
Keywords: 8FR/Cervus elaphus/daily movement/GPS/Malme/method/movement/radio telemetry/red deer/telemetry

Abstract: Differential Global Positioning System technology can provide series of accurate locations of free-ranging animals with a short, fixed interval. The sum of straight-line distances between valid locations (y) plotted against number of attempted fixes per day (x) should fit a hyperbolic function (i.e., y = x/(ax - b)) after removing inaccurate fixes and inactive periods. Its asymptotic value (1/a) can provide an estimate of real travel distance. The ratio of 1/a and y is a correction factor to apply to perceived straight-line distance to estimate real distance traveled. We achieved a good model fit on free-ranging adult red deer (Cervus elaphus) from data obtained every 15 min for a male and a female in winter 1997–1998, with a narrow range of correction factors. To validate this model, we used independent datasets from 3 other adult red deer roaming in the same area in winter 2000. We applied the procedure to distances perceived with fixed intervals ranging from 30 to 240 min and found consistent results in estimated real distances. Application of various steps of this analytical method could further development of a general approach to assess real distance traveled by individuals, thus offering new ways of studying habitat use or energetic requirements.
ASSESSING REAL DAILY DISTANCE TRAVELED BY UNGULATES USING DIFFERENTIAL GPS LOCATIONS

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Differential Global Positioning System technology can provide series of accurate locations of free-ranging animals with a short, fixed interval. The sum of straight-line distances between valid locations \(y\) plotted against number of attempted fixes per day \(x\) should fit a hyperbolic function (i.e., \(y = \frac{x}{ax - b}\)) after removing inaccurate fixes and inactive periods. Its asymptotic value \(1/a\) can provide an estimate of real travel distance. The ratio of \(1/a\) and \(y\) is a correction factor to apply to perceived straight-line distance to estimate real distance traveled. We achieved a good model fit on free-ranging adult red deer \((Cervus elaphus)\) from data obtained every 15 min for a male and a female in winter 1997–1998, with a narrow range of correction factors. To validate this model, we used independent datasets from 3 other adult red deer roaming in the same area in winter 2000. We applied the procedure to distances perceived with fixed intervals ranging from 30 to 240 min and found consistent results in estimated real distances. Application of various steps of this analytical method could further development of a general approach to assess real distance traveled by individuals, thus offering new ways of studying habitat use or energetic requirements.

Key words: Cervus elaphus, daily travel distance, differential GPS, France, red deer, telemetry, ungulate

Investigations on large- and medium-sized mammal movements have been possible through the use of very high frequency radiotracking systems since the early 1960s (Cochran et al. 1965; Heezen and Tester 1967). To describe daily movements of animals, straight-line distances between consecutive radiolocations taken at various sampling intervals have been used (Breitenmoser et al. 1992; Harris et al. 1990; Heezen and Tester 1967; Johnson et al. 2002; Musiani et al. 1998; Reynolds and Launder 1990). However, the monitoring of very high frequency radiocollared animals often remains limited by various constraints like manpower, ground access, topography, or weather. To appropriately detect small-scale movements, location accuracy (proximity to true location) is a key parameter and remains an important issue when elevation changes frequently and substantially (Keating et al. 1991) or when position estimates can be biased because of rugged topography, power lines, or mineral deposits (Findholt et al. 1996). The adaptation of Global Positioning System (GPS) devices to wildlife studies (Rodgers and Anson 1994; Rodgers et al. 1996) offered a new technological opportunity to monitor such fine-scale movements of large- or medium-sized mammals over short time periods and, consequently, to assess their cumulative daily movement (Mourão and Medri 2002).

Many preliminary studies aimed to test performance and accuracy of GPS collars that could be affected by technological constraints (intentionally degraded GPS satellite signals by United States Department of Defense until 1 May 2000, called selective availability use of differential GPS), animal behavior, or environmental parameters (canopy and topographic obstruction, weather conditions—D’Eon et al. 2002; Dussault et al. 1999; Edenius 1997; Hulbert and French 2001; Janeau et al. 1998; Merrill et al. 1998; Moen et al. 1996b; Rempel et al. 1995). Accuracy of each differential GPS location also depends on number and position of visible satellites, each location having a specific dilution of precision value, which is a measure of satellite geometry quality: closer satellites provide lower accuracy and higher dilution of precision value, so a simple filtering procedure on dilution of precision value can thus remove inaccurate locations. However, influence of satellite geometry on accuracy was considerably reduced when applying differential correction.

