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# Performance of Spread Spectrum Global Positioning System Collars on Grizzly and Black Bears

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**ABSTRACT** Global Positioning System (GPS) telemetry is a prevalent tool now used in the study of large mammals. Global Positioning Systems either store the data on board the collar or contain a remote-transfer system that allows for data recovery at more frequent intervals. Spread spectrum (S–S) technology is a new mode of data transfer designed to overcome interference problems associated with narrow-band very high frequency and ultra high frequency data-transfer systems. We evaluated performance of S–S GPS radiocollars deployed on grizzly (*Ursus arctos*) and black bears (*U. americanus*). We also evaluated variables that influenced GPS fix success rates, with particular focus on animal activity, time of year, and temperature. The S–S GPS collars performed to our expectations and met study objectives; we did not experience any major problems with the data-transfer system. We observed varying rates of fix success that were directly related to recorded activity counts. Using logistic regression, we verified that activity counts were a reasonable measure of resting or feeding–traveling in both bear species. Our results showed that 73% and 79% of missed fixes, respectively, occurred when we predicted black and grizzly bears to be resting. Temperatures measured in the canister of the collar were not correlated with air temperature, suggesting posture and activity influenced canister temperature. Both measures of temperature were predictive of fix success. We did not find that fix success was related to body morphology (i.e., neck circumference, mass, and chest girth), fix interval, position of the GPS antenna relative to the sky, or sex of the bear. We conclude that fix success for both species is strongly related to activity patterns and time of year. Activity counters appear to be a reasonable measure of this behavior, and we recommend researchers consider including an activity-count system when deploying GPS collars. We also recommend researchers explore building separate models of habitat selection based upon categories of activity to account for bias in fix success associated with bear behavior. (JOURNAL OF WILDLIFE MANAGEMENT 73(7):1174–1183; 2009)

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Scientists first used Global Positioning System (GPS) radiocollars to track caribou (*Rangifer tarandus*), moose (*Alces alces*), and black bears (*Ursus americanus*) in Canada (Rodgers and Anson 1994, Obbard et al. 1998). Two years later, the first GPS collars were deployed on brown bears (*U. arctos*) in Alaska, USA (Schwartz and Arthur 2000). Since this time, GPS telemetry has revolutionized wildlife research, improving our ability to collect accurate large-sample, fine-scaled spatial data on an array of large animals (Rempel et al. 1995, Rodgers et al. 1999).

Many factors have been shown to affect GPS fix success. Failed fix attempts have been associated with vegetation and terrain (Rempel et al. 1995, Moen et al. 1996, D'Eon et al. 2002, D'Eon 2003, Frair et al. 2004), species, behavior, morphology (Moen et al. 1996, Obbard et al. 1998, Belant and Follmann 2002, D'Eon and Delparte 2005, Moe et al. 2007), movement rates (Graves and Waller 2006, Heard et al. 2008), satellite configurations and visibility of the sky (Moen et al. 1997, Frair et al. 2004, Graves and Waller 2006), time of day and year (Belant and Follmann 2002, Heard et al. 2008), and sampling frequency (Mills et al. 2006).

Global Positioning System collars are typically configured in 1 of 4 ways: 1) data are stored on a nonvolatile memory chip and data are collected when the collar is retrieved, 2) data are transmitted at predetermined intervals to an Argos satellite and retransmitted to a base station, 3) data are retrieved from the collar using a remote data download via very high frequency (VHF) or ultra high frequency (UHF) radio modem, or 4) data are retrieved using a remote data download via the Global System of Mobil Communication (GSM) cellular network or the Iridium satellite network (mainly in Europe). Each data-retrieval method comes with its own set of advantages and limitations.

Our objective was to evaluate GPS collection units fitted with a new system of data transmission that uses spread spectrum (S–S) technology. Spread spectrum technology takes advantage of spreading information across many channels, minimizing disruptive effects of interference on the data-transfer process and increasing the effective data-transfer rate. Potentially, this represents a substantial improvement over older, narrow-band frequency modulation modems in the VHF or UHF frequency bands. Our second objective was to explore variables that affected GPS fix success.

## STUDY AREA

Our study area was located in the southern Greater Yellowstone Ecosystem, focused within Grand Teton National Park (GRTE) where grizzly bears and black bears

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are sympatric. This area included the upper Snake River drainage in a high-elevation valley, commonly referred to as Jackson Hole, which was bounded by the Teton Range to the west, the Gros Ventre and Absaroka mountains to the east, the Yellowstone Plateau to the north, and the town of Jackson, Wyoming to the south. Our work concentrated in the area roughly north of Leigh Canyon in the Teton Range and Spread Creek in the valley floor. Elevations ranged from 1,890 m in the valley floor to 4,197 m atop surrounding peaks. The climate was characterized by long, cold, snowy winters and short, cool summers. The 30-year (1971–2000) mean high and low temperatures in January and July were −3.1° C, −18.6° C, 24.7° C, and 2.6° C, respectively, at Jackson Lake Dam in the south-central portion of our study area (Western Regional Climate Center 2009). Approximately 70% of precipitation fell as snow.

Patterns of precipitation and temperature produced predictable vegetation patterns (Marston and Anderson 1991). Low elevations (<1,900 m) featured foothill grasslands or shrub steppes. With increasing moisture, open stands of Douglas-fir (*Pseudotsuga menziesii*) with some limber pine (*Pinus flexilis*) occurred. Lodgepole pine (*P. contorta*) formed the lowest-elevation forest community at around 1,900–2,200 m (Patten 1963, Waddington and Wright 1974, Romme and Turner 1991) and dominated the extensive Yellowstone Plateau at mid-elevations (2,400 m), where poor rhyolite-based soils dominated (Despain 1990). With increasing elevation, spruce–fir or subalpine forests dominated. Engelmann spruce (*Picea engelmannii*) and whitebark pine (*Pinus albicaulis*) formed the upper tree line around 2,900 m (Patten 1963, Waddington and Wright 1974, Despain 1990). Alpine tundra occurred at the highest reaches of all major mountain ranges.

