstone National Park in 1997. These collars were set to take a GPS fix every 9 hours with an Argos uplink duty cycle of 6 hours on, 42 hours off.
We also tested 2 and 8 (6 new and 2 refurbished) GPS store-on-board collars in 1996 and 1997, respectively. These collars were similar in design to the GPS-Argos collars without the Argos units. Also, each contained a non-volatile memory interface card capable of storing all GPS fixes. These units were programmed to collect GPS fixes at 5.75 hours intervals (4 or 5 fixes/day), and all data were stored on board the collar. These collars were designed to last approximately 6 months. The percent of successful fixes obtained by the store-on-board units directly reflected the functioning of the GPS units (no locations were potentially lost due to failed Argos uplinks). As the GPS receivers in the store-on-board collars were identical to those in the GPS-Argos collars, we assumed that the GPS functioning was similar between the 2 systems.

Of the 29 collars, 8 were deployed on lone bears, 9 on females with cubs of the year, and 12 on females with yearlings. Four of the females classified as alone were accompanied by 2-year-old cubs that dispersed in spring shortly after tagging. Age of collared bears ranged from 3 to 20 (median = 10) years. Eighteen females occupied areas in the Kenai lowlands, 5 used both lowland and mountain habitats, and 6 used only mountain areas. Collars were removed in autumn (10 Sep–21 Nov).

Accuracy and Factors Affecting Fix Rate

We tested accuracy of locations by plotting fixes obtained from 9 stationary collars relative to their true location at 2 sites. We chose sites in flat, open terrain to reduce the effects of vegetation and topography. True locations were determined by using a military GPS unit that determined position using the high precision P-code, which provides centimeter-level accuracy (Rodgers et al. 1996). Accuracy of non-differentially corrected civilian GPS receivers is predicted to be 40 m for about 50% of locations and 100 m for 95% (Hurn 1989). We tested the accuracy of 9 and 4 collars placed at 2 known locations for 39 and 36 days, respectively.

To test for changes in fix rate over time, we used data from 5 collars that were active over the entire season (May–Nov) in 1996. We divided the season into ten 15-day periods and calculated the percent of successful fixes for each collar in each time period. The test was a repeated-measures analysis with 3 independent variables: reproductive class (lone females or females with cubs or yearlings), time, and individual collar. To test for differences in fix success rate, we used PROC MIXED (Littell et al. 1996) with an Arcsine transformation of the square root of $p$, the percent of successful fixes (Ostle and Mensing 1975). Whereas time and reproductive class were treated as fixed variables, collar identity was considered a random variable allowing inference beyond the 5 collars tested. PROC MIXED accommodates both fixed and random variables to fit the best model. We used the following approach: (1) specify the model configuration, (2) select a covariance structure, and (3) fit the model. This process was repeated until model fits had the following covariance structure: (1) compound symmetry, (2) first-order auto-regressive, (3) antedependence, (4) unstructured, or (5) Toeplitz. Akaike's Information Criteria and Schwartz's Bayesian Information Criterion were then used to select the best model (Littell et al. 1996).

**Effects of Vegetative Cover on Fix Rate**

We tested the effects of vegetation on fix and uplink success rate of the GPS-Argos units by positioning a collar in a representative stand in 10 vegetation types and monitoring successful GPS fixes and successful Argos uplinks. The number of attempted fixes in each vegetation type ranged from 12–43 (6–21 days). To reduce the effect of terrain, we selected sites on the Kenai lowlands with topographic relief <100 m. The vegetation types we tested were representative of the major habitats present and included mature white spruce–deciduous, and mixed spruce–deciduous, plus seral stands of regeneration ranging from 5 to 49 years old. We quantified canopy characteristics in each stand by measuring stem density and mean diameter within a 3-m radius of the collar. We defined overstory closure as the proportion of the sky obliterated by tree crowns within a defined angle from a single point (Bunnell et al. 1985:181). We measured overstory closure using a spherical densiometer (Lemmons 1956) with a grid of 24 quarter-inch squares etched on its mirror. On each of these 24 squares we used 4 imaginary equally-spaced dots for a total of 96 point estimates. The number of dots that fell on open spaces in the canopy was tallied, subtracted from 96, and divided by 96 to give the proportion of canopy closure above the GPS antenna.

We used Poisson regression and fitted a general linear model (McCullagh and Nelder 1983) to the natural log of the number of failures as a function of the number of fixes attempted and 4 explanatory variables (quantified canopy characteristics). We set $\alpha$ for all tests at 0.05.
on the collar and redeployed. We tested this redesigned collar for 29 days. The GPS unit successfully obtained 95 of 116 GPS fixes (81.9%) and successfully transmitted these data to the Argos satellite at least once per day (100% success). In addition, we obtained 24 of 29 Argos position fixes.