During inactive periods, location error induces a perceived movement in GPS position, leading to erroneous biological interpretation. To remove this noninformative data, we proposed to take into account an activity value (with a 5-min count interval) given by a dual-axis motion sensor that is included in GPS collars with each attempted fix (Moen et al. 1996a). For intervals between attempted fixes longer than 5 min, recorded
activity values, ranging from 0 to 255, are automatically averaged. For instance, Moen et al. (1996a) estimated active time per day of moose (Alces alces) using activity values averaged every 10 min; however, they pointed out that exact cutoff values linked to inactive periods that should be used could not be determined precisely because of overlap in activity counts and because they believed that the counter was incremented during comfort movements and possibly when the moose was panting while bedded.

Due to a limited battery life, GPS users are still confronted with a trade-off between overall duration of monitoring and number of locations per day, making the latter a key limiting factor for field studies. The aim of this study was both to propose and apply an analytical procedure to correct straight-line distances obtained from infrequent GPS locations per day to estimate real distance traveled by monitored animals. We carried out a preliminary experimental test on removal of noninformative data from inactive periods using continuously observed tame red deer females kept in an enclosure. We then developed a hyperbolic model that could be applied in other studies and therefore could permit a comparison of small-scale movements among species. We applied this model to empirical GPS data from 2 free-ranging adult red deer during winter 1997–1998 in a mountainous area using locations recorded during 5-day field sessions. To validate model effectiveness, we used independent datasets recorded during a 10-day field session from 3 other adult red deer roaming in the same area in winter 2000.

**Materials and Methods**

**Preliminary experimental test.—**This test was carried out at the Institut National de la Recherche Agronomique of Theix, France (45°42'N, 3°30'E). Two free-ranging tame adult females fitted with differential 6-channel GPS_1000 collars (Lotek Engineering Inc., New Market, Ontario, Canada) were observed in a 1-ha enclosure covered by meadows and woodland (Quercus pedonculata, Castanea satina, Fagus sylvatica, Alibis alba, and Pinus sylvestris). We tracked them with a 10-min fixed interval and by 2 observers on foot who stayed within 3 m of each female continuously from sunset to sunrise for 3 days (16, 18, and 20 October 2000). We recorded starting and ending time of each inactive (resting, standing) or active (foraging, moving) bout. We considered each 10-min fixed interval when the animal spent all its time inactive as an inactive interval or, in a few cases, when it was partially active in only one 10-min fixed interval within a long series of inactive fixes (occasionally there were high counts in the middle of an inactive period: these were caused by grooming behavior). In all other cases, we considered fixed intervals as active intervals. We compared cumulative frequency of both active and inactive bouts to respective cumulative frequency of increasing activity values given by the dual-axis motion sensor (Fig. 1). Because such detailed behavioral information is impossible to collect in the field, we propose to use the 1st point of inflection of the cumulative function of pooled data to visually identify a threshold (i.e., activity value cutoff) splitting the two bout categories.

**Analytical modeling procedure.—**Animals rarely move in a straight-line direction and often make zigzag and loop movements (Spitz and Janeau 1990) or concentrate daily movements in a rather small area within their home range, especially in mountainous areas when they use flat trails (constant elevation level) in order to minimize metabolic cost. Consequently, with an increasing number of locations per day, an asymptotic value for estimated daily distance traveled should be reached (i.e., absolute real distance or real movement—Laundré 1987). Assuming that this asymptotic value (i.e., $y_{\text{asymp}} = 1/a$) can be directly deduced from a hyperbolic function (i.e., $y = x/[ax - b]$), we propose to compare straight-line distance covered by animals when measured with increasing fixed intervals. For that purpose, we undersampled each data set in order to obtain datasets with longer fixed intervals corresponding to multiples of the former $\Delta t$ fixed interval used (Breitenmoser et al. 1992; Heezen and Tester 1967; Musiani et al. 1998).

