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Quantification and Accuracy of Activity Data Measured with VHF and GPS Telemetry

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Abstract

*Quantifying activity budgets and determining the accuracy of behavioral data obtained by telemetry is essential to understand the behavior of animals that are difficult to observe. We fitted 8 captive white-tailed deer (*Odocoileus virginianus*) with VHF or GPS collars to determine the accuracy of VHF variable-pulse sensors and GPS dual-axis sensors and validate the performance of VHF telemetry for the measurement of activity budgets. We also evaluated whether instantaneous activity counts could measure daily activity patterns of 16 free-ranging deer fitted with GPS collars on Anticosti Island (Québec, Canada). Comparison of VHF telemetry data and visual observations of active (feeding, moving, and standing) and inactive (resting) deer behaviors were correct in 74% of the scans. Using the activity values of 3 successive VHF scans, we increased accuracy to 84% of the observed behaviors and detected 87% of observed activity bouts. The accuracy of GPS activity data varied with orientation of the sensor: activity counts of vertical sensors (92% agreement) were better able to predict observed behaviors than activity counts from horizontal sensors (83% agreement). GPS activity sensors detected peaks of activity after dawn and at dusk in free-ranging deer. We conclude that dual-axis GPS motion sensors can be used to reliably record activity data and successive scans from VHF sensors can precisely detect activity bouts in large herbivores.* (WILDLIFE SOCIETY BULLETIN 34(1):81–92; 2006)

Key words

activity, activity sensor, circadian, Global Positioning System, GPS, Odocoileus virginianus*, radiotelemetry, VHF, white-tailed deer*.

Conventional Very High Frequency (VHF) telemetry and animal tracking with Global Positioning System (GPS) collars allow animal ecologists to quantify the activity of wildlife and have been used to measure time budgets of species that are difficult to observe. Initially, signal strength (Singer et al. 1981, Cederlund et al. 1989, Hölzenbein and Schwede 1989) and linear distance between relocation points determined by radiotelemetry (Sparrowe and Springer 1970, Kammermeyer and Marchinton 1977), and later by GPS collars (Merrill and Mech 2003), were used to measure activity budgets of many species. The interpretation of signal evenness, however, has been found to be subjective and influenced by particular animals and the environment between the transmitter and the antenna (Garshelis et al. 1982, Gillingham and Bunnell 1985, Rouys et al. 2001). The use of relocation distances has been criticized because estimates of radiolocations have large errors (for VHF telemetry) and distance traveled may misclassify stationary, but active, animals as inactive (Craighead et al. 1973, White and Garrott 1990, Rouys et al. 2001). VHF and GPS activity sensors made it possible for biologists to quantify remotely continuous or instantaneous activity data.

Three types of VHF activity sensors have been used. Reset sensors are equipped with a timer and a mercury switch that initiate a pulse-rate change when the switch is not triggered within a specified time lapse. Tip-switch sensors transmit different pulse rates depending on orientation of the sensor. The number of pulse-rate changes in a specific time period may be used to index activity. Reset sensors and tip-switch sensors were found to be easily triggered by head and comfort movements made by resting animals (Garshelis et al. 1982, Gillingham and Bunnell 1985). Nonetheless, a strong correlation ($r = 0.9$) was found between distance moved by black bears (*Ursus americanus*) and activity measured by reset sensors (Garshelis et al. 1982). The proportion of time active measured with tip-switch sensors could be estimated from telemetry data with 90% accuracy in a study of black-tailed deer (*Odocoileus hemionus columbianus*; Gillingham and Bunnell 1985). To refine the use of tip-switch sensors, Beier and McCullough (1988) increased sampling interval from 1 to 5.25 minutes and this led to the correct classification of 98% of individual samples. In a validation study of tip-switch sensors used to measure time budget of Dall's sheep (*Ovis dalli*), examination of scan pattern changes rather than fixed time samples also increased accuracy of activity detection (Hansen et al. 1992). Variable-pulse sensors were developed because it was thought that by adding extra pulses to every switch movement, specific behaviors such as moving versus feeding could be identified from different pulse patterns. As for tip-switch sensors, variable-pulse sensors are triggered by individual movements and changes in pulse rates are not dependent on a specific time-delay as for reset sensors. The first versions of variable-pulse sensors assessed movement periodically (every 0.25 sec), but an increase in animal movement did not necessarily result in higher pulse rates because instantaneous samples of movements missed concentrations of rapid pulses (Gillingham and Bunnell 1985). Rather than sampling movement instantaneously, later versions of variable-pulse sensors, such as the ones we used, integrated the amount of movements by adding pulses to a base pulse rate. Depending on scan duration (1–5 min), Relyea et al. (1994) found that 74–81% of the scans discriminated resting deer from non-resting deer, but that variable-pulse sensors

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could not discriminate amongst different active or inactive behaviors. Errors with variable-pulse sensors are still associated with head and comfort movements in resting periods or with sensors that fail to detect movements while animals are active, but keep their head still for extended periods.

Methods for effectively gathering continuous VHF sensor data on numerous animals also have been developed. In the beginning researchers listened directly to signal changes (Garshelis et al. 1982). Other systems registered signal variations on strip charts (Gillingham and Bunnell 1985, Beier and McCullough 1988, Hansen et al. 1992). Gathering data was still time consuming because every signal change had to be manually recorded. In the 1990s new automated systems that recorded time and pulse rates electronically in an immediately usable form were developed (Relyea et al. 1994). We used a version of this automated data-logging system to gather and analyze data on deer activity budgets.