GPS-Argos collars obtained 500 and 1,045 locations in 1996 and 1997, respectively. Performance of individual collars was extremely variable (Table 1) over the field season; success rates for receiving GPS fixes varied from 11–62% in 1996 and 25–82% in 1997, with an overall mean of 43%.

Uplink success with the Argos satellite was similar to the GPS fix rate, ranging from 13–63% and 30–96% in 1996 and 1997, respectively, with the overall mean of 48% (Table 1). Proportions of successful GPS fixes and successful Argos uplinks were significantly correlated ($P < 0.01, r = 0.91$, Fig. 2). Three GPS-Argos collars deployed on grizzly bears in the Greater Yellowstone Ecosystem (Fig. 2) achieved more successful uplinks than ours, perhaps due to increased uplink time (6 hours versus 4 hours).

Successful fix rate for the GPS store-on-board collars ranged from 50–74% (Table 2, $\bar{x} = 66.7$%). This was significantly higher ($t = -4.009, 27$ df, $P < 0.001$) than the success rate for the GPS-Argos system ($\bar{x} = 43.1\%$).

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Table 1. Success rates for fixes and uplinks for GPS-Argos transmitters deployed on brown bears on the Kenai Peninsula, Alaska, 1996 and 1997. GPS units were programmed to take 1 fix/day in 1996 and 2 fixes/day in 1997.

<table>
<thead>
<tr>
<th>PTT#</th>
<th>Days deployed</th>
<th>Potential fixes (n)</th>
<th>Actual fixes (n)</th>
<th>Fix success (%)</th>
<th>Potential uplinks (n)</th>
<th>Actual uplinks (n)</th>
<th>Uplink success (%)</th>
</tr>
</thead>
<tbody>
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<td>1996</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10911</td>
<td>101</td>
<td>101</td>
<td>29</td>
<td>29</td>
<td>9</td>
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<td></td>
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<td>11</td>
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<td>38 (SD = 16)$^b$</td>
<td>498</td>
<td>203</td>
<td>39 (SD = 16)$^b$</td>
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<td>48 (SD = 18)$^b$</td>
<td>744</td>
<td>409</td>
<td>58 (SD = 22)$^b$</td>
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<tr>
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<td>2,348</td>
<td>4,696</td>
<td>1545</td>
<td>43$^c$</td>
<td>1,242</td>
<td>612</td>
<td>48$^c$</td>
</tr>
</tbody>
</table>

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$^a$Platform transmitter terminal identification.

$^b$Weighted by PTT.

$^c$Weighted by year.
Table 2. GPS fix success for store-on-board collars deployed on brown bears on the Kenai Peninsula, Alaska, 1996 and 1997. GPS units were programmed to take 5 fixes/day.

<table>
<thead>
<tr>
<th>Year</th>
<th>Days deployed</th>
<th>Potential fixes (n)</th>
<th>Actual fixes (n)</th>
<th>Fix Success (%)</th>
<th>Days fixed (n)</th>
<th>Days fixed (%)</th>
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<td>246</td>
<td>67</td>
<td>86</td>
<td>99</td>
</tr>
<tr>
<td>1997</td>
<td>162</td>
<td>674</td>
<td>423</td>
<td>63</td>
<td>155</td>
<td>96</td>
</tr>
<tr>
<td>1997</td>
<td>170</td>
<td>705</td>
<td>521</td>
<td>74</td>
<td>169</td>
<td>99</td>
</tr>
<tr>
<td>1997</td>
<td>152</td>
<td>630</td>
<td>389</td>
<td>62</td>
<td>146</td>
<td>96</td>
</tr>
<tr>
<td>1997</td>
<td>176</td>
<td>732</td>
<td>528</td>
<td>72</td>
<td>168</td>
<td>96</td>
</tr>
<tr>
<td>1997</td>
<td>104</td>
<td>431</td>
<td>250</td>
<td>58</td>
<td>103</td>
<td>99</td>
</tr>
<tr>
<td>1997</td>
<td>137</td>
<td>568</td>
<td>401</td>
<td>71</td>
<td>136</td>
<td>99</td>
</tr>
<tr>
<td>1997</td>
<td>101</td>
<td>418</td>
<td>267</td>
<td>64</td>
<td>98</td>
<td>97</td>
</tr>
<tr>
<td>Total</td>
<td>1,231</td>
<td>5,118</td>
<td>3,324</td>
<td>65</td>
<td>1,188</td>
<td>97</td>
</tr>
</tbody>
</table>

*a Weighted by GPS unit.