With the use of transformations $y' = 1/y$ and $x' = 1/x$, the hyperbolic function is reduced to a linear function (i.e., $y' = a - bx'$—Tomassone et al. 1983). Consequently, we obtain values and 95% confidence limits (i.e., $\pm SD$) of a and b parameters for the fitted hyperbolic function. The ratio between the asymptotic value (i.e., $y_{\text{asymp}} = 1/a$) and $y$ fitted for a given number of attempted locations per day ($n$) could be assimilated to the correction factor ($k_n$) and applied to the corresponding perceived cumulative distance to obtain the estimated real distance (i.e., $k_n = y_{\text{asymp}}y'$ fitted for $x = n$).

**A case study on free-ranging red deer in the Cévennes National Park.—**The field study was carried out in the Cévennes National Park (44°19'N, 3°45'E) located in the eastern part of the Massif Central (France). Mean distance between base station and study area was about 240 km. Within the study area, elevation ranges between 800 and 1,700 m above sea level. In this mountainous area located about 100 km away from the Mediterranean Sea, the landscape is a mosaic of mixed forest (Pinus sylvestris, Abies alba, Faagus sylvatica, Quercus, Castanea sativa) and moorland (Erica, Calluna vulgaris, Sarothamnus purgans, Vaccinium). Rainfall ranges from 900 to 1,500 mm/year.

We trapped red deer with the authorization of the Cévennes National Park and the French Ministry of Agriculture (certificates 7060 and 7382). On the basis of the condition of the study area, species being studied, and number and energy of persons available to check traps, we used 10 cage traps baited with apple and salt. We organized the 1st trapping session during winter 1997–1998 (November–April). We fitted cage traps with very high frequency transmitters to verify their status (open or closed); in this way, captured deer would not be held in the trap for more than 6 h during daytime or 12 h at night before handling as quickly as possible to prevent panic or injury. We caught a male (designated A) and a female (B) on 20 November 1997 and 5 February 1998, respectively. Animals were immobilized in the trap with the use of a dart gun containing medetomidine (Orion Pharma, Espoo, Finland) and ketamine hydrochloride (Merial, Lyon, France). Handling time did not exceed 40 min. In both cases, weight of the differential 6-channel GPS_1000 collar was <1.5% of body mass. We administered atipamezole (Orion Pharma, Espoo, Finland) as an antidote to medetomidine before releasing animals at the capture site. Deer were active 2–5 min after release and left the capture site without showing signs of stress (such as protracted or very fast movement). The male was shot by a hunter 2 months after capture. Hair loss on the neck was the only noticeable effect of the GPS collar on this animal. The GPS collar of the female failed prematurely after 4 months, but the very high frequency transmitter included in her collar allowed us to follow her for 1.5 years. Her ultimate fate is unknown.

Later, we similarly trapped 3 other adult red deer and fitted them with GPS collars to study their home range and habitat use. We trapped a female (C) on 12 October 1999, a male (D) on 10 December 1999, and a female (E) on 27 March 2000.

**Data treatment.—**We planned 5-min fixed intervals during one 5-day session for male A (beginning 2 weeks after capture, i.e., 5–10 days).
December 1997) and 15-min fixed intervals for female B during three 5-day sessions (beginning 6 days after capture, i.e., 11–16 February, then from 18–23 March and 15–20 April 1998). A 12-channel GPS Pathfinder base station (Trimble Navigation Ltd., Sunnyvale, California) located in southwest France (43°31’N, 1°30’E) was used to differentially correct all collected locations. Before and after the removal of selective availability, we selected 3-dimensional (3-D) and 2-dimensional (2-D) fixes with dilution of precision values <10 (Adrados et al. 2002; Dussault et al. 2001; Moen et al. 1997a, 1998; Rempel and Rodgers 1997).