In the past decade, GPS collars have been equipped with different motion sensors: tilt-switch activity sensors that tally head-down occurrence (Rumble et al. 2001) and activity counters composed of dual-axis motion sensors sensitive to vertical and horizontal head and neck movements (Moen et al. 1996, Turner et al. 2000, Adrados et al. 2003). The first validation tests of activity counters were conducted on GPS 1000 collars (Lotek Engineering, Newmarket, Ontario, Canada; Moen et al. 1996, Turner et al. 2000, Adrados et al. 2003). Both the vertical and the horizontal sensors of GPS 1000 collars consist of a cylinder that contains a small sphere. An integrated datalogger registers the number of times that the sphere hits the extremities of the cylinders in a specific time interval. The activity counts of GPS 1000 collars are combined values of the vertical and the horizontal sensors. When the GPS fix interval is longer than the activity observation window, the activity value recorded is averaged over the GPS fix interval. For example, if the GPS fixes are taken every 2 hours and the activity counts are recorded at 5-minute intervals, then the reported activity counts would be the average of 24 observations for every 2-hour period. Moen et al. (1996), Turner et al. (2000), and Adrados et al. (2003) validated these activity counters with captive animals and were able to classify correctly 91%, 95%, and 69% of the active samples and 75%, 91% and 89% of the inactive samples, respectively. Moen et al. (1996) also validated activity sensors on free-ranging moose (*Alces alces*) and found that the amount of time that moose were active as estimated from activity sensors was comparable to daily time active reported in other studies of moose for the same region. Moen et al. (1996) suggested that activity counts should be recorded during a time interval $\leq$10 minutes and that they should not be averaged over the entire GPS fix interval. Recently, new models of GPS collars have allowed us to record 2 activity counts, one for the vertical and one for the horizontal sensor. Furthermore, each value is the actual activity count recorded during the observation window directly preceding the reported GPS position and not an average as for the GPS 1000 collars. These new sensors, however, have never been validated in the field but may provide a considerable improvement over older models for fine-scale analysis of foraging behavior and habitat use because they allow the correlation of actual activity counts to reported GPS positions and corresponding habitat. A comparison of activity counts measured on captive deer fitted with GPS collars and the corresponding observed behavior would allow the verification of sensor accuracy. Another approach to validate activity sensor data would be to look at circadian activity patterns of free-ranging animals fitted with GPS collars. Circadian activity peaks synchronized with dawn and dusk are widely observed in white-tailed deer (*Odocoileus virginianus*; Montgomery 1963, Kammermeyer and Marchinton 1977, Beier and McCullough 1990, Rouleau et al. 2002). If the sensors can track activity peaks as daylight changes throughout seasons, then this would indicate that the sensors are reliable.

Our main objective was to validate the use of motion sensors to estimate the activity of free-ranging large herbivores. We wanted to 1) determine the accuracy of VHF variable-pulse sensors and GPS dual-axis sensors by comparing sensor data with observed behavior, 2) determine the performance of VHF variable-pulse sensors to estimate activity budgets, and 3) verify the ability of instantaneous activity counts generated by GPS motion sensors to estimate daily activity patterns of free-ranging deer.

Study Area

We conducted this study on Anticosti, a 7,943-km^2 island located in the Gulf of St. Lawrence, Québec, Canada (49°28'N, 63°00'W). The climate was maritime and characterized by cool summers and mild and long winters. Mean daily temperature was 15°C in July and −14°C in January (Environment Canada 1993). The boreal forest that prevailed on Anticosti was dominated by balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*P. mariana*), (Rowe 1972). White-tailed deer were introduced on Anticosti in 1896 and, in the absence of predators, their numbers increased rapidly to >100,000. Currently, deer density is about 20/km^2 and severe impacts of browsing on the vegetation have occurred across the whole island (Potvin et al. 2003).

Methods

Calibration of VHF and GPS Motion Sensors on Captive White-Tailed Deer Fawns

Deer captures.—We captured 8 white-tailed deer fawns between 21 November and 12 December 2003 with dartguns, Stephenson box-traps, or cannon nets. We released deer in 2 50 × 80-m semi-natural enclosures that contained cover, forage, and daily supplemental food placed in a feeder. Low tree branches and shrubs were absent in the enclosures. The Animal Care and Use Committee of Université Laval, Québec, Canada approved all capture methods (reference number 2003-014).

VHF collars.—LMRT-3 VHF collars equipped with STO-2a variable-pulse sensors (Lotek Engineering, Newmarket, Ontario, Canada) were fitted on 4 deer. Each collar had a board fitted parallel to the ground on the bottom of the transmitter case to which a tilt-switch oriented perpendicular to the spine of the animal (horizontal sensor) was attached. Pulses were automatically added each time the switch was triggered. Transmitter signals from the collars were received and recorded in a SRX-400 Version W9 receiver-datalogger (Lotek Engineering, Newmarket, Ontario, Canada) connected to a multidirectional antenna and a 12-V battery to ensure a constant electrical input.

We programmed the receiver to measure duration between 2 pulses for 65 consecutive pulses, record mean pulse rate, and automatically switch to scan another transmitter. The time needed to record 65 pulses was, thus, dependent on pulse rate. As the SRX receiver scanned one transmitter at a time and because 4 individuals were followed each day, a measure of pulse rate for each deer was obtained approximately every 4 minutes. At the end of the day, we downloaded data on a laptop computer with Winhost software 1.0.0.1 (Lotek Engineering, Newmarket, Ontario, Canada).

GPS collars.—The GPS 2200R collars (Lotek Engineering, Newmarket, Ontario, Canada) that we used were equipped with dual-axis motion sensors (vertical and horizontal) that recorded the number of times a switch was triggered during the 4 minutes immediately preceding a GPS fix. Both sensors are fixed on a board parallel to the ground in the transmitter case. The vertical sensor is oriented parallel to the spine of the animal and the horizontal sensor is oriented perpendicular to the spine of the animal. We obtained GPS locations every 5 minutes. The maximum number of events that could be recorded during each 4-minute interval was 255.

Behavioral observations.—We waited 48 hours after deer had been introduced into the enclosures before beginning visual observations so that deer could habituate to wearing a VHF or a GPS collar. We observed deer during mornings and afternoons from a 4-m-high observation tower between 21 November and 23 December 2003. When needed, we used 8×42 binoculars or 20–25×60 spotting scopes. We recorded the time and type of each behavior on tape recorders. We set watches to match the time on the receiver and the GPS collars. We recorded 4 behaviors during observations: feeding, moving, standing, or resting.

Validation of GPS Motion Sensors on Free-Ranging Deer

We monitored 16 free-ranging white-tailed deer does equipped with GPS 2200R collars between July and November 2001 ($n = 8$) and 2002 ($n = 8$). We captured does in late June or early July in peat bogs with a net gun fired from a helicopter. Handling time was <5 minutes and we released deer at the capture site. We set GPS fix interval to 2 hours and recorded activity counts during the 4 minutes immediately preceding every GPS location. We predicted that if the motion sensors recorded activity accurately, we could track activity peaks at dawn and dusk as daylight changed throughout summer and autumn.

Data Analysis

Calibration of VHF and GPS motion sensors.—All VHF mean pulse rates (BPM) were divided by the transmitter's respective base pulse rate (from 59–64 pulses per minute). A sensor that had not moved would thus give a relative BPM of 1. Due to receiver or collar variations, pulse rate could be smaller but close to base pulse rate (i.e. >0.95 of the base pulse rate). We rounded these data to 1 because we considered them as equivalent to base pulse rate. When movements occurred, scans should then give a relative BPM higher than 1 (up to about 2.5). The dual-axis motion sensors of GPS 2200R collars provided 2 distinct activity counts, one for vertical and the other for lateral head and neck movements. Number of events ranged from 0–255.

