



# Wild ungulates and environmental temperature: analysis on the possible utilization of data from sensor placed on GPS collars

Alessandro Messeri<sup>1,2</sup> · Valentina Becciolini<sup>2</sup> · Gianni Messeri<sup>3</sup> · Marco Morabito<sup>4</sup> · Alfonso Crisci<sup>4</sup> · Simone Orlandini<sup>2</sup> · Maria Paola Ponzetta<sup>2</sup>

Received: 27 July 2018 / Revised: 13 November 2018 / Accepted: 10 December 2018

© ISB 2019

## Abstract

GPS collars for wildlife provide a large amount of spatio-temporal location data and are frequently equipped with sensors that record the animal-level environmental temperature at a schedulable sampling frequency. The simultaneous collection of environmental temperature and animal location may contribute not only to deepen the understanding of animal behavior in different climatic conditions, but also to increase the knowledge of climate features in inaccessible areas. The measurement of environmental temperature provided by the sensors, however, can be biased by several factors (e.g., surface temperature of the animal, direct solar radiation, precipitation), so in-depth studies are required to verify the correlation. The aim of this study was to identify an equation for correcting the collar-recorded temperature data, allowing to improve and refine the results obtained by the analysis of spatial data and to highlight the environmental factors having the greatest impact on the accuracy of the measures. Temperature data from GPS collars were obtained within a research on spatial behavior on 11 hinds while spatialized temperature data were obtained from LAMMA-IBIMET dataset. These data showed high correlation and an identical trend, although the GPS collar temperature data was always higher. This model could represent a tool to obtain an accurate measurement of temperatures in complex geographical areas with wild animals but low density of weather stations. The availability of corrected temperature data, recorded simultaneously with the animal location, could be useful for a more accurate comprehension of animal behavior in free-ranging conditions, both in case of forthcoming studies and to valorize existing datasets.

**Keywords** Environmental temperature · GPS collar sensor · Wild ungulates habitat · Climate

---

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00484-018-01662-1>) contains supplementary material, which is available to authorized users.

---

✉ Alessandro Messeri  
alessandro.messeri@unifi.it

<sup>1</sup> Centre of Bioclimatology, University of Florence, Piazzale delle Cascine 18, 50144 Florence, Italy

<sup>2</sup> Department of Agri-food Production and Environmental Sciences, DISPAA, University of Florence, Piazzale delle Cascine 18, 50144 Florence, Italy

<sup>3</sup> Consortium LaMMa (Laboratory of Monitoring and Environmental Modelling for the Sustainable Development), Via Madonna del Piano 10, 50019 Sesto Fiorentino (Florence), Italy

<sup>4</sup> Institute of Biometeorology, National Research Council, Via Giovanni Caproni 8, 50145 Florence, Italy

## Introduction

GPS technologies for wildlife monitoring widely spread in the last decade, enabling researchers to improve their understanding of spatial behavior and resource selection for a large number of species. The application of GPS telemetry to animal tracking has upgraded the quality of wildlife monitoring and simplified the process of data collection. These advantages become essential when aiming to investigate the habits of elusive or highly roaming species, as well as the behavior of wild animals inhabiting scarcely accessible territories, especially during extreme seasons. One of the major benefits of GPS telemetry is the possibility to collect a large amount of highly precise spatial and temporal data at small time intervals (Hebblewhite and Haydon 2010), but also to access other sources of information such as the activity of animals (using accelerometers as activity sensors) and, potentially, the thermal conditions of their habitats. Collars are often equipped with sensors providing the animal-

level environmental temperature recorded at high sampling frequency, which enable researchers to collect geo-referenced thermal data in wide extensions of territories, as in the case of distant areas utilized by migratory or roaming individuals. The simultaneous collection of environmental temperature and animal location is crucial for a deepened understanding of animal behavior in response to exogenous factors. Especially for wild herbivorous mammals, local climatic and environmental conditions are known to affect directly or indirectly their habits, survival, and population dynamics, for instance by enhancing mortality during severe winters (Coulson et al. 2001; Grotan et al. 2008) or influencing indirectly their body size (Pettorelli et al. 2005; Mysterud et al. 2008), fecundity (Grotan et al. 2008), mating strategies (Apollonio et al. 2013), and reproductive success (Tveraa et al. 2013) through changes in growth and quality of food resources. Local weather, seasonality, and food availability have marked effects on the home range size of cervids (Morellet et al. 2013) and also a relevant influence on their habitat use (Ossi et al. 2015) and movements in different land cover types (Van Beest et al. 2013).