Because fixed intervals differed between individuals (5 min for male A and 15 min for female B), we first averaged male activity values to 15-min intervals. We obtained the same curve shape of cumulative frequencies for increasing activity values of both individuals (Fig. 1). Tangents of these functions at their 1st inflection point corresponded to an activity value around 10, assimilated to the activity value cutoff. Consequently, we assigned each 15-min fixed interval either to an active bout (41% of fixes for male A and 38% of fixes for female B) or to an inactive bout (48.4% of fixed intervals for female B). We calculated straight-line distance covered by red deer between relevant locations during each 5-day session (taken as reference basis).

For each session and for pooled data, we calculated straight-line distances covered when measured with increasing length of fixed intervals: we selected intervals of 30, 45, 60, 90, 120, 180, 240, 360, 480, or 720 min, which correspond to 48, 32, 24, 16, 12, 8, 6, 4, 3, and 2 attempted locations per day, respectively. We finally deduced and compared asymptotic values (\( y_{\text{asymp}} = 1/a \)), which were assimilated to real distances traveled.

Model application.—We tested the ability of our hyperbolic model to estimate real daily distance traveled by free-ranging red deer, with locations collected with various fixed intervals on a dataset obtained independently on 3 other adults in winter 2000 in the same area. We applied the procedure detailed above to correct straight-line distances traveled by animals calculated with fixed intervals ranging from 0.5 to 4 h. Because the 1st location of each day was generally recorded during a resting period (i.e., inactive fix), we did not remove them from datasets to estimate the daily distances traveled. We tested the comparison between animals by the Kruskal-Wallis test (Scherrer 1984; Sprent 1992).

RESULTS

Model Fitting

Sensor activity values versus observed activity categories.—From visual observations of 2 tame females, we discriminated 232 active and 166 inactive fixed intervals. Shapes of cumulative frequency for both active and inactive fixed intervals were clearly separated with relation to the respective cumulative frequency of increasing sensor activity values (Fig. 1). Only 2.6% of active data and 48.4% of inactive data referred to sensor activity values ≤10 (chi-square test with continuity correction: \( \chi^2 = 120.4, P < 0.001 \)).

Estimates of real distances traveled.—Strong linear correlations occurred between the inverse of cumulative straight-line distances covered by red deer during 5 days (as estimated from multiples of 15-min intervals between fixes) and the corresponding inverse number of locations per day (\( r^2 \) ranging from 0.881 for male A to 0.917 for female B in the March session and \( r^2 = 0.943 \) for pooled data, \( P < 0.001 \)). Consequently, the
hyperbolic function fits untransformed field data well (Fig. 2). With the range of parameter a, we estimated asymptotic values of the respective hyperbolic function: \( y_{\text{asymp median}} = \frac{1}{a} \), \( y_{\text{asymp min}} = \frac{1}{a + SE} \), and \( y_{\text{asymp max}} = \frac{1}{a - SE} \). All adjusted \( y_{\text{asymp median}} \) values were lower than estimated daily distances traveled from location attempts every 15 min \( (r^2 \text{ ranging from 0.720 for male A to 0.842 for female B in the April session and } r^2 = 0.807 \text{ for pooled data}) \). Consequently, the method we propose will result in an underestimate of movement for pooled data by about 20% when considering \( y_{\text{asymp median}} \) (or ranging from about 6% to about 29% when considering \( y_{\text{asymp max}} = 0.939 \) and \( y_{\text{asymp min}} = 0.708 \)).

Minimum and maximum correction factors were obtained for female B in March and February sessions, respectively (e.g., 1.052–1.119 with 0.5-h intervals and 1.417–1.951 with 3-h intervals). Subsequent analysis only refers to values obtained with pooled data. We deduced that correction factors for red deer GPS location attempts with time intervals of 0.5, 1, 1.5, 2, 3, and 4 h are 1.074, 1.144, 1.224, 1.298, 1.449, and 1.598, respectively.