# METHODS

## Trapping and Collaring

We used culvert traps to capture both species of bears (Blanchard 1985). Procedures were approved by the Animal Care and Use Committee of the United States Geological Survey, Biological Resources Division and conformed to the Animal Welfare Act and United States Government principles for the use and care of vertebrate animals used in testing, research, and training. Trapping occurred principally within GRTE. We fitted captured bears, except dependent offspring or small subadult black bears, with Telonics S–S GPS collars (Telonics, Inc., Mesa, AZ), a CR-2a programmable breakaway collar release (Telonics, Inc.), a biodegradable canvas spacer, and a motion sensor that reduced transmitter pulse rate if stationary for 4–5 hours. Transmitters also contained an activity switch positioned so that the switch was activated by movement of the bear's head through a plane 15° below the horizon. The activity switch tallied the number of seconds that showed a switch closure that was then accumulated during a 15-minute interval just prior to the GPS fix attempt. The number returned was a percentage of total seconds of switch closure during the collection interval at 0.5% resolution. Activity counts were reflective of the bear's head-up head-down movement just prior to each attempted GPS fix. A sensor recorded temperature inside the unit just prior to each fix attempt over a temperature range of −55° to +125° C, at a resolution of 1° C.

We set collars to maximize the number of fixes during deployment. Telonics, Inc. recommended longer fix intervals each year of our study. As a consequence, our fix intervals differed considerably over the duration of the study. We programmed our collars with fix intervals (min) of 35 ($n$ = 4), 37 ($n$ = 4), 48 ($n$ = 4), 63 ($n$ = 1), 65 ($n$ = 1), 76 ($n$ = 5), 84 ($n$ = 2), 103 ($n$ = 6), 118 ($n$ = 2), 180 ($n$ = 1), and 190 ($n$ = 3). With the exception of the fix interval of 180 minutes, we picked intervals not divisible by 60, to sample throughout the 24-hour clock, rather than the same time each day. We programmed GPS units to search for available satellites for up to 180 seconds. If a successful fix was not obtained, units turned off until the time of the next scheduled fix attempt. Units were off during the anticipated denning season (15 Nov–14 Apr or 31 Oct–14 Apr, for grizzly and black bears, respectively). The VHF tracking transmitter operated daily for 24 hours, 18 hours, or 12 hours, depending upon anticipated length of deployment, and with the exception of times when a data download occurred, the tracking transmitter operated independently of the S–S GPS unit.

We flew telemetry flights weekly from late April through early November to retrieve data. We had the uplink for the S–S GPS unit set to operate each Tuesday and Thursday 0800–1200 hours Mountain Standard Time. During each telemetry flight, we retrieved the previous week's GPS data and stored them on a laptop computer in the aircraft.

We recorded number of times during the study we were successful or unsuccessful in establishing a communication link with each collar. We recorded number of times the communication link, once established, was broken prior to full data recovery and approximated the time for full data recovery in minutes.

## Activity Patterns

We conducted site visits to GPS telemetry locations to determine habitat selection and activity patterns. Each week, we randomly assigned all collared bears (regardless of species or sex) a random number (>0 and <1), then ranked them by that number. For each bear, we assigned each day of the week a random number. Site visits started with the lowest-ranked bear on its lowest-ranked day of week, and continued through the list of ranked bears to sample as many individuals as possible. For each bear-day, we visited most GPS locations collected for that 24-hour period. For bears with fix interval <1/hour, we visited ≥1 GPS fix for each hour, whereas we visited all GPS fixes for those with intervals ≥1/hour. Our goal was to discern activity of each sampled bear over a 24-hour period. Based upon sign, we classified activity types as bedded (presence of day bed) or feeding (evidence of feeding activity). If neither bedding nor feeding sign were present, we classified the bear as traveling. In some cases we recorded >1 activity (e.g., bedding and feeding at a carcass).

To determine if collar activity-counts were indicative of activities recorded at site visits, we contrasted activity count with recorded activity (resting vs. active). We used a logistic regression model where the dependent variable was recorded activity (resting = 0, active = 1), the predictor variable was activity count, and bear identity was coded as a cluster. We used generalized estimating equations to estimate model parameters. Generalized estimating equations are an alternative to maximum-likelihood estimation, which is more difficult with correlated longitudinal and clustered data (Molenberghs and Verbeke 2006). We tested species as a categorical variable to ascertain if there was a difference between grizzly and black bears. Results of this model indicated species was not significant ($P = 0.566$), so we fit a second model excluding species. We interpreted the resulting model as a logistic discriminant function that accounted for repeated measures of individual bears. We used the logistic discriminant function to classify GPS fixes as belonging to either an active or resting bear, where the threshold for classifying a bear as active was given by (Seber 1984):

$$\beta_0 + \beta_1 \times \text{activity count} > \ln\left(\frac{n_1}{n_2}\right),$$

where $n_1$ and $n_2$ were sample sizes from feed-site visits where we determined activity for active and resting bears, respectively. We derived the threshold value by solving the above equation algebraically in terms of activity count.

**Fix Success**

We modeled probability of a location attempt being successful (1) or unsuccessful (0) with binomial logistic regression (Hosmer and Lemeshow 2000). We used PROC NLMIXED in Program SAS 9.1.3, (SAS Institute Inc., Cary, NC) because it allowed us to treat bear-transmitter (e.g., time period one bear wore one transmitter) as a subject variable (Frair et al. 2004). We used PROC LOGISTIC to estimate starting values for beta coefficients when running NLMIXED. We chose bear-transmitter as the subject variable rather than bear-year because some individuals retained their collar for >1 year. For this analysis, we excluded weeks 14–16 (14–22 Apr), and 43–46 (21 Oct–14 Nov) because of small sample sizes and compromised GPS fix acquisition when bears moved into or out of dens.