So far, animal responses to weather and climatic variations have been studied and quantified either by using temperature measurements from GPS collars (Street et al. 2015) or data from meteorological weather stations located within the area used by animals (Börger et al. 2006, Grotan et al. 2008). Weather stations are not widespread in wild territories and meteorological data in proximity to the studied subjects can be rarely obtained. Radiocollar built-in thermic sensors could represent a cost-effective solution both in terms of price and of battery longevity; however, the measurements of environmental temperature provided by the sensors can be biased by several factors (e.g., surface temperature of the animal, direct solar radiation), so their validation is required for a proper utilization.

Assessing a relationship between temperature data recorded by collars and by weather stations could represent an opportunity to exploit the fine-scale additional information derived from these built-in mobile sensors. A further calibration of the collar temperature data with an appropriate number of representative weather stations would be desirable, but often their geographical distribution and the continuity of data acquisition is not adequate to cover all the area utilized by animals as well as the entire study period.

At present, only few preliminary investigations attempted to evaluate the correspondence between the GPS collar temperature data and the ones from weather stations and there are no studies using spatialized temperature data for comparison. These studies suggest that temperature recorded from sensors in GPS collars, despite systematically higher, can be regarded as a reliable index of ambient air temperature (Berger and Courtiol 2013, Ericsson et al. 2015, Messeri et al. 2015); however, none of these studies has provided a model to validate temperature data from sensors in GPS collars and to explore at

the same time the effects of the main environmental and animal sources of variability of these measurements.

The aim of this study is to identify an equation for correcting the collar-recorded temperature data, allowing to improve and refine the results obtained by the analysis of spatial data and to highlight the environmental factors having the greatest impact on the accuracy of the recorded measures. The purpose of this analysis, thus, is to provide a benchmark relevant both for the valorisation of existing datasets and for planning forthcoming studies.

## Methods

The temperature data from GPS collars utilized in this work represent additional information collected within a research project focused on the study of the red deer spatial behavior. The study was conducted in northern Apennine using GPS/GSM collars, fitted on free-ranging deer, which provided the animal position (geo-localization) (Ponzetta et al. 2009; Crocetti et al. 2010). The collars were also equipped with specific sensors recording the animal-level environmental temperature at the same sampling frequency of the GPS localizations.

## Study area

The study site is located in the Tuscan-Emilian Apennines, specifically in the provinces of Prato and Pistoia. The area is characterized by hilly and low mountain territories up to 900 m above sea level. Oak (*Quercus pubescens* and *Quercus cerris*) and other deciduous species (*Fraxinus ornus*, *Carpinus betulus*, *Ostrya carpinifolia*, and *Castanea sativa*) are the most common at lower elevations. *Fagus sylvatica*, *Picea abies*, and *Abies alba* are the dominant species at higher elevations. The study area includes also arable lands, meadows, and abandoned open areas.

## Data collection and analysis

Eleven free-ranging hinds (aged 2–9 years) were captured by narcosis (protocol approved by Istituto Superiore per la Protezione e Ricerca Ambientale—ISPRA) and fitted with GPS/GSM Pro Light4 radio-collars (Vectronic Aerospace GmbH, Berlin, Germany), during winter 2008–2009. Data collection ranged from January 2009 to December 2010.

Fix positions were collected every hour, together with the animal-level environmental temperature (ALET); for every fix, elevation was calculated from a Digital Terrain Model 10 × 10 m (Regione Toscana, Sistema Informativo Territoriale ed Ambientale). A land cover map was used to assign each fix to the corresponding land use category; these categories were subsequently merged to obtain two cover types: woodland and open areas.

In a second step, the area frequented by the hinds was divided into 100 square grids ( $2 \times 2$  km) and each animal was assigned daily to the square containing the highest number of its localizations per day. This type of approximation was possible, thanks to the reduced movement of the animals and therefore in every day most of the fixes of each animal fell within a single square. The calculation of the maximum, minimum, and average daily spatialized temperature data (STmax, STmin, STave) for each of the 100 squares was performed using the LAMMA-IBIMET dataset based on the Daymet program, originally proposed by Thornton et al. (1997, 2000, 2016) to describe a method for generating daily surface variables, such as temperature, over large regions of complex terrain; this method takes into account the temperature observation (like minimum and maximum temperature variables), their elevation, and the elevation of the grid points; the program generates a spatialized interpolation of these data. The spatialized temperature was calculated using data from about 150 weather stations located in the Tuscan territory in order to compensate for their inhomogeneous distribution in the investigated area.