To test whether we could relate ranges of relative BPM and GPS activity counts to different behaviors, we selected the periods when deer were observed performing only 1 of the 4 behaviors identified for the whole sampling period. We then compared means and ranges of relative BPM and GPS activity counts (Fig. 1). We determined the percentage of correctly classified scans for VHF and GPS sensors when deer were active (i.e. feeding, moving or standing) or inactive (resting) for the entire sampling period using different mean relative BPM for VHF collars and different activity counts for GPS collars as separation thresholds. Samples with relative BPM and activity counts under the threshold value were considered inactive and samples over the threshold value were considered active. We determined the value of the best threshold by plotting the percentage of correctly classified samples when deer were active and inactive against all possible relative BPM or activity count thresholds (Fig. 2).

Calculation of activity bouts with VHF collars.—To compare the results obtained with VHF collars to observed activity budgets and calculate the accuracy of scans, we combined the information from 1 scan with that of the following 2 successive scans (i.e., a time interval of 10–15 minutes). We depicted activity bouts using the following criterions: an inactive bout began when at least 3 consecutive scans considered as inactive were recorded, and, conversely, an animal was classified as active when at least 3 consecutive scans considered as active were recorded (Fig. 3). To compare our method of estimating active and inactive bout durations from telemetry-derived data to observed data, we simply correlated the observed and estimated proportions of time active and quantified the number of correctly classified activity bouts for each day of observation. We also calculated the mean daily duration of active and inactive bouts and compared the estimated and observed results with Student's t-tests. When needed, we either square-root or log-transformed bout length to achieve data normality (Zar 1999).

Validation of activity counts of GPS collars on free-ranging deer.—GPS collars recorded 12 4-minute activity counts per day (every 2 hr) for each free-ranging deer for both vertical and horizontal motion sensors. We classified data into 4 periods of the day and the numbers of 4-minute activity counts varied for each period: dawn (from half an hour before sunrise to an hour after, $n = 1$), dusk (from an hour before sunset to half an hour after, $n = 1$), day ($n = 4$–7), and night ($n = 3$–6). Mean activity counts were, thus, used for day and night. For each sensor, we used repeated-measures ANOVAs (proc GLM (General Linear Models Procedure); SAS Institute 1989) to evaluate the influence of the period of the day on activity counts from July–November and we compared the results with the LSMEANS statements of SAS Institute (1989). We ensured that the residuals were normally distributed (Shapiro–Wilk test) and were homogeneous by visual examination of the plots. We square-root-transformed horizontal activity counts to normalize the residuals (Zar 1999). Unless specified, all results are presented as $\bar{x} \pm 1$ SE.

Results

We collected 102 hours of observation on 4 captive deer wearing 4 different VHF collars and 105 hours on 4 other captive deer wearing 3 different GPS collars. We observed each deer with a VHF collar for a total of 6 days and each deer with a GPS collar for 3 to 6 days (approx 4 hr of observation per day). Deer spent 30 $\pm$ 2% of their time feeding, 13 $\pm$ 1% standing, 13 $\pm$ 2% moving, and 43 $\pm$ 4% lying ($n = 42$ deer-days) during the daily observations. We obtained simultaneous data of relative BPM and

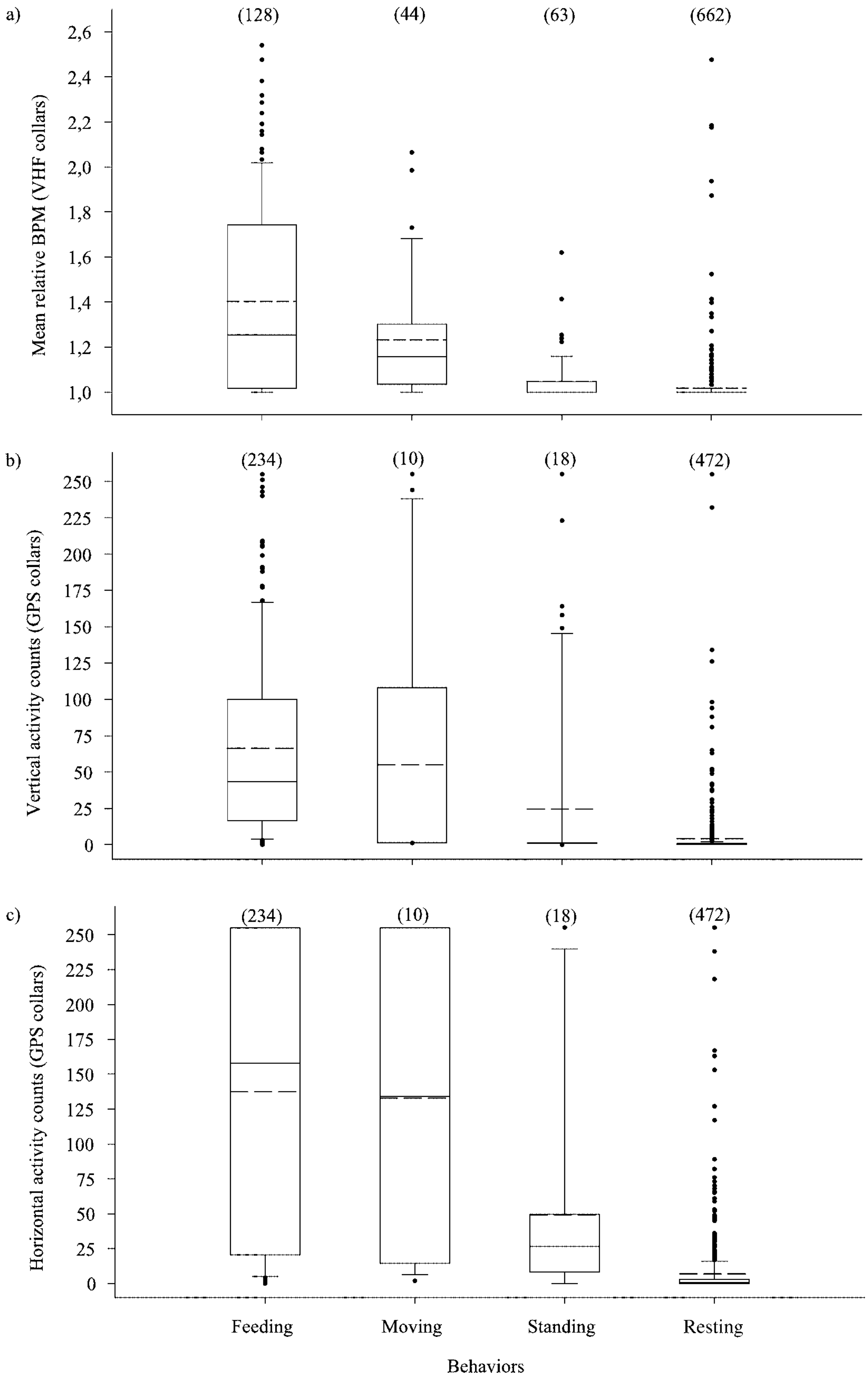


Figure 1. Box plot representations of relative mean pulse rates (BPM) for (a) VHF variable-pulse sensors and of (b) activity counts for vertical, and (c) horizontal GPS activity sensors for the 4 different behaviors observed. Collars were fitted to white-tailed deer fawns that were simultaneously observed on Anticosti Island, Québec during 21 November–23 December 2003. Solid middle bars correspond to the median for each behavior observed and dashed bars symbolize the mean value. Error bars represent 90% quantiles and dots are outlier values ($<$10% of data). Numbers in parentheses represent the number of telemetry samples for each behavioral category. Distribution of VHF relative BPM and GPS activity counts show clearly how values overlap between active (feeding, moving, and standing) and inactive (resting) behaviors.