We built different models for the 2 species because we hypothesized differences in behavioral patterns and habitat use likely affected fix success. We could have attempted to do this by incorporating species as a covariate in a more general model, but incorporating interactions would have resulted in complex models that would have been difficult to fit in NLMIXED. Covariates tested included sex, activity count, time of year (Julian day [jday], week, or month), fix interval, collar-recorded temperature, ambient temperature, and morphometric measurements of bears at time of capture. We measured air temperature hourly at a fixed station in GRTE (GTGW4), approximately 10 km south of our study area (MesoWest 2009). Some temperature records were missing. We excluded associated records from our analysis so that our Akaike's Information Criterion (AIC) values would be comparable among models.

Graves and Waller (2006) found significant negative correlations between fix success and neck circumference, chest circumference, and body mass. We combined these 3 variables using principal-components analysis. We used the first principal component, which explained 96% of variation and was a weighted mean of the 3 variables based on loadings (girth = 0.975, neck = 0.980, mass = 0.984). Finally, for grizzly bears, we tested the angle of the antenna relative to the sky at time of collar deployment. We fitted collars to bears so that the GPS antenna was positioned as close to dorsal surface of the animal's neck as possible. If this was not possible, we recorded the angle from the dorsal surface of the neck and used this angle in models to determine if deviations were predictive of fix success. We only used data from grizzly bears because we had an adequate sample distribution only for this species. Angles recorded varied from 0° (pointing directly up) to 60° in 15° increments.

We compared linear and quadratic models for some covariates (activity, time, temp) because we hypothesized that fix success might vary in a nonlinear fashion. We used the information-theoretic approach (Burnham and Anderson 1998, 2002) and selected best approximating models from the candidate set using AIC adjusted for small sample sizes (i.e., $AIC_c$; Burnham and Anderson 2002). For models that were nearly identical based on $AIC_c$ values, we used an evidence ratio (Burnham and Anderson 2002) of Akaike weights.

We evaluated model fit in 3 ways. We plotted the logit ($\ln[p/1 - p]$) of the proportion of successful fixes ($p$) for covariates categorized into 10 ordinal 10% quantile bins of the data. We visually contrasted distribution of the raw logit against modeled logit for each covariate in the top model. We also compared fit of our top model for both species using Receiver Operating Characteristic (ROC) curves, plots of true positives versus false positives (Fielding and Bell 1997). The area under the curve is the probability that a model will rank a randomly chosen successful fix higher than a randomly chosen failed fix. Finally, we used the top model from our black bear data set and, using ROC curves, fit it to an independent data set collected for black bears collared during the same period in GRTE just south of our study area.

Based upon our visual inspections of logit plots, we constructed post hoc models considering cubic terms for collar temperature and air temperature. Inspection of the plotted raw logit suggested that a third-order polynomial might provide a better fit to the data.

## RESULTS

From 2004 to 2006, we captured 26 grizzly and 77 black bears. We deployed 39 S–S GPS collars on 29 unique individuals (10 grizzly [4 F, 6 M] and 19 black bears [8 F, 11 M]). These 39 collars were deployed for 6,669 days, including days bears were in dens and GPS units were off.

We averaged 20 (range = 18–22) download flights/season with a median of 8 bears/flight (range = 1–15). On each flight, the pilot–observer located each bear using the VHF beacon, and the observer initiated the download sequence while the plane circled above the bear. Downloading 1 week of data (approx. 50–400 attempted fixes/bear) normally took <4 minutes/bear. Data transfer typically occurred at 1,900–5,400 bits/second. We typically located and downloaded data from 5 bears/hour. During roughly 10% of download attempts, line-of-sight between receiving and transmitting antennas was interrupted, requiring subsequent download attempts. Interruptions occurred as the moving airplane passed behind dense vegetation or terrain that blocked subsequent signal transfer. Repositioning the aircraft allowed for complete data transfer in most cases. On rare occasions (approx. 3 times/yr) an active bear was in a location that precluded complete data transfer even after multiple attempts. We attributed this to rugged terrain. At the close of each field season, we downloaded complete data sets from each transmitter. These downloads (up to 4,500 fix attempts/bear) required more time and were more prone to interruptions. Successful downloads generally required <10 minutes/bear. We were unable to download data from about 30% of denned bears, but successfully recovered those data the following spring.

On days when poor weather conditions precluded flying, we occasionally downloaded data using a handheld receiving antenna extended 2 m above the ground. Success of this approach depended on our ability to establish line-of-sight contact with the bear, but in one case we downloaded data from a bear >4 km away across the surface of a large lake.

### Activity Patterns

We visited 3,269 GPS locations to ascertain bear activity and foraging behavior. We recorded bears as resting, active, or both at 612, 2,344, and 313 sites, respectively. When fitting models we excluded individual sites where we recorded both activities. For black bears, we had 1,749 site visits, with 332 and 1,417 where bears were either resting or active, respectively (Fig. 1A). For grizzly bears we had 1,207 sites visits, with 280 and 927 where the bear was either resting or active, respectively (Fig. 1B). Similar observed frequencies between species supported our findings that there was no difference between them ($P = 0.566$). Histograms showed overlap between active and resting bears when activity counts were low but little overlap when activity counts were high (Fig. 1).

The threshold value (16.23) we derived from the data successfully classified bears as resting for 552 of 612 (90.2%) site visits where we recorded bears as resting, and active for 1,570 of 2,344 (67.0%) site visits where we recorded bears as active. However, of 1,326 sites classified as resting bears based on the modeled break point of activity count ($\leq$16.23), we recorded 774 (58.4%) as an active bear based on site visits. Likewise, of 1,630 sites classified as active bears based on the modeled break point of activity count (>16.23), we recorded 60 (3.68%) as a resting bear based on site visits.