In addition, in the same territory, precipitation data (mm/day) were obtained from a weather station (Hydrologic Service of Tuscany Region) located at 890 m a.s.l. ( $44^{\circ} 00' 03.7''\text{N}$ ,  $11^{\circ} 00' 35.7''\text{E}$ ) and each day has been categorized with a YES or NO (precipitation  $> 0.1$  mm, precipitation 0 mm). Maximum daily solar radiation data ( $\text{w/m}^2$ ) were obtained from a weather station located in Vernio (Pistoia) at 303 m s.l.m ( $44^{\circ} 00' 755''\text{N}$ ,  $11^{\circ} 15' 052''\text{E}$ ).

Animal level environmental temperature (ALET) data were averaged on a daily basis; and maximum (ALETmax), minimum (ALETmin), and average (ALETave) temperatures were calculated. Pearson correlation coefficients were calculated between each spatialized environmental temperature and the corresponding collar-recorded data. In addition, a detailed multivariate analysis was applied by an extension of the linear multiple regression analysis, the Linear Mixed-effect Model

(LMM), which allows both fixed and random effects (Fox 2002). For the multivariate evaluation (Table 1), ALETmax, ALETmin, and ALETave were considered as dependent variables. The fixed factors selected for the analysis were: (a) the proportion of daily time (expressed as percentage of fixes) spent by the animals in woodlands, hereafter daily time under woodland cover (TWC): values were split in three classes, according to tertile calculation; (b) the rain precipitation (Prp), considered with two levels: presence or absence; and (c) the season in the climatological definition (Winter from December up to February, Spring from March up to May, Summer from June up to August, and Autumn from September up to November). The “animal” effect was inserted in the LMM as a random factor in order to take into account the variability of each sensor. Maximum daily solar radiation was included in the model as covariate. The statistical analyses were carried out using R, version 3.1.3 (R Core Team 2015), package lme4 (Bates et al. 2015).

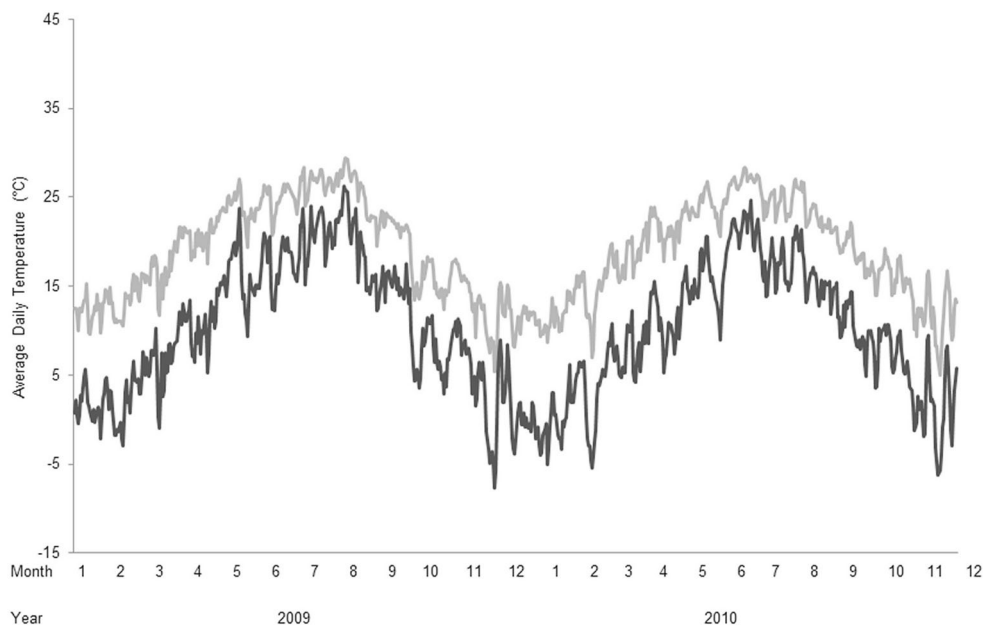
## Results

Pearson coefficients showed high correlation between spatialized and collar-recorded temperatures, especially for the minimum ( $r_p = 0.97$ ) (Online resource 1) and average ( $r_p = 0.96$ ) (Online resource 2) thermal values, while daily maximum temperatures resulted less correlated ( $r_p = 0.80$ ) (Online resource 3). A preliminary comparison between ALETave and STave, carried out on raw data averaged over the 11 hinds, showed that collar-recorded temperatures were always higher than the spatialized data, although with a similar trend (Fig. 1). This difference appeared higher in some seasons, particularly in winter when ALETave showed an average of  $11.8^{\circ}\text{C}$  while STave was just  $3.3^{\circ}\text{C}$ . Substantial differences appeared also in spring with an average value of  $19.3^{\circ}\text{C}$  for the ALETave and of  $11.4^{\circ}\text{C}$  for the STave. Less different values were