**Model Effectiveness on Independent Datasets**

After removing inactive periods and inaccurate fixes, remaining locations attempted every 30 min in winter 2000 for red deer C, D, and E represented 58.4%, 62.2%, and 53.8% of data, respectively. When we applied correction factors to daily distances traveled by these individuals and we recorded less than one-third of total attempted locations per day, we systematically obtained an undervaluation of the straight-line distances. Consequently, we did not use the corresponding days to estimate real distances. In all other cases, a very low range of estimated real daily distances was found (Fig. 3). High coefficients of variation (≥25%) were only noted for male D on day 1 and for female E on day 9, during which more than one-third of attempted locations was obtained with time intervals of 1.5, 2, and 3 h \( (n = 3; \text{Table 2; Fig. 3}) \).

Using average values of estimated real distances \( (n = 5 \text{ or } 6 \text{, except for female C on day 5 and for female E on day 9; Table 2}) \), we estimated mean locomotor activity of all 3 red deer during the 10-day field session \( (\bar{X} \pm SE, 2.94 \pm 0.80 \text{ km for female C, } 4.04 \pm 1.20 \text{ km for male D, } 4.40 \pm 2.10 \text{ km for female E; Kruskal-Wallis test: } H = 4.5, d.f. = 2, P = 0.105) \). Estimated daily distance traveled did not change significantly from one day to the next (Kruskal-Wallis test: \( H = 7.41, d.f. = 9, P = 0.595 \)).

**DISCUSSION**

**Methodological considerations.**—We believe that the fundamental advantage of our analytical approach to predict cumulative movement distance of animals is that it could be adapted to take into account differences in location accuracy, in the activity value cutoff threshold, or in both, depending both on technical capacities and good neck fit of GPS collars and on species behavior. Using data sets obtained with a short fixed interval, we showed how real distance covered by animals, assimilated as an asymptotic value, could be estimated by fitting perceived straight-line distance against corresponding number of locations per day and by applying an appropriate correction factor. However, we could identify a few limitations for an accurate application of correction factors from validation tests. When reducing data sets (i.e., widening time intervals between GPS locations due to missing, inaccurate, and inactive data; described in “Materials and Methods”), we obtained underestimated real distances traveled. This was the case when we collected less than one-third of daily attempted locations.
and when the remaining location data were not evenly distributed throughout the day, as in the case of male D, for which many data were missing during the 1st half of day 1. The best way to strictly calibrate straight-line distance traveled by an animal would be to track it on snow in parallel with a continuous GPS location series and to compare cumulated straight-line distances with real distances traveled. Musiani et al. (1998) effectively used this procedure on the day following a night of radiotracking wolves for nearly 70 km in Poland. We never had the opportunity for such control in our study because of good weather conditions (absence of or not enough snow on ground).

As pointed out by Heezen and Tester (1967), the major problem working with distance is that most location errors are additive; that is, if at any location, every time an error is made in which the animal did not actually move, distances to an erroneous location and back will be added. The problem of additive errors could be especially important to take into account if the location errors are large relative to animal movements (R. Moen, pers. comm.) and if the time interval between location attempts is short. To reduce this problem, we used a filtering procedure to remove inaccurate locations using fixed status locations (2-D and 3-D with dilution of precision ≥10) and locations corresponding to inactive bouts with a cutoff threshold activity value of 10. Due to location errors, additional daily distance would have been taken into account if locations recorded during inactive periods were not removed. We evaluated such effect on data collected in winter 1997–1998: using a 15-min sampling interval, we found a relatively low difference (ranging from +11.2% for female B in the March session to +29.9% for female B in the February session; Table 1). Consequently, we believe that with animal locations taken every 2–4 h, additive errors will be very low. Location data associated with high activity values corresponded to active animals but not systematically to a move from a previous location. Indeed, animals, and in particular herbivores such as deer, can be active when not engaged in locomotion (e.g., when foraging). We calculated straight-line distances between successive locations even if the deer remained in the same foraging site. Such methodological artifacts certainly explain why traveled distances estimated with a 15-min fixed interval were systematically higher than all adjusted \( \text{y}_{\text{asympt}} \) median values, by definition assimilated to real distances.