In most cases, when the activity count was above the threshold of 16.23, the recorded activity at sites represented an active bear; but when activity count was $\leq$16.23, recorded activity was a mixture of resting and active bears. Although we more accurately predicted a resting bear when the bear was recorded as resting based on the threshold, activity counts <16.23 misclassified some active bears. On the other hand, predictions above the threshold were nearly all associated with active bears.

### Fix Success

On average, the 39 collars we deployed were available to collect data for 118 days (range = 5–320 days) when bears were not denned. Due to GPS antenna cable fatigue, 7 collars malfunctioned, reducing data collection to 105 days; total lost information equaled 524 days. Global Positioning System units attempted 92,438 fixes and successfully obtained 76,796. Success rates averaged 80.8% (range = 59.3–94.9%). After removing weeks 14–16, and 43–45, plus records with missing estimates of air temperature, our data set contained 85,752 records, including 36,544 records from 15 grizzly bears and 49,208 records from 24 black bears.

For all models, in all cases, AIC and $AIC_c$ values were identical, so we only present AIC values. For univariate models, significant ($P \leq 0.05$) variables included both quadratic and linear fits for activity count, air temperature, and collar temperature for both species; models fit with a quadratic term had lower AIC values compared to models fit with a linear term, with the exception of air temperature for black bears. The quadratic of activity count was the best univariate model for both species, based on AIC values. Time covariates varied between species. For grizzly bears, week, jday, and month were significant, as were the quadratic fits. The quadratic fits for week and jday were nearly identical and only differed by 1 $\Delta$AIC unit (change in AIC value from top model). For black bears, the linear fits for jday, week, and month were significant, but the quadratic fits were not. The linear fits for week and jday were nearly identical and only differed by 1 $\Delta$AIC unit. Sex, the principal component of morphology, and fix rate were not significant for either species. Antenna angle relative to the sky was not significant for grizzly bears. Fix success ranged from 71.2 to 96.6 ($\bar{x}$ = 84.3%) when the antenna was in the dorsal position, and the confidence interval overlapped the mean fix success for the other angles (15° = 86.4%, 30° = 87.6%, 45° = 83.9%, and 60° = 78.5%). Sample sizes were 9 collars with the antenna pointing directly up (0°), 3 at 30°, and 1 each for 15°, 45°, and 60°, respectively.

We combined significant covariates and constructed complex models (Tables 1 and 2). For grizzly bears, the top model contained quadratic terms for activity, week, collar temperature, and air temperature (Table 1). For the second-best model, the quadratic of week was replaced with the quadratic for jday. Models with other combinations of significant variables were not supported based on Akaike weights. Covariates that were significant in individual models all contributed to the general model. Logit plots of collar and air temperature suggested addition of a cubic