**Table 1** Independent variables used in the LMM calculation

Acronym	Parameter
STmin	Minimum daily spatialized temperature ( $^{\circ}\text{C}$ )
STmax	Maximum daily spatialized temperature ( $^{\circ}\text{C}$ )
STave	Average daily spatialized temperature ( $^{\circ}\text{C}$ )
ST*season	Interaction between the variables “spatialized temperature” and “season”
TWC	Proportion of the animal daily time under woodland cover (%) split in three classes ( <sup>1, 2, 3</sup> ) according to tertile calculation
Rad	Maximum daily Solar radiation ( $\text{W/m}^2$ )
Prp	Precipitation (categorical variable (yes or no))
Season	<sup>a</sup> Winter (from 1 December up to 28(29) February); <sup>b</sup> Spring (from 1 March up to 31 May); <sup>c</sup> Summer (from 1 June up to 31 August); <sup>d</sup> Autumn (from 1 September up to 30 November)
Animal	Animal effect (a random factor in order to take into account the variability of each sensor)

**Fig. 1** Trend of ALETave (averaged over 11 hinds) and STave during the 2 years of the monitoring. ALETave = light gray line. STave = dark gray line



registered in summer when the average ALETave temperature was 25.5 °C while the STave was about 21 °C.

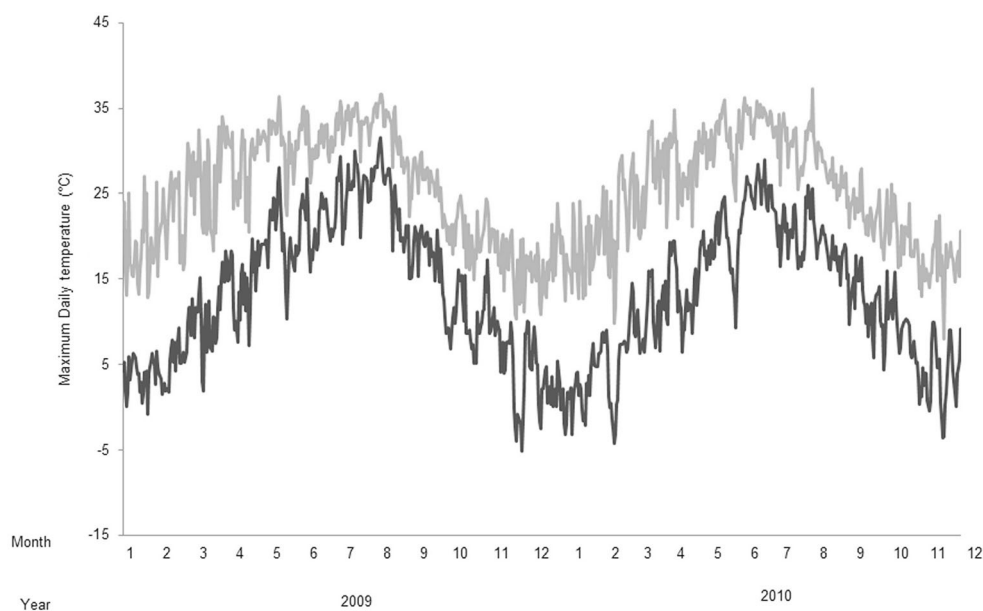
A similar trend was observed in maximum daily temperature (Fig. 2) where the most important differences between the two values occurred in winter (ALETmax 18.1 °C, STmax 6.3 °C) and the minimum in summer (ALETmax 32.3 °C, STmax 26.4 °C). Instead, as regards the minimum daily temperature (Fig. 3), the differences appeared more steady during the year.

In order to test the effect of the above-mentioned environmental parameters, Linear Mixed-effects Models were fitted for ALETave (Table 2), ALETmin (Table 3), and ALETmax, (Table 4) according to the following equation (Bates et al. 2015):