Another possibility would have been to check straight-line distances between consecutive fixes and to accept the 2nd fix only if the distance from the former is greater than a threshold value related to location accuracy (i.e., significant displacement—Breitenmoser et al. 1992). However, such a method might systematically reduce true small-scale movements occurring on feeding sites (i.e., activity zone—Spitz and Janeau 1990).

**Biological considerations.**—With the exception of Heezen and Tester’s (1967) pioneering work on radiotagged white-tailed deer, in which some animals were located at short time intervals from 2 fixed tracking towers during 4 days, few researchers have attempted to document small-scale movements of ungulate species. The choice of appropriate sampling intervals depends on the biological question to be answered. If autocorrelated data violate the assumption of statistical independence and therefore cannot be used for some estimates of spatial habitat use patterns, restricting sampling effort might sacrifice information of biological significance, as pointed out by Reynolds and Laundré (1990). Consequently, to maximize information available from radiotelemetry studies, they recommend collecting data with a short sampling interval to meet a more precise objective, such as to accurately estimate real daily distance traveled. For studies involving short observation periods of a few days, in the interest of efficiency, the minimum number of fixes required for an accurate evaluation should be used. Within the limitations revealed by the present experimental and field tests, we found that this can be accomplished by planning a short fixed interval (30 min) during a few days throughout the study period to record calibration data. It might be possible to save memory and battery power in the GPS collar by switching to a different scheme with long time intervals. In their study, Reynolds and Laundré (1990) found that estimates of daily movements based on sampling intervals >4 h for pronghorns (Antilocapra americana) and >3 h for coyotes (Canis latrans) were not correlated with the actual distance traveled (based on 30-min intervals during 24-h tracking sessions). However, with our method, real distances could be estimated from location data recorded at intervals of at least 0.5 to 3 h. By this method, daily ranges of different animals could be compared for the same day. With similar environmental and weather conditions during a 10-day session, we also found close mean locomotor

**Table 1.**—Daily distances traveled by 2 adult free-ranging red deer (male A and female B) in the Cévennes National Park as estimated from straight-line distances between differential GPS locations attempted every 15 min during 5-day sessions, winter 1997–1998. All fixes with a dilution of precision value ≥10, due to poor satellite geometry quality, were excluded. Fixes recorded during inactive periods were also excluded, the last 2 columns showing additional distance perceived if those fixes were not removed.

<table>
<thead>
<tr>
<th>Red deer</th>
<th>Field session</th>
<th>Number of GPS locations removed</th>
<th>Remaining GPS locations</th>
<th>Estimated daily distance traveled (m)</th>
<th>Additional distance when including inactive periods (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Missing fixes</td>
<td>Fixes with dilution of precision ≥10</td>
<td>Inactive periods</td>
<td>( X )</td>
</tr>
<tr>
<td>Male A</td>
<td>5–10 December</td>
<td>65</td>
<td>21</td>
<td>159</td>
<td>236</td>
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<tr>
<td>Female B</td>
<td>11–16 February</td>
<td>12</td>
<td>3</td>
<td>225</td>
<td>241</td>
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<tr>
<td>Female B</td>
<td>18–23 March</td>
<td>10</td>
<td>10</td>
<td>168</td>
<td>293</td>
</tr>
<tr>
<td>Female B</td>
<td>14–19 April</td>
<td>37</td>
<td>6</td>
<td>129</td>
<td>309</td>
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</tbody>
</table>
activities for all 3 red deer, as no significant change occurred from 1 daily real distance traveled to the next. So, individual differences or similarities in moving behavior due to snow depth, forage availability, or competing animals can be detected.

Because many accurate locations can be obtained with various time intervals from differential GPS collars, it will be possible to describe more precisely foraging or random trajectories (Adrados et al. 2003; Atkinson et al. 2002; Focardi et al. 1996; Viswanathan et al. 1999) and daily or seasonal movements (Bergman et al. 2000; White and Garrott 1990). For 3-D locations, the GPS technology gives the coordinates of recorded positions, including elevation. This last information could be quite important across a mountainous terrain in knowing whether an animal is moving up- or down-slope, so it allows one to calculate movement costs and evaluate energetic requirements of free-ranging animals at temporal and spatial scales very difficult to comprehend until now (Hudson and White 1985; Mann et al. 2002; Moen et al. 1997b).