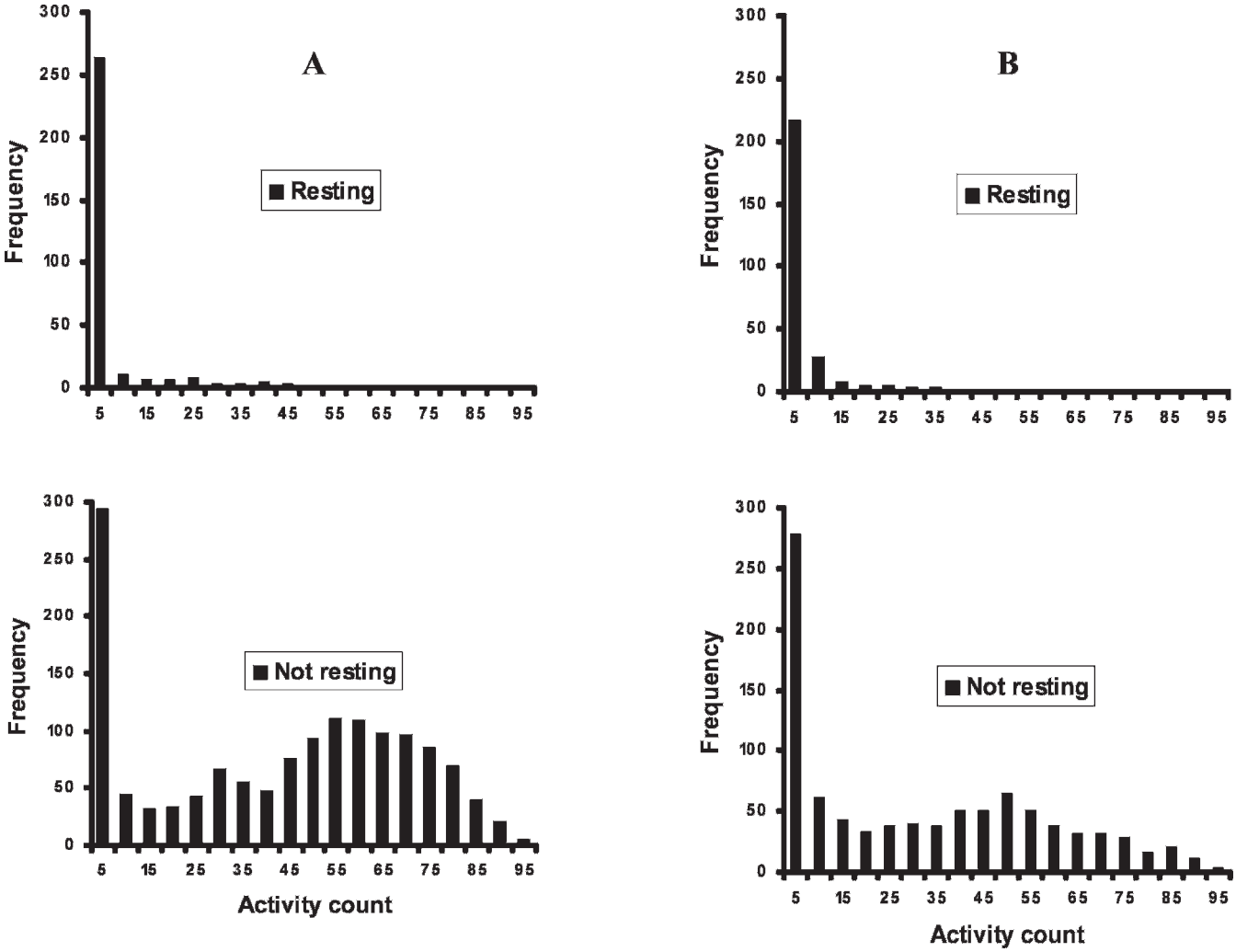


**Figure 1.** Frequency of observations by activity count from Global Positioning System spread-spectrum telemetry collars deployed on black bears (A; $n$ = 1,749 sites visited, with 332 and 1,417 resting or active, respectively) and grizzly bears (B; $n$ = 1,207 sites visited, with 280 and 927 resting or active, respectively). Data from Grand Teton National Park, Wyoming, USA, 2004–2006.

term might provide a better fit. Consequently, we fit post hoc models where we compared models with cubic terms fit to collar and air temperature to our top a priori model (Table 1). We chose to build these models using week as the time variable rather than jday, although based on model weights, we could have used either (evidence ratio = 1.65). Adding a cubic term for air temperature and collar temperature improved model fit (Table 1). The top 2 models (ΔAIC = 0) both contained cubic terms for air temperature, and models with either a cubic or quadratic term for collar temperature were identical based on AIC values (Table 3). These models were 6 ΔAIC units less than the top a priori model.

**Table 1.** Model variables, Akaike's Information Criterion value (AIC), number of parameters ($K$), change in AIC values from top model (ΔAIC), and Akaike weight ($w_i$) for Global Positioning System fix success for collars deployed on grizzly bears ($n$ = 15) in Grand Teton National Park, Wyoming, USA, 2004–2006. We present $w_i$ and ΔAIC values separately for a priori and post hoc models.

| Variables | AIC | $K$[a] | ΔAIC | $w_i$ |
|---|---|---|---|---|
| A priori models | | | | |
| Activity$^{2b}$ + week$^2$ + collar temp$^2$ + air temp$^2$ | 26,103 | 9 | 0 | 0.565 |
| Activity$^2$ + jday$^{2b}$ + collar temp$^2$ + air temp$^2$ | 26,104 | 9 | 1 | 0.343 |
| Activity$^2$ + jday + collar temp$^2$ + air temp$^2$ | 26,108 | 8 | 5 | 0.046 |
| Activity$^2$ + week + collar temp$^2$ + air temp$^2$ | 26,108 | 8 | 5 | 0.046 |
| Post hoc models | | | | |
| Activity$^2$ + week$^2$ + collar temp$^{3b}$ + air temp$^3$ | 26,097 | 11 | 0 | 0.450 |
| Activity$^2$ + week$^2$ + collar temp$^2$ + air temp$^3$ | 26,097 | 10 | 0 | 0.450 |
| Activity$^2$ + week + collar temp$^3$ + air temp$^3$ | 26,100 | 10 | 3 | 0.100 |

[a] Includes an intercept term.
[b] Squared terms also included a linear term; cubic terms include linear and quadratic terms. jday = Julian day.

**Table 2.** Model variables, Akaike's Information Criterion value (AIC), number of parameters ($K$), change in AIC values from top model (ΔAIC), and Akaike weight ($w_i$) for Global Positioning System fix success for collars deployed on black bears ($n$ = 24) in Grand Teton National Park, Wyoming, USA, 2004–2006. We present $w_i$ and ΔAIC values separately for a priori and post hoc models.

| Variables | AIC | $K$[a] | ΔAIC | $w_i$ |
|---|---|---|---|---|
| A priori models | | | | |
| Activity[2b] + week$^2$ + collar temp$^2$ + air temp | 41,723 | 8 | 0 | 0.506 |
| Activity$^2$ + week$^2$ + collar temp$^2$ + air temp$^2$ | 41,724 | 9 | 1 | 0.307 |
| Activity$^2$ + jday[2b] + collar temp$^2$ + air temp$^2$ | 41,725 | 9 | 2 | 0.186 |
| Post hoc models | | | | |
| Activity$^2$ + week$^2$ + collar temp$^2$ + air temp[3b] | 41,717 | 10 | 0 | 0.604 |
| Activity$^2$ + week$^2$ + collar temp$^3$ + air temp$^3$ | 41,719 | 11 | 1 | 0.366 |
| Activity$^2$ + week$^2$ + collar temp$^3$ + air temp | 41,724 | 9 | 6 | 0.030 |

[a] Includes an intercept term.
[b] Squared terms also included a linear term; cubic terms include linear and quadratic terms. jday = Julian day.

The top a priori model for black bears contained quadratic terms for activity, week, and collar temperature, and a linear term for air temperature (Table 2). The second-ranked model (ΔAIC = 1) contained quadratic terms for all these variables and was identical to the top a priori model for grizzly bears. The evidence ratio between these 2 models was 1.65, suggesting both had support. Covariates that were significant in individual models all contributed to the general model. Week was significant, but the quadratic of week was not. However, models containing only the linear term for week were not supported compared to those with the quadratic based on ΔAIC values. The top 2 post hoc models were identical to those for grizzly bears, and the evidence ratio between these 2 models was 1.65, suggesting both had support (Table 3).

Activity counts were predictive of fix success. The proportion of successful fixes was not consistent over the 24-hour period (Fig. 2A) with more missed fixes occurring at night from around 2100 hours to 0400 hours, and midday. Activity counts from 3,269 site visits, categorized into either active ($\bar{x}$ = 35.2) or bedded ($\bar{x}$ = 8.0) were different ($t$ = 26.8, df = 3,267, $P$ = 0.00), suggesting that most missed fixes occurred when bears were bedded. Plots of activity versus fix success for 10 ordinal 10% quantile bins plotted against predicted fix success from the top post hoc models for black and grizzly bears suggested a reasonable fit to the data (Fig. 2B, C).