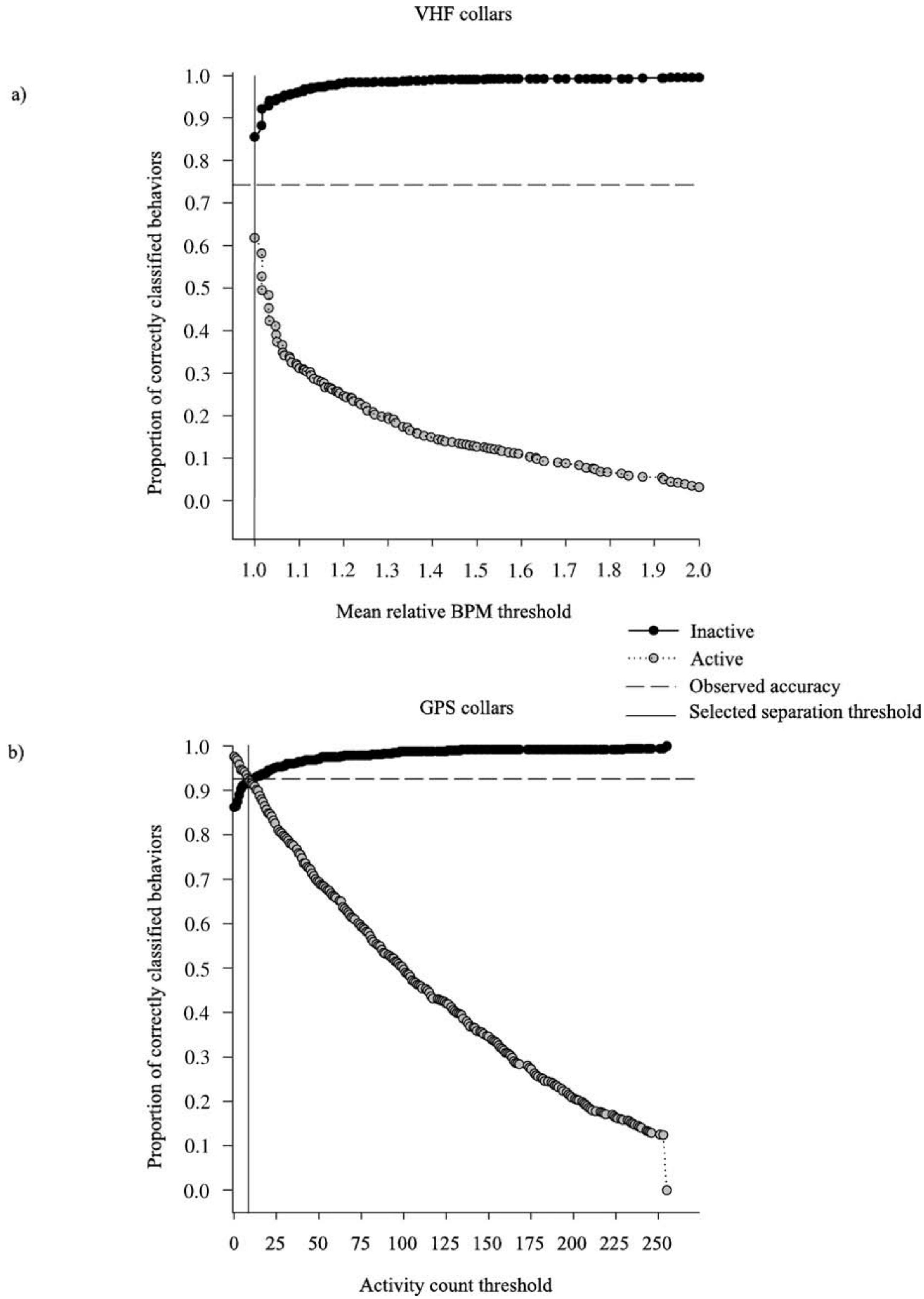


Figure 2. Determination of a criterion to separate (a) relative mean pulse rates (BPM) for VHF collars equipped with variable-pulse motion sensors, and (b) activity counts for GPS collars equipped with double-axis motion sensors into active and inactive behaviors of white-tailed deer on Anticosti Island, Québec. The percentages of correctly classified samples in relation to all possible separation thresholds of relative BPM or activity counts are illustrated. The best separation threshold is found where the 2 curves intersect or where the classification error of active and inactive behaviors is the smallest.

