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SHORT COMMUNICATION

Down a hole: missing GPS positions reveal birth dates of an underground denning species, the red fox

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Abstract

Global positioning system (GPS) technology is increasingly used to study animal behavior. However, some animals exhibit behaviors that may result in the failure to acquire a GPS position, such as for species with underground denning behavior. This creates a challenge for researchers to identify the timing of important life-history events such as birth. Here, we tested if information gaps arising from unsuccessful GPS positions, in connection with intrinsic and extrinsic factors, can identify parturition events in an underground denning species, the red fox. Using data from 30 GPS collared female red foxes during the approximate parturition period of 1 March–31 May, we calculated the proportion of successful GPS positions per day. We then compared the patterns of successful GPS positions for females of known reproductive status to those known not to have reproduced and a subset of females for which reproductive status was unknown. Females confirmed to have pups ($n = 11$) and two females of unknown reproductive status showed a significant difference in the proportion of successful GPS positions compared to females without pups, illustrating that parturition and denning activity could be identified from GPS data. None of the 12 subadult females were identified as denning. Parturition date, identified as the day with the lowest GPS fix rate within the five-day period with the lowest proportion of successful GPS positions, ranged from 20 March–14 May, with a mean parturition date of 12 April. We, therefore, conclude that important biological information, such as reproductive status and parturition dates, can be identified from patterns of missing GPS positions for some underground denning species.

Keywords GPS · Parturition · Denning behavior · Birth date · Fix success · Carnivore · Canid · Reproduction · *Vulpes* · Scandinavia

Global positioning system (GPS) technology is becoming an increasingly utilized tool to assess the spatial dynamics and behaviors of wild animals (Cagnacci et al. 2010; Hofman et al. 2019). However, studies utilizing GPS telemetry rarely achieve 100% fix success rates (Tomkiewicz et al. 2010; Hofman et al. 2019). Missing GPS positions and subsequent data loss may occur, either randomly among marked individuals within a population, or non-randomly leading to consistent patterns of missing data, relating to specific animal behaviors (Mattisson et al. 2010; Cristescu et al. 2015).

Reproductive events in mammals, such as the timing of birth (i.e. parturition) and the subsequent care of dependent young, often result in sudden changes in female movements and behavior (Edelhoff et al. 2016; Gurarie et al. 2016; Weinstein et al. 2018; Hurme et al. 2019). For instance, declines in movement rates or localization identified from GPS positioning data have been used to determine reproductive state and timing of parturition in ungulates (DeMars et al. 2013; Bonar et al. 2018; Cameron et al. 2018). However, for species that give birth underground, parturition events can limit satellite coverage, resulting in missing GPS positions (Tomkiewicz et al. 2010; Wiesel et al. 2019). This creates a challenge for researchers to identify the occurrence

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and timing of birth using remote monitoring methods such as telemetry. Thus, for many species, information on parturition is limited or untested in wild, free-ranging populations, resulting in management actions that are incompletely informed (Smith et al. 2020).

Determining the timing of breeding and parturition for hunted or managed species is of great interest because of its implications for hunting regulations and species management. Hunting seasons that overlap with the birth and denning period of game species bring up ethical considerations regarding their appropriateness (Parker and Rosell 2001). This may be particularly relevant for species in highly seasonal environments where the timing of reproduction may be temporally synchronized (Ims 1990; Aronsson 2017) but variable along a latitude gradient (Lloyd and Englund 1973), whereas hunting seasons are not. Previously, methods for assessing mating and birth dates in many game species have relied on measurements of embryos from dead animals obtained from hunters and trappers (Lindström 1994; Kauhala 1996; Asano et al. 2003; Elmeros and Hammershøj 2006; Kristiansen et al. 2007). However, such data is not available or applicable for all species and opens the door for applying other methods of data collection to determine the timing of parturition.