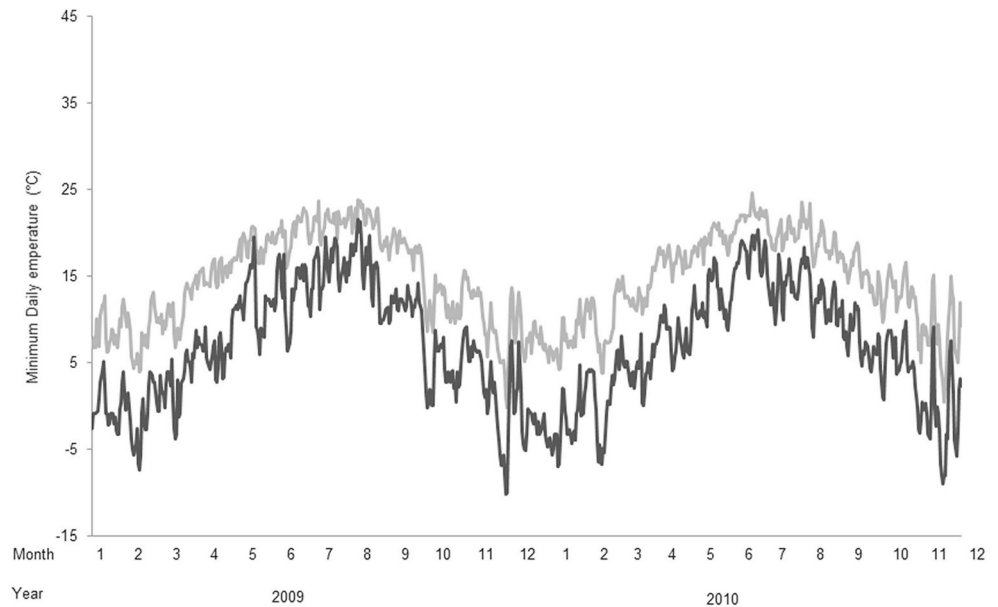
$$ALET = ST + Season + TWC + Animal + Rad + Season*ST + Prp$$

Average, minimum, and maximum daily temperature (ALETave, ALETmin, ALETmax) recorded by the collars appeared to be affected by all the variables taken into account (Tables 2, 3, and 4). The only exception is the proportion of the animal daily time under woodland cover (TWC) that is not significant for the average daily temperature Table 2. In particular, daily temperature recorded by the collars (Tables 2, 3, and 4) were

**Fig. 2** Trend of ALETmax (averaged over 11 hinds) and STmax during the 2 years of the monitoring. ALETmax = light gray line. STmax = dark gray line



**Fig. 3** Trend of ALETmin (averaged over 11 hinds) and STmin during the 2 years of the monitoring. ALETmin = light gray line. STmin = dark gray line



significantly affected by the seasonal effect ( $p < 0.001$  for all seasons;  $p < 0.01$  only in autumn for ALETave) and the interaction between season and spatialized environmental temperature was always significant ( $p < 0.001$ ; only in STmax\*spring for ALETmax  $p < 0.05$ ), revealing that the reliability of collar-recorded thermal data within season also varies in relation to environmental temperature.

Regarding the solar radiation ( $p < 0.001$ ), it determined higher values in the temperatures collected by the collars, particularly for ALETave. On the contrary, rain precipitations affected significantly measured

temperatures ( $p < 0.001$ ), producing a general decrease of the collar-recorded values.

## Discussion

The study showed that temperatures measured by the GPS collars were highly correlated with spatialized temperature data. The strong correlation between the environmental temperatures and the ones recorded by collar emerged also in the low presence of research about this topic, performed on different species and latitudes (Berger and Courtiol 2013, Ericsson et al. 2015).

**Table 2** LMM equation parameters of the Average Daily Temperature (ALETave) and significance  $R^2 = (0.934)$

	Estimate	Std. error	Df	T value	Pr(> t )	Sign
Intercept	9.766 + 00	2.707 e-01	1.100e+01	36.081	3.88e-13	***
Stave	6.671e-01	9.420e-03	6.306e+03	70.819	<2e-16	***
Season <sup>b</sup>	1.050e+00	8.678e-02	6.305e+03	12.095	<2e-16	***
Season <sup>c</sup>	3.730e+00	1.889e-01	6.305e+03	19.748	<2e-16	***
Season <sup>d</sup>	-2.586e-01	9.859e-02	6.304e+03	-2.623	0.008748	**
TWC <sup>2</sup>	-4.377e-02	5.644e-02	6.305e+03	-0.776	0.438009	
TWC <sup>3</sup>	-6.548e-02	6.201e-02	6.313e+03	-1.056	0.291010	
Rad	2.967e-08	3.557e-09	6.305e+03	8.343	<2e-16	***
Prp	-6.659e-01	5.067e-02	6.304e+03	-13.141	<2e-16	***
Stave * season <sup>b</sup>	4.892e-02	1.137e-02	6.304e+03	4.302	1.72e-05	***
Stave * season <sup>c</sup>	-1.228e-01	1.280e-02	6.304e+03	-9.595	<2e-16	***
Stave * season <sup>d</sup>	4.259e-02	1.153e-02	6.304e+03	3.693	0.000224	***