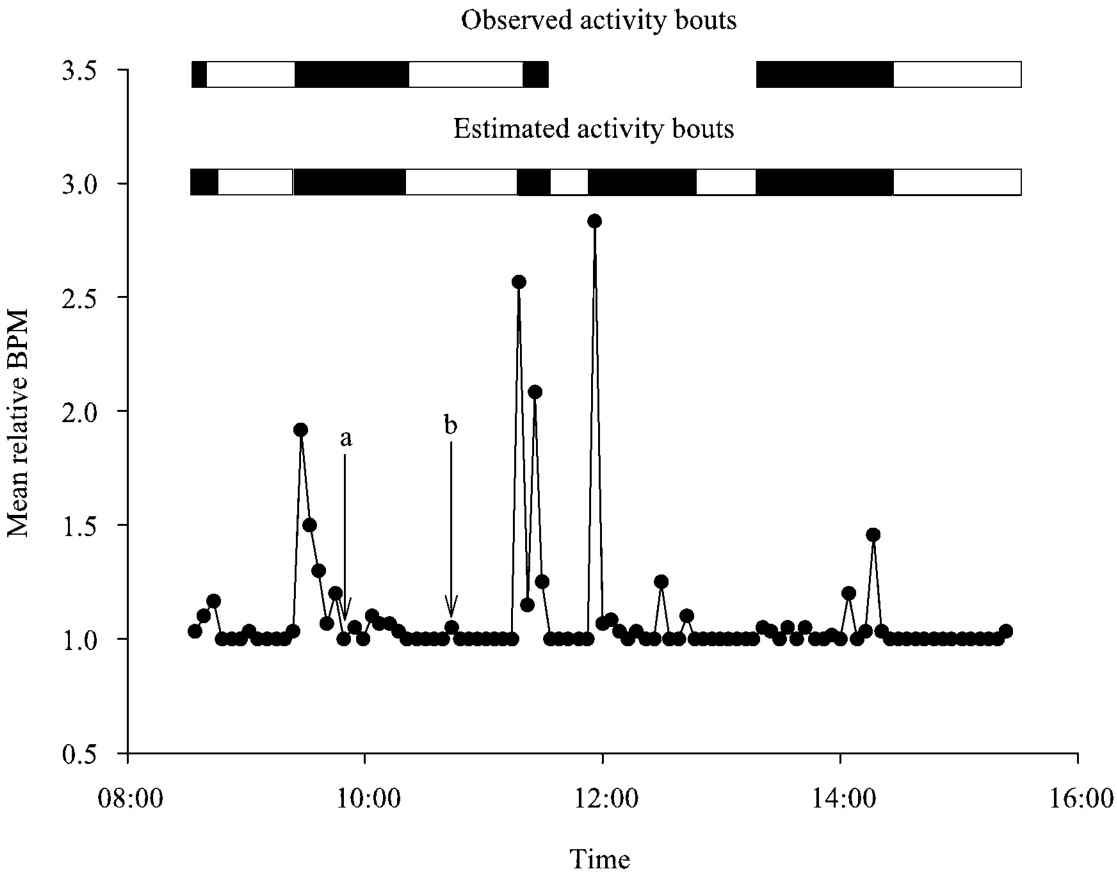


Figure 3. Observed behavior and relative mean pulse rate (BPM) obtained during one day for a white-tailed deer fawn fitted with a VHF collar equipped with a variable-pulse sensor on Anticosti Island, Québec. An inactive bout (white rectangles) began when at least 3 inactive scans (relative BPM of 1) were observed. To return to an active bout (black rectangles), at least 3 active scans (relative BPM higher than 1) had to be observed. Note the presence of single inactive scans surrounded by (a) active scans, and (b) single active scans surrounded by inactive scans that did not change the calculation of the duration of the bout.

behavioral observations for 1,357 relative BPM samples from VHF collars and 1,126 4-minute samples from GPS collars.

Determination of Specific Behaviors

For VHF collars, the ranges of 90% quantiles for relative BPM of resting (1–1.02), standing (1–1.16), feeding (1–2.02) and moving (1–1.69) overlapped considerably (Fig. 1a) because they all included 1. Ranges of active behaviors, however, were much larger than for inactive behaviors (Fig. 1a). For GPS collars, 90% quantiles for vertical activity counts ranged from 0–4 for lying, from 2–148 for standing, from 4–166 for feeding and from 2–237 for moving and, thus, also overlapped considerably (Fig. 1b). Overlap ranges were even greater for horizontal activity counts (Fig. 1c). Even if relative BPM and activity counts of standing deer resembled those of lying deer, standing deer were considered active because they were observed during active bouts and were standing only for short periods (VHF: $\bar{x} = 33 \pm 1$ seconds; GPS: $\bar{x} = 19 \pm 2$ seconds).

Calibration of VHF and GPS Motion Sensors

Deer were either 100% active ($n = 662$) or 100% inactive ($n = 662$) for 1,324 scans of the VHF collars. We identified the best separation threshold of relative BPM as 1 (i.e. the smallest classification error, Fig. 2a). The best separation criterion was found where the 2 curves intersected or where the classification error of active and inactive behaviors was the smallest (Relyea et al. 1994). For example, if we had used a separation threshold of 1.3 mean relative BPM for VHF collars, we would have correctly classified 97% of the inactive samples (Fig. 2a, top curve), but only 20% of the active samples (Fig. 2a, bottom curve). We correctly discriminated 87% and 61% of inactive and active samples, respectively, for a total of 74% of correctly classified samples (Table 1). Most errors occurred when deer were observed feeding or moving, but VHF telemetry signals indicated that they were inactive. Using all 4-minute intervals when deer were completely inactive ($n = 472$) or active ($n = 614$) (Fig. 2b), we found that for GPS collars the best cut-off activity count to separate active from inactive samples was a value of 10 for both vertical and horizontal sensors. This separation criterion allowed us to correctly classify 92% and 83% of the samples for the vertical and the horizontal activity sensor, respectively (Table 2).

Calculation of Activity Bouts

Using the values of 3 successive VHF scans, we correctly estimated 92% ($n = 662$) of the scans related to inactive behaviors and 77% ($n = 662$) of the scans related to active behaviors and thus correctly classified 84% of the scans (Table 1). A strong correlation existed between the proportion of time active observed and estimated by VHF activity sensors ($r = 0.81$; $n = 24$ deer-days; $P \leq 0.001$; Fig. 4). Mean time observed active per day was slightly higher ($\bar{x} = 56 \pm 5\%$, $n = 24$ deer-days) than estimated time spent active ($\bar{x} = 50 \pm 6\%$, $n = 24$ deer-days; $t_{23} = 1.86$; $P = 0.08$). In addition, we

Table 1. Individual and combined relative mean pulse rates (BPM) from variable-pulse activity sensors that correctly classified[a] the observed behaviors of captive white-tailed deer fawns fitted with VHF collars during 21 November–23 December 2003 on Anticosti Island, Québec.

		Percentage of relative mean BPM correctly classified					
		Individual scans			Combination of 3 scans[c]		
Deer ID	***N*[b]**	**Inactive**	**Active**	**Total**	**Inactive**	**Active**	**Total**
30	297	90	61	74	93	86	89
35	341	88	50	70	95	72	84
39	310	84	99	92	82	99	91
40	376	86	32	60	95	53	75
Total	1,324	87	61	74	92	77	84

[a] The threshold value for relative mean BPM was determined graphically (Fig. 2a).
[b] *N* refers to the number of scans when deer were observed either 100% active or 100% inactive.
[c] To determine whether each individual scan should be considered active, we used the information of the following 2 scans. Samples were considered active until at least 3 successive scans changed to inactive relative mean BPM values and vice versa.

Table 2. Activity counts recorded during 4-minute intervals that corresponded[a] to observed behaviors from captive white-tailed deer fawns fitted with GPS collars during 21 November–23 December 2003 on Anticosti Island, Québec.