In this study, we assessed the occurrence and timing of birth in an underground denning species, the red fox *Vulpes vulpes*, by quantifying temporal variation in fix rate of GPS collared female foxes during their reproductive period. More specifically, we examined if patterns of missing GPS positions could be used to determine the parturition of foxes. Missing GPS positions may provide 'information' gaps, which, rather than being viewed as missing data, can potentially be used to make inferences about female reproductive status, natal denning behavior and timing of parturition (McClintock et al. 2017). We predicted that reproductive status and parturition could be identified by a sudden and marked loss of GPS positions coinciding with the estimated birth period of red foxes, thereby providing a GPS data-driven method to evaluate parturition date of underground denning species, such as red foxes (DeMars et al. 2013; Picardi et al. 2019).

Between 2012 and 2019, we opportunistically live captured red foxes using baited wooden box traps. Foxes captured in Sweden were then either immobilized using a mixture of 2 mg/kg ketamine and 0.08 mg/kg medetomidine, where the medetomidine was later reversed with 0.4 mg/kg atipamezole or with 10 mg/kg tiletamine-zolazepam, for which there is no reversal (Kreeger and Arnemo 2012). In Norway, a noose pole was used to restrain captured foxes, which were then processed quickly and safely without chemical immobilization. Total processing time of fox removal from the trap to fox release at capture site was approximately 25–35 min for Sweden and 10–15 min for Norway. All captured foxes were sexed, weighed, aged and marked with plastic ear tags (Rototags, Dalton Supplies, Ltd.). We outfitted those foxes meeting necessary weight requirements (≥ 5 kg) with GPS collars (Tellus Ultralight, 210 g, Televilt, Inc. Lindesberg, Sweden). Age of foxes was approximated, assuming a birth date of 15th April (Englund 1970), as either pup (<6 months), sub-adult (6 months to <1 year) or adult (>1 year), using the date of capture in combination with the amount of tooth wear and tooth coloration.

Fox captures occurred within three study areas in Sweden and Norway representing a latitudinal gradient of decreasing landscape productivity and human land use (Fig. S1; Walton et al. 2017). The southernmost study area, Kolmården, Sweden (~59° N), consists of boreonemoral forests, agricultural lands, and scattered human settlements. The central study area, Grimsö (~60° N) is located in south-central Sweden and consists of a transitional border zone between boreonemoral forests in the south and boreal forests in the north. Northern boreal forests and alpine tundra of low diversity and productivity characterize the northernmost study area in Hedmark County (~62° N), Norway.

In Scandinavia, red fox parturition is estimated to occur between mid-March and mid-May (Lloyd and Englund 1973). We, therefore, refined our GPS data to only include female red foxes that were monitored during the months of March–May. The GPS-programming of the collars varied, with collars deployed before October 2015 programmed to take 3 positions per day with a drop-off after 270 days (9 months), and collars deployed after October 2015 programmed to take 6 positions per day with a drop-off after 180 days (6 months). Additionally, three females had 14-day periods of intensive 10-min positioning during their standard monitoring.

Reproductive events were confirmed in the field for monitored females either through visible pregnancy or lactation when captured, field visits confirming active den sites (presence of fresh prey remains and pup scats) or subsequent observation of pups in the field. In cases where reproduction could not be determined, we classified the female as of unknown reproductive status. As foxes were captured over multiple years, we converted date-time record to Julian day to enable comparison of females across all years. We then determined the proportion of successful GPS positions per day for each individual based on their expected fix rate programming. We also binned days into five-day long periods starting January 1 of the Julian calendar for all foxes to smooth fix rate, thus reducing the effects of single days with low fix success rate. General fix success rate was then compared using a Kruskal–Wallis chi-squared to test differences between females with and without pups during the estimated denning period(1 March–31 May). For females with pups, we identified the 5-day period with the largest proportion of missing positions. We then identified parturition date as the first Julian day within this period having the lowest GPS fix success rate. We estimated the average parturition date and range of parturition dates for all females with pups for the three different study areas. We then used a generalized linear model (GLM) to examine differences in parturition dates by study area (i.e. latitude). All analyses were preformed using R 3.6.0 (R Core Team 2019).

Twenty-nine female red foxes (12 subadults and 17 adults) were monitored for a total of 30 parturition periods (1 March–31 May). Of these females, 45% were confirmed to have reproduced. Parturition events were only identified in adult females with no evidence of reproduction in all 12 subadult females.