$R^2 = 0.934$

Sign  $p \leq 0.001$  (\*\*\*),  $p \leq 0.01$  (\*\*),  $p \leq 0.05$  (\*)

In "Season" spring = <sup>b</sup>; summer = <sup>c</sup>; autumn = <sup>d</sup>

TWC = proportion of the animal daily time under woodland cover, (<sup>2</sup> second tertile, <sup>3</sup> third tertile)

**Table 3** LMM equation parameters of the Minimum Daily Temperature (ALETmin) and significance ( $R^2 = 0.909$ )

	Estimate	Std. error	df	T value	Pr(> t )	Sign
Intercept	7.264e+00	2.539e-01	1.200e+01	28.612	1.56e-12	***
STmin	7.163e-01	1.116e-02	6.299e+03	64.196	< 2e-16	***
Season <sup>b</sup>	7.905e-01	8.215e-02	6.298e+03	9.622	< 2e-16	***
Season <sup>c</sup>	3.697e+00	2.159e-01	6.298e+03	17.122	< 2e-16	***
Season <sup>d</sup>	4.862e-01	9.892e-02	6.299e+03	4.915	9.10e-07	***
TWC <sup>2</sup>	2.632e-01	6.969e-02	6.300e+03	3.776	0.000161	***
TWC <sup>3</sup>	4.362e-01	7.660e-02	6.307e+03	5.694	1.29e-08	***
Rad	1.969e-08	4.159e-09	6.298e+03	4.735	2.24e-06	***
Prp	- 2.127e-01	6.323e-02	6.297e+03	- 3.363	0.000775	***
STmin * season <sup>b</sup>	7.991e-02	1.424e-02	6.297e+03	5.613	2.07e-08	***
STmin * season <sup>c</sup>	- 1.337e-01	1.761e-02	6.297e+03	- 7.592	3.60e-14	***
STmin * season <sup>d</sup>	5.713e-02	1.452e-02	6.297e+03	3.935	8.43e-05	***

$R^2 = 0.909$

Sign  $p \leq 0.001$  (\*\*\*),  $p \leq 0.01$  (\*\*),  $p \leq 0.05$  (\*)

In "Season" spring = <sup>b</sup>; summer = <sup>c</sup>; autumn = <sup>d</sup>

TWC = proportion of the animal daily time under woodland cover, (<sup>2</sup> second tertile, <sup>3</sup> third tertile)

In our study, the collar-recorded and the spatialized daily temperatures (maximum, average, and minimum) showed a similar trend, although the values recorded by collars were always higher. This difference probably depends on the influence of fur, of animal's body temperature, of the sensor's position (above the neck), which is thus subject to direct solar radiation, and of the absence of air circulation inside the sensor case.

The magnitude of the offset, according to the results of LMM analysis, varied in relation to the period of the year (i.e., season). The seasonal differences were more pronounced for ALETmax, followed by ALETave and ALETmin, suggesting that collar sensors are less reliable at higher

environmental temperatures. Moreover, the greater values recorded by collars in summer could be also ascribed to the fact that the sensor is located in a dark and waterproof box, without thermal shelters and air circulation. The lowest values recorded for ALETmin in winter could be accordingly explained by the minor overheating within the sensor case due to the daylight duration, the angle of the sun's rays.

All the environmental parameters and behavioral factors considered for LMM were significant with regard to the maximum and minimum daily temperatures. On the contrary, different proportions of time spent by the hinds under woodland cover did not appear to affect ALETave, probably owing to

**Table 4** LMM equation parameters of the Maximum Daily Temperature (ALETmax) and significance ( $R^2 = 0.726$ )

	Estimate	Std. error	df	T value	Pr(> t )	Sign
Intercept	1.523e+01	4.287e-01	2.200e+01	35.531	< 2e-16	***
STmax	7.248e-01	2.596e-02	6.313e+03	27.917	< 2e-16	***
Season <sup>b</sup>	2.156e+00	3.193e-01	6.306e+03	6.754	1.57e-11	***
Season <sup>c</sup>	4.344e+00	5.734e-01	6.308e+03	7.577	4.05e-14	***
Season <sup>d</sup>	- 1.599e+00	3.442e-01	6.304e+03	- 4.645	3.48e-06	***
TWC <sup>2</sup>	- 1.115e+00	1.722e-01	6.309e+03	- 6.474	1.03e-10	***
TWC <sup>3</sup>	- 1.404e+00	1.888e-01	6.257e+03	- 7.435	1.19e-13	***
Rad	6.606e-08	1.112e-08	6.311e+03	5.940	3.00e-09	***
Prp	- 2.771e+00	1.528e-01	6.303e+03	- 18.130	< 2e-16	***
STmax * season <sup>b</sup>	- 6.305e-02	3.032e-02	6.305e+03	- 2.079	0.0376	*
STmax * season <sup>c</sup>	- 2.452e-01	3.256e-02	6.304e+03	- 7.530	5.80e-14	***
STmax * season <sup>d</sup>	- 7.435e-02	3.083e-02	6.306e+03	- 2.412	0.0159	***