TABLE 2.—Estimated real daily distances traveled by 3 free-ranging adult red deer in the Cévennes National Park during winter 2000 from GPS locations attempted a variable number of times a day (48, 24, 16, 12, 8, or 6). Data were obtained from the product of straight-line distances covered by animals when measured with a given frequency and the corresponding correction factor (1.074, 1.144, 1.224, 1.298, 1.449, and 1.598 for time intervals of 0.5, 1, 1.5, 2, 3, and 4 h, respectively).

<table>
<thead>
<tr>
<th>Red deer</th>
<th>Day 1</th>
<th>Day 2</th>
<th>Day 3</th>
<th>Day 4</th>
<th>Day 5</th>
<th>Day 6</th>
<th>Day 7</th>
<th>Day 8</th>
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<th>Day 10</th>
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<td>Female C</td>
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<td>6</td>
<td>1</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>5</td>
<td>6</td>
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<tr>
<td>X (m)</td>
<td>2,288</td>
<td>4,432</td>
<td>3,287</td>
<td>2,325</td>
<td>3,322</td>
<td>3,514</td>
<td>3,332</td>
<td>1,627</td>
<td>2,666</td>
<td>2,603</td>
</tr>
<tr>
<td>Range (m)</td>
<td>2,229–2,357</td>
<td>3,855–4,826</td>
<td>2,631–4,126</td>
<td>1,509–2,716</td>
<td>—</td>
<td>2,770–4,020</td>
<td>3,117–3,591</td>
<td>1,281–1,874</td>
<td>2,050–3,037</td>
<td>2,267–2,852</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>1.9</td>
<td>9.3</td>
<td>16.0</td>
<td>19.3</td>
<td>—</td>
<td>13.5</td>
<td>5.7</td>
<td>14.2</td>
<td>15.9</td>
<td>7.3</td>
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<td>Male D</td>
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<tr>
<td>X (m)</td>
<td>2,059</td>
<td>5,151</td>
<td>2,907</td>
<td>6,274</td>
<td>3,290</td>
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<td>4,475</td>
<td>4,418</td>
<td>4,418</td>
<td>3,949</td>
</tr>
<tr>
<td>Range (m)</td>
<td>1,078–2,927</td>
<td>4,833–5,708</td>
<td>1,996–3,658</td>
<td>5,998–6,611</td>
<td>2,302–4,330</td>
<td>2,997–3,881</td>
<td>4,305–4,811</td>
<td>4,014–5,134</td>
<td>4,052–4,992</td>
<td>3,505–4,685</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>37.4</td>
<td>6.2</td>
<td>20.6</td>
<td>4.1</td>
<td>20.6</td>
<td>8.4</td>
<td>4.0</td>
<td>9.1</td>
<td>7.6</td>
<td>11.3</td>
</tr>
<tr>
<td>Female E</td>
<td></td>
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<tr>
<td>X (m)</td>
<td>5,300</td>
<td>6,966</td>
<td>6,520</td>
<td>1,728</td>
<td>3,980</td>
<td>1,936</td>
<td>5,900</td>
<td>6,425</td>
<td>1,659</td>
<td>3,605</td>
</tr>
<tr>
<td>Range (m)</td>
<td>3,833–6,308</td>
<td>6,274–8,184</td>
<td>6,114–7,085</td>
<td>1,366–1,986</td>
<td>3,372–4,327</td>
<td>1,767–2,067</td>
<td>5,527–6,532</td>
<td>5,629–7,387</td>
<td>872–2,761</td>
<td>3,423–3,744</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>18.6</td>
<td>10.2</td>
<td>5.1</td>
<td>13.1</td>
<td>8.2</td>
<td>5.6</td>
<td>6.3</td>
<td>9.5</td>
<td>59.2</td>
<td>0.3</td>
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Literature Cited


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