The average GPS fix rate was 0.81 ± 0.15 SD for all females combined from 1 March to 31 May. However, adult females confirmed to have pups ($n = 11$), as well as two adult females originally categorized as of unknown reproductive status, showed a significantly lower proportion of successful GPS positions than for females without pups and females where pups were not confirmed (Kruskal–Wallis chi-squared $= 19.867$, $p < 0.001$; Table 1; Fig. 1). This confirmed that gaps in GPS-fix success could be used to identify parturition and denning seasonally (Fig. 1, Fig. S2) or annually (Fig. S3).

Table 1 The mean proportion of successful GPS positions (i.e. GPS fix rate) and standard deviation for female red foxes monitored between the dates of March 1–May 31. Females of different reproductive status were categorized as adult females with pups (Pups), adult females without pups (No Pups), and subadult females of unknown reproductive status (Pups Unknown). Sample sizes of each category are given in parenthesis

Female status	GPS fix rate	SD
Pups unknown ($n = 12$)	0.90	0.13
Pups ($n = 13$)[a]	0.70	0.31
No Pups ($n = 5$)	0.93	0.10

[a]Includes a recaptured female with confirmed pups both years and two adult females that were originally classified as unknown but subsequently identified as having pups

The average parturition date for all red fox females was identified as April 12 (± 4.3 SE, range March 20–May 14) though local and latitudinal variation were evident (Table 2). Parturition date in the northern study area (Hedmark) occurred significantly later than in the more southern areas, Grimsö (GLM; $\beta = -27.5 \pm 7.7$ SE, $p = 0.005$) and Kolmården ($\beta = -37.5 \pm 6.0$ SE, $p < 0.005$; Fig. 2).

Analysis of animal movement data has primarily focused on understanding patterns of space use and the behavioral processes driving them. This study illustrates how a lack of data within GPS datasets can provide important biological information such as female reproductive status and reproductive patterns. We showed that the loss of satellite signal associated with underground denning (Wiesel et al. 2019) resulted in a sudden and noticeable decline in the proportion of GPS positions, coinciding with the denning period for red foxes. The birth and care of dependent young modifies female behavior and movements, making it possible to draw inferences about the timing of reproductive events using GPS telemetry data (Hofman et al. 2019; DeMars et al. 2013). Under the assumption that reproducing females remain inside the den in the days immediately after giving