Sign  $p \leq 0.001$  (\*\*\*),  $p \leq 0.01$  (\*\*),  $p \leq 0.05$  (\*)

In "Season" spring = <sup>b</sup>; summer = <sup>c</sup>; autumn = <sup>d</sup>

TWC = proportion of the animal daily time under woodland cover, (<sup>2</sup> second tertile, <sup>3</sup> third tertile)

different behaviors of the animal during the day. In fact, the permanence of the animals in woodland, which for ungulates as red deer is driven by the necessity of protection from disturbance (Strohmeyer et al. 1999), predation or thermal stress (Myserud and Østbye, 1999), is generally longer during the daylight hours (Adrados et al. 2008): such behavior could consequently lead the sensor to benefit of woodland covering effect that tends to moderate the thermal extremes. Accordingly, as time spent in woodlands increase, collar-recorded average and maximum collar-recorded temperatures tend to reduce, as an effect of thermal mitigation offered by canopy in comparison to grasslands (Morecroft et al. 1998).

The solar radiation, as predictable, influenced all the measured values and appeared to determine an additional overestimation of temperatures in days when cloud cover is absent or moderate.

This aspect is confirmed by the fact that during the rainy days, the temperature values measured by the collars are generally lower, probably due not only to the cloudy sky (and therefore low solar radiation) but also to the direct effect of water drops which, by wetting the sensor case, limits its overheating and decreases its surface temperature during the evaporation process and this phenomenon could be further accelerated in the event of wind.

Considering these aspects, the Linear Mixed-effect Models identified could be regarded as valuable tools to increase the accuracy and precision of the air temperatures measured by collar sensors, which could be useful in complex geographical areas where the density of weather stations is very low.

Other environmental factors could also be taken into account, such as wind that can increase the dispersion of heat accumulated by the fur of the animal and the surface of the sensor, especially in the event of rainfall. Also, the snow cover and its duration on land can significantly increase the daily temperature range and probably it can change the behavior of animals and for this reason it might be interesting to consider these aspects in further LMM analysis.

Concerning the temperature sampling frequency, it can be varied in order to obtain less or more detailed data. An adequate scheduling of data collection, with an elevated number of position fix, is pivotal to achieve a realistic approximation of environmental temperature. Increasing the sampling frequency, however, reduces the lifetime of battery and archival memory (Cagnacci et al. 2010), so this limitation should be considered in relation to the primary aim of the study. Finally, opportune improvements of the collar design and ergonomics would allow a reduction of undesired effects biasing the sensor measurements. Few improvements in collar manufacturing could enhance the reliability of the collar-recorded temperatures: the use of light colors for the sensor's case could reduce the effect of incident solar radiation, as well as the use of waterproof but air permeable materials could allow for a greater circulation of air in sensor case. A further

improvement could be made using a case equipped with a fan that allows forced air circulation around the sensor.

## Conclusion

Knowing the responses of wild species to climatic conditions represents a crucial aspect for the study of their daily and seasonal activity and their spatial distribution. The possibility to reconstruct environmental temperature data starting from the temperature measured by GPS radiocollars appears a promising tool to increase the knowledge of environmental variables in particularly inaccessible areas with a good temporal resolution. The availability of the animal-level environmental temperature might represent a further opportunity for studying the behavior of wild ungulates, especially when representative data from weather stations are not available or lacking. The proposed method could be replicated in different areas as well as for the other animal species, but a new LMM analysis should be recalculated according to the new animal species and the new characteristics of the study area.