Temperatures recorded within the canister on the collar were not correlated with air temperature (Fig. 3). Temperatures recorded in collars were warmer than recorded air temperatures, especially when air temperatures were low. We did not record temperatures <0° C in collars on live bears. At high air temperatures, collar temperatures tended to be slightly lower than air temperatures. These relationships were similar for both species. Plots of air or collar temperatures versus fix success for 10 ordinal 10% quantile bins plotted against predicted fix success from the top post hoc models for black and grizzly bears suggested a reasonable fit to the data (Fig. 4). The ROC scores fit to the best model for grizzly and black bears were 0.72 (SE = 0.004) and 0.69 (SE = 0.003), respectively. The ROC score (0.61, SE = 0.005) fit to the independent black bear data set was lower ($P$ = 0.05), suggesting poor fit.

## DISCUSSION

According to Clark et al. (2006), S–S radio transceivers have several advantages over tracking systems using GSM (i.e., cellular telephones), satellite (i.e., Argos), and narrow-band telemetry radio frequencies for data transition. Cellular telephone coverage is limited in many wildlands (Sundell et al. 2006), including our study area. Commercial satellite communication is expensive and has restricted data-transition capacity (Chadwick and Garner 2002, Clark et al. 2006). Narrow-band radios operate on frequencies

**Table 3.** Best post hoc models describing Global Positioning System fix success for collars deployed on grizzly bears ($n$ = 15) and black bears ($n$ = 24) in Grand Teton National Park, Wyoming, USA, 2004–2006.

| | Grizzly | | | | Black | | | |
|---|---|---|---|---|---|---|---|---|
| Parameter | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE |
| Intercept | 7.584 | 0.484 | 7.413 | 0.571 | 2.611 | 0.530 | 2.599 | 0.563 |
| Activity | 0.055 | 0.002 | 0.055 | 0.002 | 0.062 | 0.003 | 0.062 | 0.003 |
| Activity$^2$ | $-4.8 \times 10^{-4}$ | $2.7 \times 10^{-5}$ | $-4.80 \times 10^{-4}$ | $2.7 \times 10^{-5}$ | $-6.2 \times 10^{-4}$ | $3.5 \times 10^{-5}$ | $-6.1 \times 10^{-4}$ | $3.5 \times 10^{-5}$ |
| Collar temp | −0.081 | 0.015 | −0.054 | 0.050 | 0.097 | 0.015 | 0.141 | 0.041 |
| Collar temp$^2$ | 0.001 | 0.000 | $5.8 \times 10^{-5}$ | 0.002 | −0.003 | 0.000 | −0.006 | 0.002 |
| Collar temp$^3$ | | | $2.0 \times 10^{-5}$ | $3.6 \times 10^{-5}$ | | | $4.0 \times 10^{-5}$ | $3.4 \times 10^{-5}$ |
| Air temp | −0.004 | 0.011 | −0.004 | 0.011 | −0.018 | 0.013 | −0.018 | 0.013 |
| Air temp$^2$ | 0.002 | 0.001 | 0.002 | 0.001 | 0.002 | 0.001 | 0.002 | 0.001 |
| Air temp$^3$ | $-6.0 \times 10^{-5}$ | $2.0 \times 10^{-5}$ | $-6.0 \times 10^{-5}$ | $2.0 \times 10^{-5}$ | $-6.0 \times 10^{-5}$ | $2.2 \times 10^{-5}$ | $-7.0 \times 10^{-5}$ | $2.2 \times 10^{-5}$ |
| Week | −0.403 | 0.031 | −0.402 | 0.032 | −0.085 | 0.034 | −0.098 | 0.034 |
| Week$^2$ | 0.007 | 0.001 | 0.007 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 |
| Error | 0.300 | 0.089 | 0.299 | 0.089 | 0.379 | 0.147 | 0.372 | 0.143 |