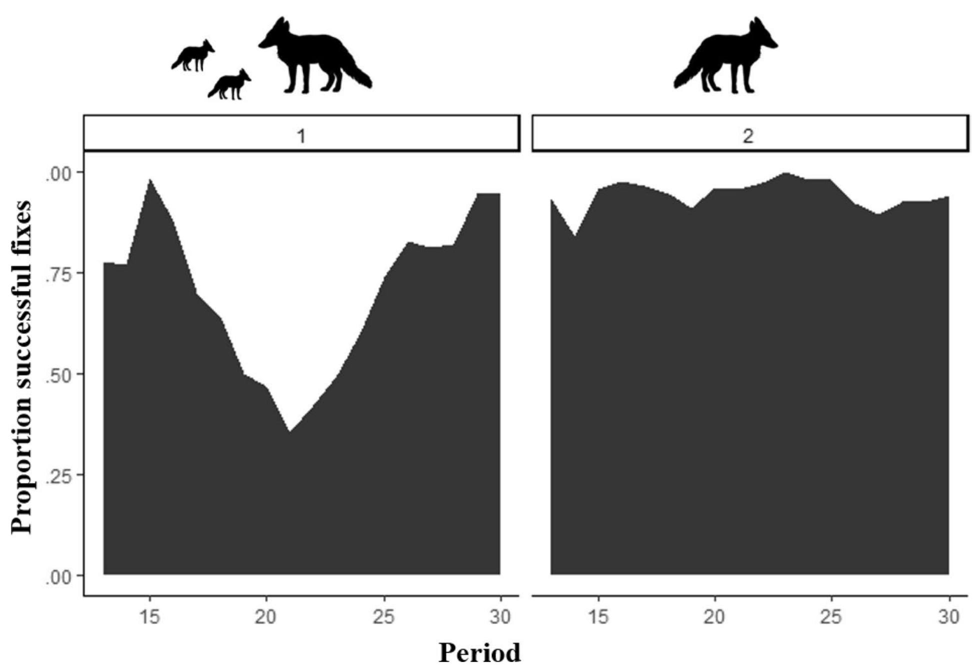

Fig. 1 The average proportion of successful GPS fixes for female red foxes with pups (1, $N = 13$) and without pups (2, $N = 17$). Daily data are smoothed by binning into five-day periods beginning January 1. The periods shown (13–30) represent a date range of 1 March–31 May, corresponding to the red fox denning period

Fig. 2 Date of parturition (predicted means with 95% CI) at the different study areas (names given with latitudes). Means = Hedmark May 11, Grimsö April 14 and Kolmården April 4

Table 2 The mean parturition date for 13 adult red fox females, defined as the day with the lowest proportion of successful GPS positions within the five-day period with the lowest GPS fix success rate between March 1 and May 31. The range of parturition dates and sample size (N) for the different study areas and the latitude of each study area arranged from south to north are provided

Area	Latitude	N	Parturition date range[a]
Kolmården	58.8°	9	20 Mar–17 Apr ($\bar{x}$ = 4 Apr ± 2.6 SE)
Grimsö	59.7°	2	13 Apr–15 Apr
Hedmark	61.8°	2	9 May–14 May

[a]Mean is only estimated for the area with more than 2 birth dates

birth, we predicted that the observed patterns of data loss can indicate that parturition had occurred. Indeed, we found that this pattern was consistent amongst all reproductive females, here only adult females, and not evident in non-reproductive adult females and subadult female red foxes. It was also possible to estimate the date that parturition occurred due to a sudden drop in the proportion of successful positions as the reproducing female entered the den.

We, therefore, suggest that it is possible to use GPS fix rate data to infer reproductive status and parturition dates for underground denning species (Hofman et al. 2019). When a sudden behavioral change results in the failure to acquire a GPS position, this may create 'information gaps' over time, which, in connection with intrinsic and/or extrinsic factors, can contain important biological information (Hebblewhite and Haydon 2010). Though all foxes could show single days of low fix rate occasionally during monitoring, these were not followed by subsequent days of low success rates in adult females without pups or subadult females, as seen for adult females with pups (Fig. S3). Here, we used a simple binning approach to identify periods of low fix success alleviating the effect of the single day low fix success rates. However, alternative statistical methods such as moving averages would also be applicable to filter out the "noise" from single day fix fluctuations and may give more precise estimates of parturition date. In all cases, however, species-specific knowledge of the target animal's annual cycle and behavior are prerequisites to making inferences from missing data. Examining GPS fix success rates daily, seasonally or annually for patterns, in conjunction with knowledge of the species' biology, can potentially reveal hidden behaviors and ecological relationships that would otherwise be difficult or impossible to infer from location data alone.

Red fox parturition dates varied between study areas, presumably in response to latitudinal variation in spring chronology. This follows the local and latitudinal variation in parturition date found in other areas of central and northern Europe (Llyod and Englund 1973, Zapata et al. 1997; Cavallini and Santini 1995). The birth dates in our study ranged from March 20 to May 14 (Table 2). Unfortunately, we had small sample sizes across our different study areas but there were strong indications of later birth dates in the northern area compared to the two more southern areas. This fits the hypothesis of Llyod and Englund (1973) that timing of reproduction in the red fox is constrained by a winter trophic bottleneck with breeding occurring later in the north and earlier in the south. They found no effect of light availability or day length as contributing factors to the latitudinal variation in estrus and subsequent parturition, however.

Interestingly, no subadult females were determined to have given birth in this study. Juvenile red foxes are sexually mature at 8–10 months of age (Englund 1970; Harris 1979), and up to 48% of subadult female red foxes have been found to give birth their first year of life (Harris 1979; Devinish-Nelson et al. 2013). However, this varies depending on food availability, population density (Harris 1979) or social mechanisms (Cavallini and Santini 1995). The lack of subadult reproduction in our study indicates that there are likely social mechanisms or resource limitations preventing breeding and reproduction of this age class of female red foxes in our study populations.