## References

- Adrados C, Baltzinger C, Janeau G, Pepin D (2008) Red deer resting places characteristics obtained from GPS data in a forest habitat. *Eur J Wildl Res* 54(3):487–494
- Apollonio M, Brivio F, Rossi I, Bassano B, Grignolio S (2013) Consequences of snowy winters on male mating strategies and reproduction in a mountain ungulate. *Behav Process* 98:44–50
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67(1):1–48. <https://doi.org/10.18637/jss.v067.i01>
- Berger A, Courtiol A (2013) The radio-collared animal as a moving weather station? Belgium, 263
- Börger L, Franconi N, Ferretti F, Meschi F, De Michele G, Gantz A, Coulson T (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *Am Nat* 168:471–485
- Cagnacci F, Boitani L, Powell RA, Boyce M (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Phil Trans R Soc B* 365:2157–2162. <https://doi.org/10.1098/rstb.2010.0107>
- Coulson T, Catchpole EA, Albon SD, Morgan BJ, Pemberton JM, Clutton-Brock TH, Crawley MJ, Grenfell BT (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292(5521):1528–1531
- Crocetti C, Ponzetta MP, Minder I, Messeri A, Cervasio F, Argenti G, Maccelli S (2010) Analysis of land utilisation by red deer in the Apennine Mountains, vol 15. European Grassland Federation, Kiel, pp 265–267
- Ericsson G, Dettki H, Neumann W, Arnemo JM, Singh NJ (2015) Offset between GPS collar-recorded temperature in moose and ambient weather station data. *Eur J Wildl Res* 61(6):919–922
- Fox J (2002) Linear mixed models. Appendix to An R and S-PLUS Companion to Applied Regression

- Grotan V, Saether BE, Filli F, Engen S (2008) Effects of climate on population fluctuations of ibex. *Glob Chang Biol* 14:218–228
- Hebblewhite M, Haydon DT (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Phil Trans R Soc B* 365:2303–2312
- Messeri A, Becciolini V, Messeri G, Morabito M, Crisci A, Orlandini S, Ponzetta MP (2015) Influence of climatic and local environmental conditions on deer: comparison between air temperatures measured by a weather station and GPS collars. IX International Symposium On Wild Fauna Košice:159–161
- Morecroft MD, Taylor ME, Oliver HR (1998) Air and soil microclimates of deciduous woodland compared to an open site. *Agric For Meteorol* 90(1–2):141–156
- Morellet N, Bonenfant C, Börger L, Ossi F, Cagnacci F, Heurich M, Kjellander P, Linnel JDC, Nicoloso S, Sustr P, Urbano F, Mysterud A (2013) Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *J Anim Ecol* 82(6):1326–1339
- Mysterud A, Østbye E (1999) Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildl Soc Bull* 27(2):385–394
- Mysterud A, Yoccoz NG, Langvatn R, Pettorelli N, Stenseth NC (2008) Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. *Phil Trans R Soc B* 363(1501):2357–2366
- Ossi F, Gaillard JM, Hebblewhite M, Cagnacci F (2015) Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer. *Eur J Wildl Res* 61(1):111–124
- Pettorelli N, Mysterud A, Yoccoz NG, Langvatn R, Stenseth NC (2005) Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proc R Soc Lond B Biol Sci* 272:2357–2364
- Ponzetta MP, Sacconi F, Crocetti C, Cervasio F, Minder I (2009) GPS/GSM collars monitoring of red deer in the Tosco-Emiliano Apennine Mountains. *Ital J Anim Sci* 8(2):646–648
- R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria Version 3.1.3. <http://www.R-project.org>
- Street GM, Rodgers AR, Fryxell JM (2015) Mid-day temperature variation influences seasonal habitat selection by moose. *J Wildl Man* 79: 505–512
- Strohmeier DC, Peek JIM, Bowlin TR (1999) Wapiti bed sites in Idaho sagebrush steppe. *Wildl Soc Bull* 27:547–551
- Thornton PE, Running SW, White MA (1997) Generating of daily meteorological variables over large regions of complex terrain. *J Hydrol* 190:214–251. [https://doi.org/10.1016/S0022-1694\(96\)03128-9](https://doi.org/10.1016/S0022-1694(96)03128-9)
- Thornton PE, Hasenauer H, White MA (2000) Simultaneous estimation of daily solar radiation and humidity from observed temperature and precipitation: an application over complex terrain in Austria. *Agric For Meteorol* 104:255–271. [https://doi.org/10.1016/S0168-1923\(00\)00170-2](https://doi.org/10.1016/S0168-1923(00)00170-2)
- Thornton PE, Thornton MM, Mayer BW, Wei Y, Devarakonda R, Vose RS, Cook RB (2016) Daymet: daily surface weather data on a 1-km grid for North America, version 3. ORNL DAAC, Oak Ridge. <https://doi.org/10.3334/ORNLDAAAC/1328>
- Tveraa T, Stien A, Bårdsen BJ, Fauchald P (2013) Population densities, vegetation green-up, and plant productivity: impacts on reproductive success and juvenile body mass in reindeer. *PLoS One* 8(2): e56450. <https://doi.org/10.1371/journal.pone.0056450>
- Van Beest FM, Vander Wal E, Stronen AV, Brook RK (2013) Factors driving variation in movement rate and seasonality of sympatric ungulates. *J Mammal* 94(3):691–701