		Percentage of 4-minute intervals correctly classified			
		Vertical sensor		Horizontal sensor	
Deer ID	***N*[b]**	**Inactive**	**Active**	**Inactive**	**Active**
29	451	90	96	87	63
32	219	95	96	64	100
33	296	95	79	94	97
41	120	88	90	59	99
Total	1,086	92		83	

[a] The threshold value for activity counts was determined graphically for each sensor (Fig. 2b).
[b] *N* refers to the number of periods observed when each deer was either 100% active or 100% inactive.

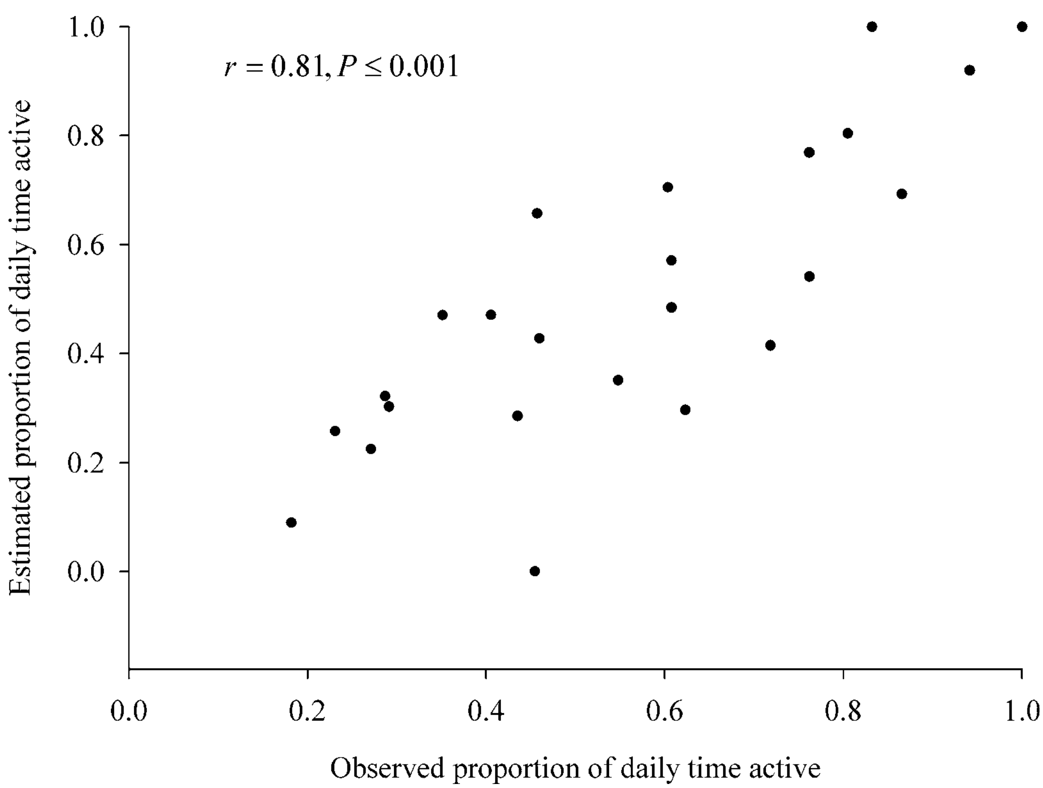


Figure 4. Relationship between observed and estimated proportion of daily active time obtained with variable-pulse activity sensors of VHF collars fitted to 4 white-tailed deer fawns each observed for 6 days ($\bar{x}$ = 4 hr of observation per day) on Anticosti Island, Québec.