Information on parturition is, for many species, limited or unknown in wild populations, resulting in management actions that are incompletely informed (Smith et al. 2020). Much of the previous information available on red fox reproduction was obtained through studies using hunted or trapped foxes where date of birth is estimated considering embryo development and a gestation period of 53 days (Englund 1970; Llyod 1980). Similarly, evaluating the timing of parturition of red foxes allows us to estimate the timing of other relevant life-history characteristics, particularly the timing of estrus and mating, by subtracting the 53 day gestation period from the parturition dates. Such life history information can provide a better understanding of the drivers of ecological relationships that would otherwise be difficult or impossible to infer from animal movement and location data alone.

Evaluation of the timing of birth in red foxes is also relevant to managers and hunters regarding the most appropriate times of the year to carry out hunting and management actions. Hunting seasons that overlap with the birth and denning period of game species bring up ethical considerations regarding their appropriateness (Parker and Rosell 2001). Our results provide additional information on the timing of parturition of red foxes in Scandinavia and are consistent with the hunting season for red foxes within Sweden (Swedish Environmental Protection Agency 2020). In Sweden, hunting ceases the 28 February in the south with stop date gradually increasing with latitude in two-week steps until ceasing April 15th in the northernmost parts of the country (Fig. 1). However, in Norway hunting is allowed until April 15th for the whole country (Norwegian Environment Agency 2017). When hunting of red foxes is allowed towards the end of the gestation period, ethical considerations arise concerning the hunting of heavily pregnant females or those that recently gave birth and have dependent young in the den. This brings up concerns as to the appropriateness of the hunting season and management regulations of red foxes (Fig. S1).

Taken together, our results indicate that the timing of specific behaviors, such as parturition, which changes the ability of GPS units to acquire a position; can be determined through patterns of GPS position fix rates. Our study shows that the GPS fix rate provides reliable data regarding when red fox females give birth to pups and how parturition dates vary with latitude. This information, in turn, is important to guide and align hunting seasons to mitigate orphaning pups when they are the youngest and most vulnerable.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Ethics approval All capture and handling protocols were approved by the Swedish Animal Ethics Committee (permit numbers NV-03459-11, DNR 70-12, DNR 58-15, DNR 13-47) and the Norwegian Experimental Animal Ethics Committee (permit numbers 2009/122825, 2012/20038, 2014/207803). In addition, permits to capture wild animals were provided by the Norwegian Directorate for Nature Management and the Swedish Environmental Protection Board (NV-03459-11).

References

Aronsson M (2017) 'O Neighbour, Where Art Thou?' Spatial and social dynamics in wolverine and lynx, from individual space use to population distribution. PhD thesis No. 2017:24. Swedish University of Agricultural Sciences

Asano M et al (2003) Reproductive characteristics of the feral raccoon (Procyon lotor) in Hokkaido. Japan J Vet Med Sci 65:369–373

Bonar M et al (2018) Implementing a novel movement-based approach to inferring parturition and neonate caribou calf survival. PLoS One 13(2):e0192204

Cagnacci F et al (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philos Trans R Soc B Biol Sci 365:2157–2162

Cavallini P, Santini S (1995) Timing of reproduction in red fox. Vuples vuples. Int J Mamm Biol. 60:337–342

Cameron MD et al (2018) Movement-based methods to infer parturition events in migratory ungulates. Can J Zool 96:1187–1195

Cristescu B et al (2015) Predicting multiple behaviors from GPS radiocollar cluster data. Behav Ecol 26:452–464

DeMars CA et al (2013) Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. Ecol Evol 3:4149–4160

Devenish-Nelson ES, Harris S, Soulsbury CD, Richards SA, Stephens PA (2013) Demography of a carnivore, the red fox, Vulpes vulpes: what have we learnt from 70 years of published studies? Oikos. 122(5):705–716

Edelhoff H et al (2016) Path segmentation for beginners: an overview of current methods for detecting changes in animal movement patterns. Mov Ecol 4:21