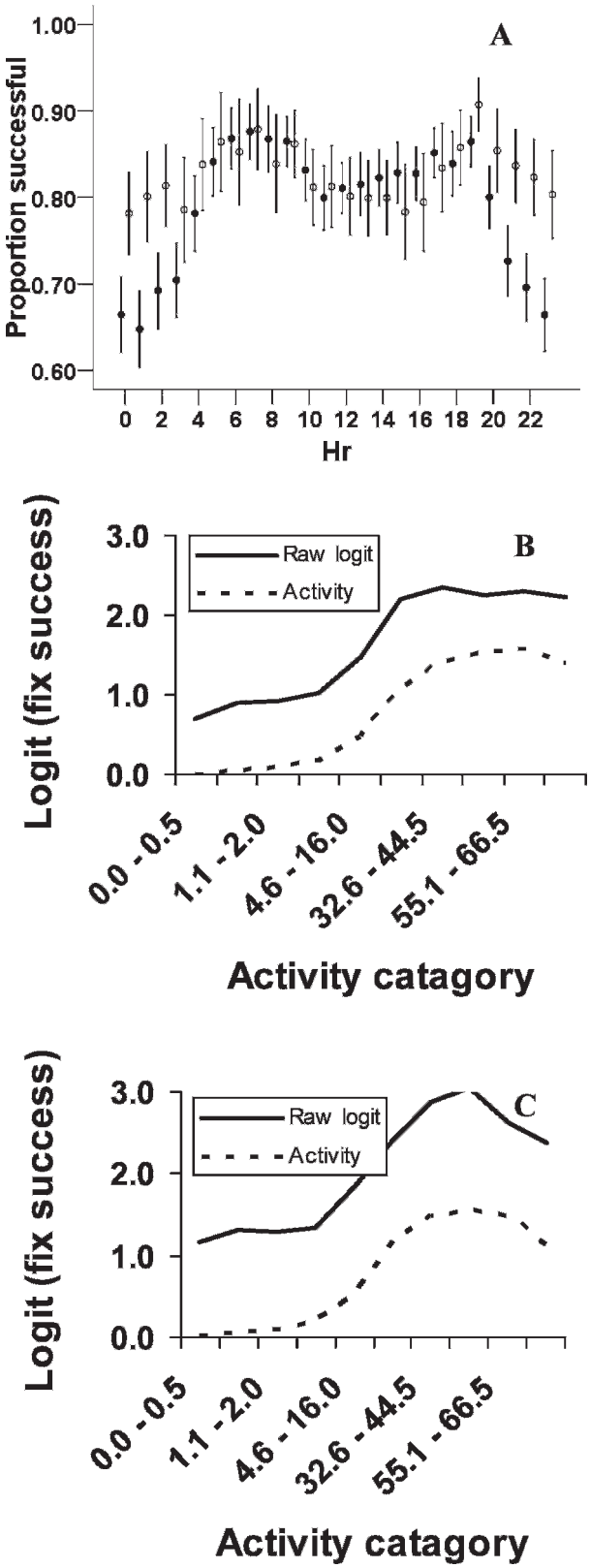


**Figure 2.** Proportion (95% CI) of hourly successful fixes (A) from Global Positioning System collars deployed on grizzly (open dots) and black (solid dots) bears, and plots of fix success (logit) for 10 ordinal 10% quantile bins of the raw data, and from the top post hoc models for black (B) and grizzly bears (C). For clarity, plots of raw and predicted logit do not include the intercept term. Data from Grand Teton National Park, Wyoming, USA, 2004–2006.

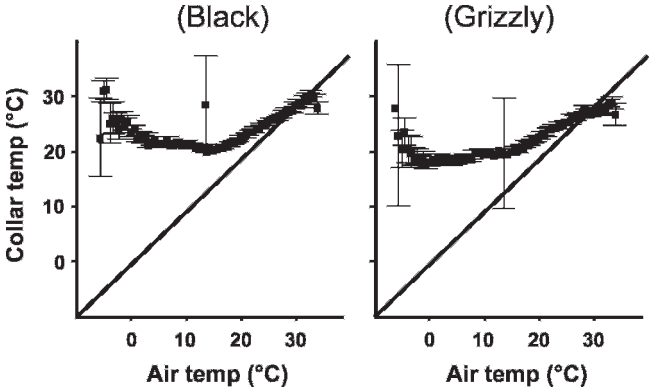


**Figure 3.** Error bar (95%) plot of the relationship between air temperature and collar temperature on black and grizzly bears. Diagonal line represents a perfect relationship between collar and air temperature. Data from Grand Teton National Park, Wyoming, USA, 2004–2006.

reserved by the Federal Communications Commission (FCC) for wildlife telemetry. Users must obtain narrow-band frequency allocation before deployment. The FCC has authorized S–S radio transceivers to operate throughout the 902–928-MHz bandwith, so frequency allocation is not required.

The S–S communication system we tested performed well. With the exception of breaking line-of-sight between the collar and receiving unit, we did not experience any major problems. We successfully met our objective of recovering GPS location data weekly. The data-transfer system performed to our expectations. We did incur additional costs associated with aircraft time when retrieving data, but some of those costs were reduced when we successfully retrieved data from the ground. Like others using GPS technology, the problems we encountered centered on fix success of the GPS units and were unrelated to the data-transfer system per se.

Based upon AIC values, the variable activity count was the most important predictor in logistic regression models, supporting previous findings that animal behavior has a major impact on fix success rates. Obbard et al. (1998) were the first to demonstrate that successful fixes were associated with time of day. Subsequent research by Graves and Waller (2006), Moe et al. (2007), and Heard et al. (2008) detected similar patterns. Most missed fixes occur when bears are passive. Moe et al. (2007) found that 78% of failed fixes in Scandinavian brown bears occurred when animals were passive. Our results showed that 73% and 79% of missed fixes occurred when we predicted black and grizzly bears, respectively, to be resting. Our findings support recommendations of Moe et al. (2007) that for studies of habitat selection, obtaining data from all 24 hours and dividing these data into relevant categories based on activity counts seems prudent.

Collar temperature was not an accurate measure of air temperature. We suspect that temperature in the collar was influenced by body posture and that resting bears likely insulated the canister. Hence, warm collar temperatures likely reflected resting behavior.