Accuracy and Factors Affecting Fix Rate

Successful fix rate declined significantly \((P = 0.0002)\) with time for the GPS-Argos units based on the arcsine transformed data, which is an order-preserving scale. Hence the trend was also evident on the proportional scale (Fig. 4a). By backward elimination, we were able rule out a reproductive effect (females with cubs versus yearlings versus lone females). Fix success rates were highest during May and June and declined thereafter. Successful fix rate for GPS store-on-board units did not change through time (Fig. 4b, Table 2).

Accuracy of fixes obtained from collars at known sites was less than expected. Of 325 GPS fixes at the first location, only 28% were within the 40-m radius predicted to contain 50% of locations (circular error probable) and 70% within the 100-m radius predicted to contain 95% of locations; 50 and 95% of all fixes were within 68 and 248 m of the true location, respectively. The remaining 5% of errors were scattered out to 570 meters (Fig. 5). Angular distributions of errors were not significantly
different \( (R = 27.38, \ 324 \text{ df}, \ P > 0.05) \) from random (Rayleigh’s test, Zar 1974). Of 112 GPS fixes at the second location, only 38% were within the 40-m 50% circular error probable and 87% were within the 100-m 95% circular error probable. Fifty and 95% of all fixes were within 51 and 143 m of the true location, respectively. The remaining 5% were scattered out to 228 meters (Fig. 5). Angular distributions of errors at this site were significantly different \( (R = 22.57, \ 112 \text{ df}, \ P < 0.02) \) from random (Rayleigh’s test, Zar 1974).

Precision of fixes was approximately 5 and 11 meters in longitude and latitude, respectively. We projected these coordinates to universal transverse mercator Zone 5 using the program UTMS, obtained from the US National Geodetic Survey over the World Wide Web (http://www.ngs.noaa.gov/PC-PROD(pc_prod.html).

Effects of Vegetative Cover on Fix Rate

Tests with a GPS-Argos collar in various vegetation types indicated that the GPS receiving unit was relatively unaffected by plant cover (Table 3). Fix success in all vegetation types was high \( (\bar{x} = 95\%, \ \text{range} \ 88-100\%) \) relative to success rates on collared bears. Vegetative closure as measured by the spherical densiometer was the only significant \( (\chi^2 = 6.53, \ P = 0.0106) \) predictor of fix rate, whereas stem density \( (P = 0.45) \), overstory height \( (P = 0.13) \), and stem diameter \( (P = 0.062) \) did not add significantly to the model. The final form of the model was \( \ln(Y_i) = \ln(N_i) - 6.6941 + 0.0471X_{li}^2 \), where \( Y_i \) = the number of fix failures at the ith location, \( X_{li} \) = the %
Fig. 6. Distribution of (a) accuracy of fixes relative to their true location and a scattergram (b) of GPS fixes and distance (meters) from the true location (center of crosshair) at site 2 on the Kenai Peninsula, Alaska, 1996–97. Data are from 4 collars placed concurrently at the site for 37 days, beginning on 21 November 1996.

Table 3. Fix success for a GPS–Argos transmitter placed at ground level in various vegetation types on the Kenai Peninsula, Alaska, 1997.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Potential fixes (n)</th>
<th>Successful fixes (%)</th>
<th>Stems/m²</th>
<th>Oversony closure x(SD)</th>
<th>Oversony height (m)</th>
<th>Mean stem diameter (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mature spruce and paper birch (open)</td>
<td>26</td>
<td>100</td>
<td>0.28</td>
<td>54(4)</td>
<td>12.8(2.1)</td>
<td>13.6(7.4)</td>
</tr>
<tr>
<td>Closed alder (short)</td>
<td>12</td>
<td>92</td>
<td>0.97</td>
<td>81(2)</td>
<td>3.3(0.2)</td>
<td>4.7(0.8)</td>
</tr>
<tr>
<td>Closed alder (tall)</td>
<td>18</td>
<td>94</td>
<td>0.92</td>
<td>92(2)</td>
<td>9.4(0.5)</td>
<td>6.2(0.4)</td>
</tr>
<tr>
<td>Closed alder (tall horizontal to ground)</td>
<td>18</td>
<td>89</td>
<td>0.92</td>
<td>92(2)</td>
<td>9.4(0.5)</td>
<td>6.2(0.4)</td>
</tr>
<tr>
<td>Aspen regrowth</td>
<td>30</td>
<td>100</td>
<td>2.08</td>
<td>89(2)</td>
<td>7.5(0.4)</td>
<td>4.1(1.4)</td>
</tr>
<tr>
<td>Riparian cottonwood*</td>
<td>43</td>
<td>88</td>
<td>0.44</td>
<td>85(1)</td>
<td>18.5(4.6)</td>
<td>32.8(17.0)</td>
</tr>
<tr>
<td>Open mature birch (open)</td>
<td>35</td>
<td>97</td>
<td>0.50</td>
<td>55(5)</td>
<td>13.6(1.0)</td>
<td>8.5(6.3)</td>
</tr>
<tr>
<td>White spruce regrowth (dense)</td>
<td>20</td>
<td>90</td>
<td>1.98</td>
<td>82(3)</td>
<td>7.0(0.8)</td>
<td>5.3(2.2)</td>
</tr>
<tr>
<td>Mature aspen (open)</td>
<td>12</td>
<td>100</td>
<td>0.04</td>
<td>60(6)</td>
<td>13.4(0.9)</td>
<td>13.4(0.9)</td>
</tr>
<tr>
<td>Birch regrowth</td>
<td>37</td>
<td>100</td>
<td>1.70</td>
<td>29(3)</td>
<td>3.0(0.1)</td>
<td>0.4(0.1)</td>
</tr>
</tbody>
</table>