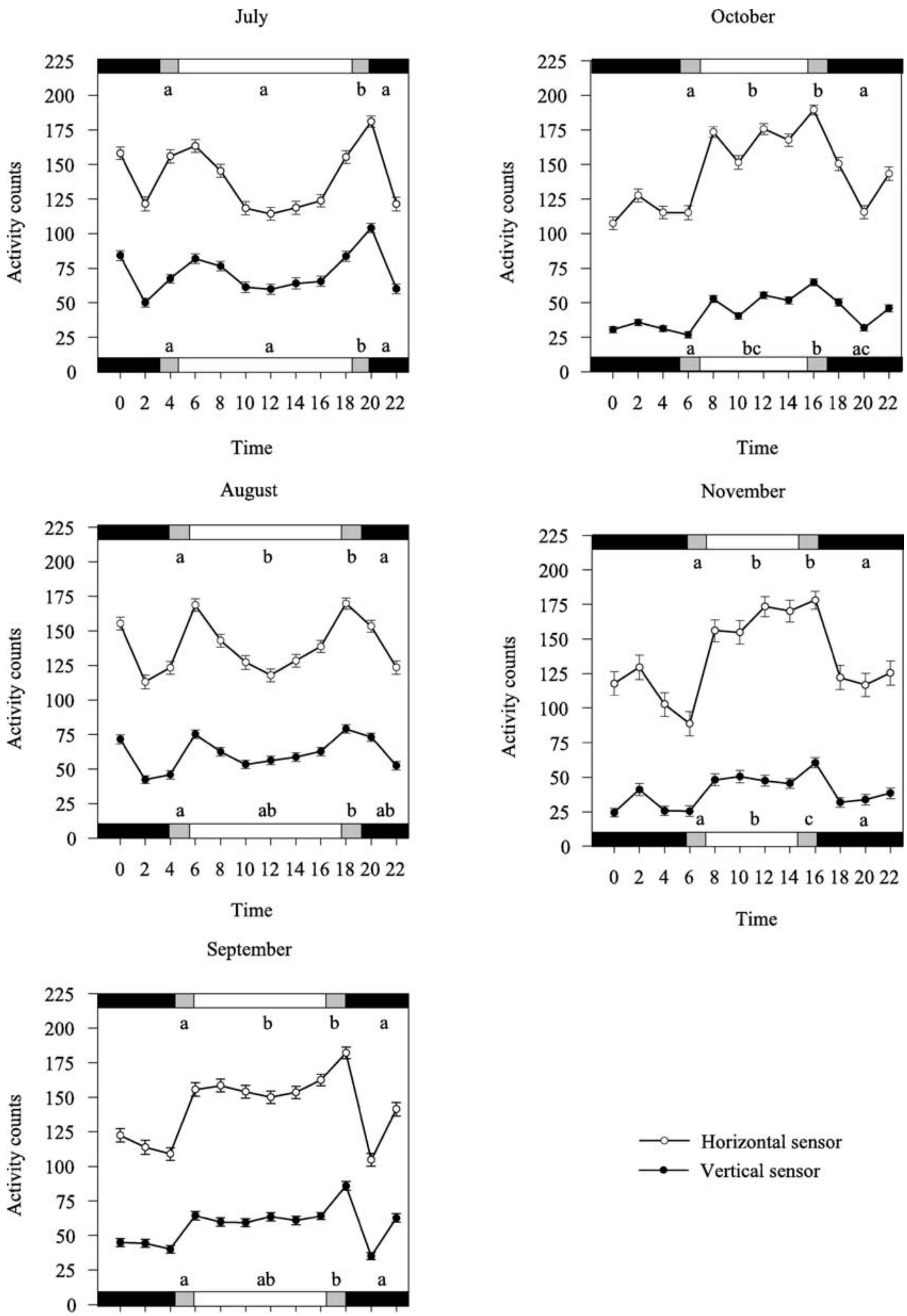


Figure 5. Mean activity counts (±1 SE) recorded by horizontal and vertical sensors of GPS collars fitted on free-ranging deer on Anticosti Island in summer and autumn 2001 ($n = 8$ deer) and 2002 ($n = 8$ deer). Grey sections indicate dawn and dusk, white sections daytime and black sections nighttime. Identical letters identify mean activity counts that did not differ statistically between periods of the day: the top row shows the results for the horizontal sensor and the bottom row for the vertical sensor. Analyses were performed separately every month for each sensor.

correctly estimated 89% of inactive bouts and 82% of active bouts. We found no difference between the mean duration of active bouts estimated by variable-pulse sensors ($\bar{x}$ = 62 ± 9 minutes, n = 23 deer-days) and those observed ($\bar{x}$ = 64 ± 8 minutes, n = 23 deer-days; t_{22} = −0.45; P = 0.65). The duration of inactive bouts estimated ($\bar{x}$ = 75 ± 9 minutes, n = 23 deer-days) and observed ($\bar{x}$ = 71 ± 8 minutes, n = 23 deer-days; t_{22} = −0.90; P = 0.44) also were comparable. We also compared each deer separately to account for individual deer-collar effects, and found no differences.

Activity of Free-Ranging Deer

During the summer and autumn of 2001 and 2002, we found an influence of the period of the day (vertical: $F_{3,54} = 7.69$, $P \leq 0.001$; horizontal: $F_{3,54} = 6.89$, $P \leq 0.001$) and month (vertical: $F_{4,216} = 46.93$, $P \leq 0.001$; horizontal: $F_{4,216} = 4.67$, $P \leq 0.001$) on mean activity counts of free-ranging does. Mean activity counts decreased from July to November (Fig. 5). The vertical and horizontal activity sensors revealed 2 daily activity peaks synchronized just after dawn and during dusk from July to November (Fig. 5). The activity peaks closely tracked the changes of daytime duration. The interaction between period of the day and month was highly significant for horizontal sensors ($F_{12,216} = 6.80$, $P \leq 0.001$) but, although the direction of the results was similar, the interaction was not significant for vertical sensors ($F_{12,216} = 1.43$, $P = 0.15$).

Discussion

Our study revealed that activity sensors of both VHF and GPS collars can provide reliable information on activity budgets and patterns of large herbivores. Data from VHF and GPS activity sensors allowed us to determine accurately 74% and 88% of observed behaviors, respectively, by using a unique separation criterion for each type of collar. In addition, activity sensors of VHF collars accurately detected 87% of activity bouts.

Determination of Specific Behaviors

Particular behaviors could not be identified from mean relative BPM for VHF collars or activity counts for GPS collars. Validation studies have never been successful in assigning distinct patterns or ranges of activity sensor data to more specific behaviors than active and inactive behaviors (Gillingham and Bunnell 1985, Beier and McCullough 1988, Hansen et al. 1992, Relyea et al. 1994). A deer may engage in several different activities during a 1-minute interval. Feeding and walking deer often move their heads similarly and, thus, trigger switches equally. Standing deer do not trigger the switch often and pulse patterns resemble those of resting deer. This resulted in strong overlap of relative BPM and activity counts between behaviors, and observations were, thus, classified by the proportion of time that deer were observed active or inactive. Deer feeding, moving, or standing were considered active and resting deer were considered inactive. Distinguishing between feeding and walking is not essential in most studies interested in foraging behavior because deer spend most (90–95%) of their active time foraging during the plant-growing season (Beier and McCullough 1988, Gillingham et al. 1997).

VHF Collars

We developed a criterion that correctly distinguished 74% of relative BPM samples. The accuracy of our collars was comparable to other validation studies of variable-pulse sensors (73–81% Gillingham and Bunnell 1985, Relyea et al. 1994), but lower than for tip-switch activity sensors (>90% Gillingham and Bunnell 1985, Beier and McCullough 1988). Tip-switch sensors have possibly given more accurate results than variable-pulse sensors because switches are oriented parallel to the spine of the animal (vertical sensors) and are, thus, more sensitive to foraging and walking movements.

Inactive samples were correctly classified in 87% of the cases and accuracy was high and constant among deer (84–90%). Sensors transmitted an active signal only 13% of the time when deer were lying compared to 27% for mule deer (*Odocoileus hemionus*; Relyea et al. 1994) and 14% for black-tailed deer (Gillingham and Bunnell 1985). A large proportion of active behaviors (39%), however, were misclassified into inactive behaviors. By analyzing the information of 3 successive scans, we reduced this percentage to 23% and correctly classified 87% of active bouts. Misclassification of active behaviors was also rather high (10–63% of inactive pulses depending on the type of active behavior) for variable-pulse sensors fitted on captive black-tailed deer (Gillingham and Bunnell 1985). Relyea et al. (1994) found a higher and more constant accuracy (74–82%) for active samples of free-ranging deer who had greater movement rates than captive deer. Differences in study results might be due to the observation of captive deer that move slowly (Gillingham and Bunnell 1985, Beier and McCullough 1988, this study). Many active sequences did not induce a change in pulse rates because deer walked slowly with their heads in a horizontal position or kept their heads down to feed for several minutes, with imperceptible sensor movement.

Inaccuracy also varied between individuals (1–68%). Variability could be attributed to individual differences in movement such as more head tipping while walking. The fit of the collar around the neck also could influence how easily the switch is triggered by movements. For example, a tighter fit could help to trigger the sensor more easily and provide higher rate values. On the contrary, a looser fit could allow the collar to slide on the neck rather than tilt the mercury switch during certain behaviors. We consider this possibility as a minor problem in our study however, because all collars were adjusted the same way. Head movements and tightening of the collar can vary depending on the age-sex class of an individual and on the season. Researchers should, therefore, be careful in analyzing activity data collected through long periods of time over many animals.