Elmeros M, Hammershøj M (2006) Experimental evaluation of the reliability of placental scar counts in American mink (Mustela vison). Eur J Wildl Res 52:132

Englund J (1970) Some aspects of reproduction and mortality rates in Swedish foxes (Vulpes vulpes), 1961–63 and 1966–69. Viltrevy 8:1–82

Gurarie E et al (2016) What is the animal doing? Tools for exploring behavioural structure in animal movements. J Anim Ecol 85:69–84

Harris S (1979) Age-related fertility and productivity in red foxes, Vulpes vulpes, in suburban London. J Zool. 187(2):195–199

Hebblewhite M, Haydon DT (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philos Trans R Soc B Biol Sci. 365(1550):2303–2312. https://doi.org/10.1098/rstb.2010.0087

Hofman MPG et al (2019) Right on track? Performance of satellite telemetry in terrestrial wildlife research. PLoS ONE 14:e0216223

Hurme E et al (2019) Acoustic evaluation of behavioral states predicted from GPS tracking: a case study of a marine fishing bat. Mov Ecol 7:21

Ims RA (1990) The ecology and evolution of reproductive synchrony. Trends Ecol Evol 5:135–140

Kauhala K (1996) Reproductive strategies of the raccoon dog and the red fox in Finland. Acta Theriol (Warsz) 41:51–58

Kreeger TJ, Arnemo JM (2012) Handbook of wildlife chemical immobilization, 4th edn. International Wildlife Veterinary Services Laramie, Wyoming, USA

Kristiansen LV et al (2007) Mortality and reproductive patterns of wild European polecatsMustela putorius in Denmark. Acta Theriol (Warsz) 52:371–378

Lindström ER (1994) Placental scar counts in the red fox (*Vulpes vulpes* L.) revisited. Zeitschrift fur Saugetierkd 59:169–173

Lloyd HG, Englund J (1973) The reproductive cycle of the red fox in Europe. J Reprod Fertil Suppl 19:119

Llyod HG (1980) The red fox. BT Batsford, London, UK

Mattisson J et al (2010) Effects of species behavior on global positioning system collar fix rates. J Wildl Manage 74:557–563

McClintock BT et al (2017) Bridging the gaps in animal movement: hidden behaviors and ecological relationships revealed by integrated data streams. Ecosphere 8:e01751

Norwegian Environmental Agency (2017) (Miljødirektoratet) Forskrift om jakt- og fangsttider samt sanking av egg og dun for jaktsesongene fra og med 1. April 2017 til og med 31. mars 2022

Parker H, Rosell F (2001) Parturition dates for Eurasian beaver Castor fiber: when should spring hunting cease? Wildlife Biol 7:237–241

Picardi S et al. (2019) Nest-site detection and estimation of avian reproductive outcome from GPS-tracking data. bioRxiv: 562025.

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Smith KP et al (2020) Using reintroduction to elucidate breeding system, breeding phenology and infanticide for a solitary carnivore. Can. J Zool 98:433–447

Swedish Environmental Protection Agency (2020) Jakttidsöversyn 2019/2020 Naturvårdsverkets preliminära förslag, paket 1 remissversion. https://www.naturvardsverket.se/Var-natur/Jakt/jakttid/.

Tomkiewicz SM et al (2010) Global positioning system and associated technologies in animal behaviour and ecological research. Philos Trans R Soc B Biol Sci 365:2163–2176

Walton Z et al (2017) Variation in home range size of red foxes Vulpes vulpes along a gradient of productivity and human landscape alteration. PLoS One 12(4):e0175291

Weinstein BG, Irvine L, Friedlaender AS (2018) Capturing foraging and resting behavior using nested multivariate Markov models in an air-breathing marine vertebrate. Mov Ecol 6(1):16

Wiesel I et al (2019) The use of GPS telemetry data to study parturition, den location and occupancy in the brown hyaena. African J. Wildl. Res. 49:1–11

Zapata SC, Travaini A, Delibes M (1998) Reproduction of the red fox, Vulpes vulpes, in Donana. Southern Spain. Mammalia. 62(1):139–142