*Populus spp.
overstory closure at the \(i\)th location, \(N_i\) = the number of fixes attempted at the \(i\)th location.

Average cost/fix using the GPS-Argos units was $42, including cost of collar purchase and data acquisition (Argos charges $10/PTT day), or $63/fix with capture time ($1,100/capture) for deployment and removal included. Cost for GPS store-on-board units was $23/fix, including capture, whereas data obtained using fixed-wing aircraft and conventional VHF units was $40–80/fix, depending upon proximity of animals and search time. Costs/fix obtained with the GPS collars was averaged over a 2-year period but would decrease with additional years because annual refurbishing costs are only about 20% of the original purchase price. All costs are based on 1997 U.S. dollars.

**DISCUSSION**

Moen et al. (1996) reported GPS fix success rates of about 95% for moose in open habitats, diminishing to 60% under closed canopies of conifer or deciduous trees with leaves. Rempel et al. (1995) measured GPS location error and fix success rates in mixed boreal forest. Fix rates varied from 10% in dense red pine (Pinus resinosa) to 97% in open habitats. Rempel et al. (1995) felt that fix success in red pine forest was primarily related to stem density and trunk diameter, which directly affect the available view of the sky for the GPS antenna. Leaf coverage apparently has less effect on fix success because GPS radio signals can pass through leafy coverage. Our measure of canopy coverage integrated stem density, basal area, and leaf coverage into 1 estimate, which probably explains why this variable was the only significant measure useful in predicting fix success rate.

Based on these results, we do not believe that the highly variable GPS fix success and Argos uplink rates measured during this study were solely associated with vegetative cover. Our data suggest that habitat condition, geographic features, and possibly bear behavior reduced collar performance. Comparing our GPS store-on-board fix success (65%) with the fix success of the GPS-Argos units (43%) suggests that we may have lost some GPS data because of the Argos component. This could happen if the Argos unit failed to successfully transmit stored GPS fixes before older data were overwritten. Recall that the internal storage capacity for the GPS-Argos unit was 5–7 locations depending upon proximity. Loss of GPS fixes due to poor Argos uplink success is also supported by the significant and positive correlation between fix and uplink success (Fig. 2). Brown bears on the Kenai Peninsula generally move to salmon (Oncorhynchus spp.) streams to feed on fish in early July. We suspect movements by bears or other factors related to bear behavior contributed to the variable success we measured. Reduced GPS fix rates associated with bear movement are supported by the very high rate of success obtained by a stationary collar placed in various vegetation types compared to our success from collars on bears. Additional research is needed to determine what factors affect fix success. If GPS receivers are to be used to sample bears and other large mammals within their environments, we must understand how vegetation, movement, terrain, and other factors affect fix success. With such information, we can correct these biases and make stronger inferences about resource selection, habitat use, and impacts of humans.

The technology we tested did not store the necessary data to differentially correct GPS locations. Errors associated with uncorrected fixes were greater than predicted using the C/A code. This error rate undoubtedly is related to the proportion of 2 dimensional (2-D) versus 3-D fixes (Rempel et al. 1995, Moen et al. 1997), a statistic we were unable to measure. Two-D fixes, obtained from only 3 satellites, are less precise than 3-D fixes obtained from \(\geq 4\) satellites. Location errors of the magnitude we measured suggest our data would be most useful in monitoring daily movement patterns, identification of travel corridors and ecocenters (Craighead et al. 1995), or coarse-grained habitat selection studies (i.e., \(>100\) m pixels), where accuracy of location is not critical.