Taking into account 3 successive scans in our quantification of the length of activity bouts allowed us to accurately determine 87% of active and inactive bouts. Active periods were characterized by fast pulses interspersed by slow pulses. Using 3 successive scans considerably decreased the effect of misclassified individual scans. Inactive bouts were depicted by lasting and constant signals equal or very similar to base pulse rates and could also be differentiated from active bouts, even if some individual scans were misclassified. We conclude that variable-pulse sensors are a reliable method to quantify activity budgets for behavioral studies when the information of successive scans is used, but individual samples are less precise.

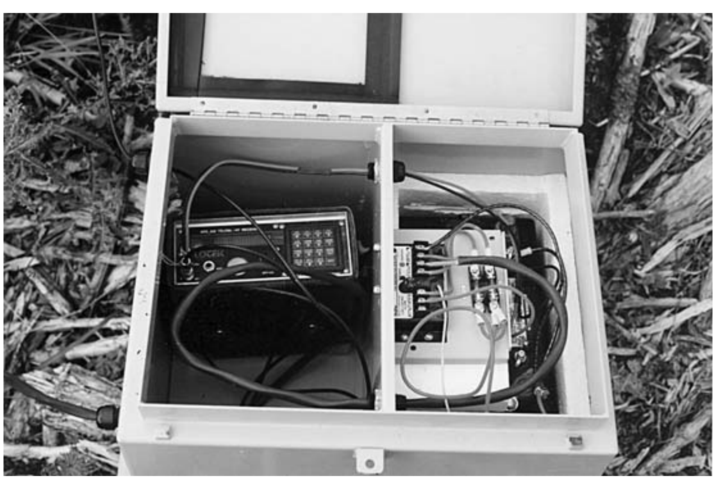
GPS Collars

The horizontal sensor of GPS collars was more sensitive than the vertical one and detected head movements even when captive deer were lying or standing. These results are consistent with the study

VHF receiver-datalogger connected to a multidirectional antenna and solar panel. Photo by S. Côté.

White-tailed doe fitted with a GPS 2200R collar equipped with dual-axis activity sensors. Photo by J.-P. Tremblay.

of Relyea et al. (1994) who also found that horizontal sensors of VHF collars were activated when deer were lying or standing. Due to its greater sensitivity, the horizontal sensor lost some information because it reached the maximum activity count (255) more often than the vertical sensor. Over-sensitivity to slight movements is not necessarily recommended for activity sensors because it then becomes more difficult to discriminate active from inactive behaviors and greater variations of activity counts are recorded between individuals. Better classifications of active and inactive samples with VHF motion sensitive tip-switches were also found using vertical sensors (Beier and McCullough 1988, Hansen et al. 1992).



VHF receiver-datalogger that allowed recording of 24 h activity budgets. Photo by S. Côté.

Deer fitted with a LMRT-3 VHF collar equipped with STO-2a variable-pulse sensors, Anticosti Island. Photo by S. Côté.

Our method provided a valid classification of active and inactive samples. Using a cut-off value of 10 for both sensors allowed us to classify correctly 92% and 83% of the samples for vertical and horizontal sensor, respectively. Other studies (Moen et al. 1996, Turner et al. 2000) on GPS activity sensors used higher cut-off values to discriminate active from inactive behaviors, but these sensors recorded a combined value of vertical and horizontal sensor instead of 2 separated values. Adrados et al. (2003) developed an individually based method to discriminate active from inactive behaviors using the mean daily activity count of each collar as a reference. This method is useful because it avoids bias due to potential variations in collar tightening among animals and seasons. The horizontal sensor of our GPS collars was more sensitive and variable than the vertical sensor and, thus, may need to be calibrated for each individual or used with an individually-based method. An individually-based method, however, is not necessary when using a vertical sensor that records actual activity counts. The vertical sensor of our collars was very accurate and using a cut-off value of 0 instead of 10, would still have correctly identified 86% and 97% of active and inactive samples, respectively. The calibration of GPS motion sensors on captive deer allowed us to validate the use of these sensors to quantify activity of free-ranging animals. We also compared the magnitude and distribution of activity counts from captive deer to those from free-ranging deer and found that they were similar. Therefore, we are confident that the magnitude of the activity of free-ranging animals can be reliably captured with the sensors.

GPS collars are widely used to study habitat use of large herbivores across seasons or years. GPS positions are usually taken at intervals varying from 1 to 4 hours. Moen et al. (1996) suggested that activity counts should be recorded during a time interval $\leq$10 minutes and that activity counts should not be averaged over the whole GPS fix interval. The GPS 2200R collars that we used recorded actual activity counts over 4-minute intervals immediately preceding every GPS fix and, thus, allowed the correlation of actual activity counts to specific periods of time. The use of GPS activity sensors on free-ranging deer on Anticosti Island allowed us to detect 2 activity peaks that were synchronized just after dawn and during dusk from July–November, as well as a daytime decrease in activity for July and August. Mean activity counts during daytime possibly increased from September–November because of the approaching rut. The horizontal activity counts are higher and more variable than the vertical activity counts and this may explain why the interaction between period of the day and month was significant for the horizontal sensors, but not for the vertical sensors. Circadian activity peaks are widely observed in white-tailed deer (Montgomery 1963, Ozoga and Verme 1970, Kammermeyer and Marchinton 1977, Rouleau et al. 2002). Similarly to our study, Beier and McCullough (1990) observed morning activity peaks after sunrise and evening activity peaks during dusk. Even if we used a coarse measure of activity taken every 2 hours, activity sensors could reliably track the daily activity peaks of deer as daylight changed from summer to autumn. Our results indicate that GPS activity sensors can be used to estimate activity and are, therefore, an advantageous tool to monitor the daily activity patterns of large herbivores.

Research and Management Implications

Activity sensor technology allows the possibility to quantify activity of animals, especially for species difficult to observe in nature. We found that vertical sensors were more accurate than horizontal sensors for both GPS and VHF collars (Gillingham and Bunnell 1985, Beier and McCullough 1988). We encourage scientists and managers to use activity sensors to record activity of their study animals, but we suggest using VHF vertical variable-pulse sensors because they will possibly give more reliable results than horizontal sensors.

VHF and GPS activity sensors allow the quantification of continuous activity information (i.e., active and inactive) to study the foraging behavior and assess fine-scale habitat use and temporal activity patterns of wild mammals. For example, activity sensors can be used to examine the influence of population density and resource abundance on activity budgets. In addition, each GPS fix obtained from free-ranging individuals is accompanied by an activity value that can be related to the environmental characteristics of each position. This information can be used, for example, to analyze the effects of habitat quality on the time budget of free-ranging deer at a fine scale. Activity data are necessary to improve our understanding of foraging behavior and, more generally, of plant–herbivore relationships. In the context of high deer density on Anticosti Island and elsewhere, activity data can contribute to generate predictive models that will help wildlife managers and land use planners to integrate plant–herbivore relationships into forest and wildlife management.

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