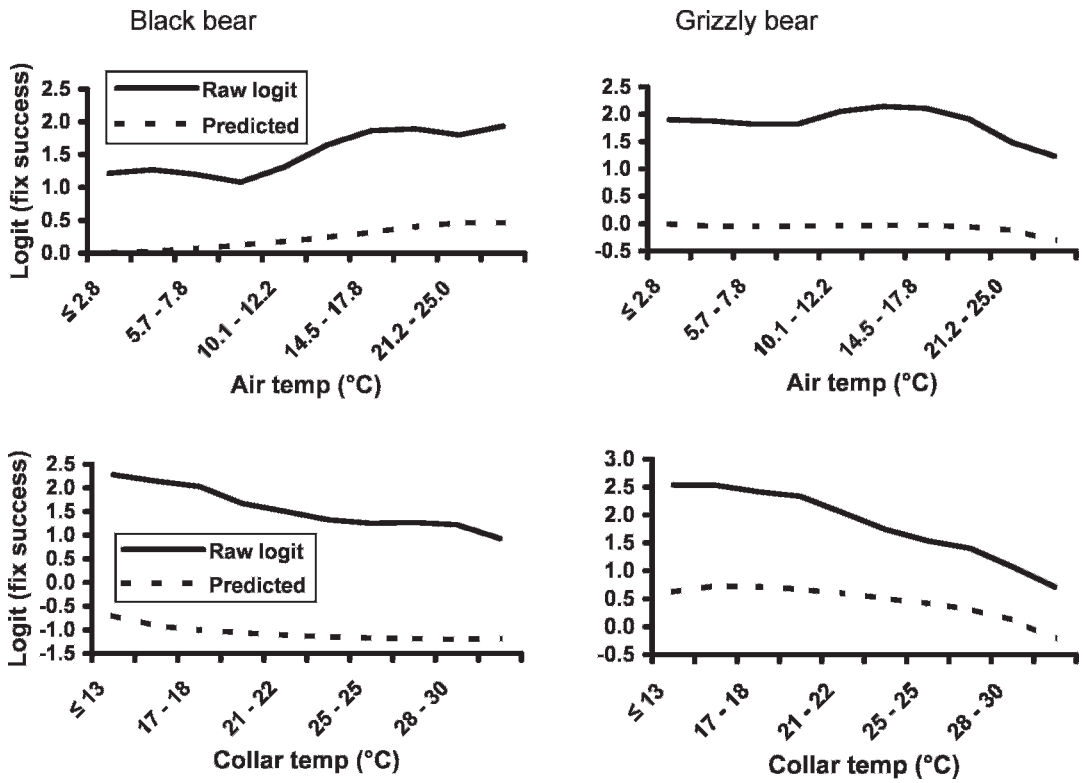


**Figure 4.** Plots of fix success (logit) for 10 ordinal 10% quantile bins of the raw data, and from the top post hoc models for black and grizzly bears. Logits of predicted fix success for black and grizzly bears based on results from the best post hoc models for both species using only beta coefficients for air or collar temperature, respectively. For clarity, plots of the raw and predicted logit do not include the intercept term. Data from Grand Teton National Park, Wyoming, USA, 2004–2006.

Both Graves and Waller (2006) and Heard et al. (2008) found positive relationships between fix success and distance moved between fixes. We likewise found a positive relationship between activity count and distances moved. Graves and Waller (2006) further recommended that future studies of fix success rate explore the relationship between activities like bedding with fix success. Our results clearly demonstrated a strong link between activity and fix success, with fewer successful fixes recorded when bears were likely to be resting. Our relationship between activity counts and distance moved likewise confirmed that movement rates are a reasonable measure of activity.

We recognize that the activity count recorded in the telemetry collar correctly identified most GPS fixes when bears were active but misclassified some active bears as resting. We also conclude that our discriminant function analysis did a reasonable job of discriminating between resting and active bears. We recognize that when counts are low, some bears are resting, whereas others may be feeding in a manner that returns low activity counts. As a result, we probably overestimated the true proportion of resting bears (low activity counts) whereas when bears are active we likewise underestimated the true proportion of active bears. Hence the peaks and troughs of activity were under- rather than over-amplified.

We did not focus on vegetation or terrain factors because they were addressed in a separate study (D. Ouren, United States Geological Survey, unpublished data), and findings indicated that fix success was invariant to most vegetation–terrain categories, with the exception of north facing slopes with heavy conifer cover. We also question whether fix success rates obtained with collars placed at fixed vegetation–terrain sites where multiple fix attempts occur in sequence (i.e., over a 24-hr period) are directly comparable to fix success for collared animals that are constantly moving on the landscape. However, we suspect that fix acquisition for stationary collars may represent an optimistic success rate for collars deployed on animals because our results and those of others clearly suggested animal behavior plays a strong role in GPS fix acquisition and there is likely an interaction between animal behavior and terrain–vegetation (Graves and Waller 2006, Heard et al. 2008).

We did not detect a relationship between our principal components of body size and fix success, which contrasts with the findings of Graves and Waller (2006). Likewise, fix interval did not appear in our top model predicting fix success and was not a significant predictor in models where it was the only covariate, which contrasts with findings of Mills et al. (2006) who found it took longer to get a successful fix with increasing intervals between fix events. We did not detect a relationship between angles of the GPS antenna relative to the sky and fix success for grizzly bears. Heard et al. (2008) found an interaction between collar orientation and canopy cover with lower fix success in heavy vegetation when the collar was on its side (90° orientation). Because we do not know what vegetation types bears were in

when fixes failed, we were unable to evaluate this. However, our results suggested that antenna orientation at deployment, across the range we tested, was not an important predictor of fix success. Of course, our test did not consider the bear's posture and potential changes in collar orientation after deployment. Our comparisons with results of Graves and Waller (2006), Mills et al. (2006), and Heard et al. (2008) must be tempered with caution because of differences among collar designs and associated software, which affect fix success and accusation times, making direct comparisons difficult.

The low ROC score from the independent black bear data somewhat surprised us, because both black bear populations were studied in the same ecosystem at the same time. However, models fit to the latter data set were not identical to those fit to our data. For example, the quadratic of activity count was important, but time did not occur in the top model, and the sign on betas for air and collar temperature changed. These results suggested there is considerable variability when analyzing factors that affect fix success and suggested researchers must be cautious when applying models built from a different sample to their data.

## MANAGEMENT IMPLICATIONS

Our tests of the S–S data-transfer system showed promise for this means of obtaining GPS telemetry fixes in near real time. This system thus has potential for other researchers where location information is required at frequent intervals.

We also demonstrated that GPS fix success was clearly linked to bear activity patterns, season of year, and measures of temperature both within the collar and in the environment. All appeared to be linked with behavioral patterns associated with resting or foraging–traveling. Activity counters appeared to be a reasonable measure of this behavior, and we recommend researchers consider including an activity-count system when deploying GPS collars. We also recommend researchers explore building separate models of habitat selection based upon categories of activity to account for bias in fix success associated with bear behavior. Finally, differences we observed between black and grizzly bears, and differences we observed between the 2 groups of black bears, demonstrated that researchers must take the time to evaluate their GPS telemetry system in their study areas to evaluate causes and consequences of missed fixes.

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