Because the memory on board the GPS-Argos collar can only store 5–7 GPS fixes at any one time, infrequent Argos uplinks may result in lost GPS data. This might explain why GPS success rate for a given level of uplink success rate was less for the Yellowstone collars compared to the Alaska collars (Fig. 2). GPS fixes from the Yellowstone collars usually were transmitted during only one uplink cycle, whereas fixes from the Alaska collars usually were included in 2–3 consecutive uplink cycles (depending on number of fixes contained in each uplink). If some of our GPS data were lost due to failed Argos uplinks, then increasing the frequency of uplinks might increase GPS success rate. However, frequent uplinks needlessly use battery power to transmit the same data multiple times. Ideally, all GPS fix data would be stored-on-board the collar (potentially available in the next generation of collars) for later retrieval when the collar was recovered. Any data lost during transmission could then be obtained. Such a system would allow for both short-term data retrieval via Argos and long data storage using a memory chip. This would also allow for more detailed analyses on the effects of activity, terrain, season, time, and the independence of these variables on GPS versus Argos uplink success.
The application of GPS-Argos technology to determine habitat use by bears is useful when part of the sampling protocol requires intensive ground searches of feeding sites (Mattson 1997a,b). The rapid transmittal of data provided by the system allowed us to visit sites used by bears within 1–2 days of when the bear was at the site. This quick response time allowed for determining more precisely why a bear was using a location, particularly when changes in the environment were rapid (i.e., vegetative growth), or when sign was likely to disappear rapidly (i.e., meat scats). Data collection by the GPS collars occurred through all hours of the day and night and during weather when aircraft telemetry was not possible. Hence, the GPS-Argos system provided a less biased sample of locations used by bears (Arthur and Schwartz This Volume) compared to conventional VHF telemetry from fixed-winged aircraft. Also, because the GPS-Argos system is remote relative to the bear, it provides the additional advantage of allowing the researcher to determine bear locations without the disturbance associated with ground tracking or low-flying aircraft. We were able to observe bear movements and only visit location sites after the animal had left the area. Consequently, our field operations did not influence bear movements (i.e., disturbance and displacement). One could argue that VHF locations are more precise than undifferentially corrected GPS fixes because it is often possible to determine the exact location of an animal via fixed-wing aircraft when a visual sighting occurs. However, there can be error associated with VHF fixes when determining the coordinates of an animal. This occurs if the location of the animal is determined with GPS technology on board the aircraft, because this technology is subject to the same errors as our collars (C/A code) unless differentially corrected. Visually plotting the location on a detailed map can also be subject to error, especially where landscape is uniform across vast areas.

The system is not without problems. The technology is expensive, collars are too large for small bears, and multiple captures are necessary. Also, transmission of data appears to be affected by canopy cover, so the potential exists for habitat biases in the data collected by GPS and Argos technology. GPS technology and its usefulness must be determined by study objectives. Our cost analysis suggests that if cost/fix is important, GPS store-on-board collars are most appropriate. However, one must wait until the end of the field season before any data are obtained. If short-time data retrieval is important or if bears are collared in remote locations where aircraft flights are difficult or impossible, GPS-Argos technology is more practical.

**RESEARCH IMPLICATIONS**

Use of GPS for animal telemetry is a recent development (Rodgers et al. 1996). The Telonics technology reported here is the first to link GPS technology with the Argos system. Our tests demonstrate the potential application of GPS-Argos technology to large wilderness mammals, and specifically to brown bears. As GPS technology advances, so will its usefulness and number of applications. Some models already allow for differential correction (Moen et al. 1997). Although this option was not available for units that transmit data via the Argos system, future models will store positions on the unit for later downloading when the unit is recovered and differentially corrected, while still providing a subsample of C/A fixes through the Argos system (S. Tomkiewicz, Telonics Inc., Mesa, Az., personal communication, 1998). As component size is reduced and power requirements for the system are further reduced, battery size can be reduced and packages will become available for smaller animals. Smaller components with lower power demands can also translate into more fixes or longer operational life. Linking Argos technology with the GPS system allows for near-real-time data acquisition without relying on VHF telemetry. Animal movements, habitat use, travel patterns, avoidance of humans, impacts of roads, and other effects can be addressed without concern for weather, ground or air tracking, human error, or terrain (Arthur and Schwartz 1999). Current limitations of these systems include the frequent inability to obtain fixes, possible influences of vegetation, animal movement, terrain, and cost.

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