Research Article

Dealing with intra-individual variability in the analysis of activity patterns from accelerometer data

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Abstract

Over the past few years, research on remote monitoring of animal behaviour by means of accelerometers integrated in GPS collars considerably increased. Use of accelerometers allows for long-term fine-scale behavioural measurements, which are extremely useful to study activity patterns. As the values generated by accelerometers are strongly affected by individual factors, season-related environmental effects, and the position of the collar on the animal, comparisons of accelerometer data among different individuals and time-periods may yield misleading results. Researchers have to find an easy-to-use method in order to turn accelerometer data into behavioural data, one which enables them to take into consideration inter- and intra-individual variations. We propose an easy individual-based method, which generates threshold values to distinguish between active and inactive behaviours with no need of direct observation. By treating each animal independently and adopting ad hoc temporal scales, this method is able to take into consideration the influence of individual factor modifications (e.g., body size, collar tightness) on the data recorded by the accelerometer. We validated this approach and showed its potential by testing it with an activity dataset from 26 free-ranging Alpine ibex (*Capra ibex*). We managed to distinguish between active and inactive behaviours with a high percentage (93%) of correctly classified binary behavioural state. We showed that, when the threshold values are calculated at a large temporal scale, the accuracy decreases and activity pattern predictions may yield misleading results. By adopting the method proposed and by transforming the accelerometer data provided by the collars into time spent active, it may be possible to analyse how the activity levels of the monitored individuals change over the seasons, to appreciate fine variations of individual characteristics, and to compare the activity patterns of different populations as well as of different species.

Introduction

Data on activity patterns are important as they provide key information about animal biology and ecology such as foraging strategy, bioenergetics, evolutionary adaptations, and responses to environmental cues (McLellan and McLellan, 2015; Murray and St. Clair, 2015; Bloch et al., 2013; Hut et al., 2013; Gleiss et al., 2011). Assessing the activity patterns of a species may help provide indices of its welfare and accordingly identify critical challenges individuals have to face. Such assessment thus potentially plays a crucial role in the development of conservation and management strategies.

Measuring the activity patterns of free-ranging animals is often a challenging task. Although direct observation is a powerful tool to document animal behaviour, it poses several problems, especially during periods of darkness (e.g., Willisch and Ingold, 2007), and has obvious limitations when dealing with elusive, forest-dwelling, and wide-ranging species (e.g., Botts et al., 2020). Furthermore, direct observations of animal behaviour are time and manpower consuming and can also be affected by different kinds of bias (Martin and Bateson, 2007). Technological advances now enable one to monitor animal behaviour throughout the 24-hr cycle and collect large amounts of temporal high-resolution data, with no researcher needed in the field. Improvements in micro-electromechanical systems allowed the construction of accelerometers, i.e., spring-like piezoelectric sensors generat-

ing a wave-like voltage signal which is proportional to the acceleration (change in velocity) they experience (Brown et al., 2013). For biological applications to studies on terrestrial mammals, accelerometers are mainly integrated into activity sensors in Global Positioning System (GPS) collars, which provide summary statistics of activity, calculated by subtracting the static acceleration (gravity) component from the total acceleration values. Some of the most important collar factories (e.g., Vectronic Aerospace, Lotek) chose to provide activity data as dimensionless values averaged over the duration of a programmed sampling interval (hereinafter referred to as "averaged raw activity data - ARAD"; Krop-Benesch et al., 2011). In so doing, they drastically reduced the battery and memory consumption due to activity data storage, thus enabling their remote download.

In terrestrial mammals, the study of activity patterns by means of ARAD was implemented by i) analysing ARAD directly provided by GPS collars (e.g., Rabaiotti and Woodroffe, 2019; Brambilla and Brivio, 2018; Grignolio et al., 2018; Brivio et al., 2017, 2016), ii) processing ARAD to distinguish between active and inactive periods (e.g., Petroelje et al., 2020; Becciolini and Ponzetta, 2018; Bose et al., 2018; Isbell et al., 2017; McLellan and McLellan, 2015; Podolski et al., 2013), iii) processing ARAD to distinguish among different behavioural categories (e.g., Abáigar et al., 2018; Zhang et al., 2015; Grünewälder et al., 2012; Löttker et al., 2009). As collar manufacturers are unable to provide a standard classification system to turn collar ARAD values into behavioural categories, researchers need to define a classification system for their focal species in order to be able to dis-

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tinguish among different behaviours. The classification process consists in correlating activity values to detailed behavioural observations of collared animals and results in a mathematical model that can be used to classify animal behaviours according to the activity data remotely collected from the collar. Thus, in order to transform data from the collars into behavioural categories, direct observations are mandatory, though this may be a strong constraint for elusive wild species. To overcome this constraint, direct observations of captive individuals and a restricted number of free-living animals are conducted (e.g., Abáigar et al., 2018; Gaylord et al., 2016; Löttker et al., 2009; Adrados et al., 2003). However, on the one hand, the behaviour of captive individuals may differ from that of wild living individuals, as several behavioural patterns do not occur in captivity on account of the different environmental and, often, social context. On the other hand, the age and sex of an animal can affect the amount of movement associated with different behaviours, thus affecting the classification process (Löttker et al., 2009; Coulombe et al., 2006; Gervasi et al., 2006). The inference of behaviour by means of the classification process poses another critical issue: accelerometer data are strictly linked to the movement experienced by the sensor on the collar, which is obviously influenced by animal motion as well as indirectly affected by several factors. Recently, Dickinson et al. (2020) clearly showed that the tightness of the collar on the animal neck strongly affected values recorded by the accelerometer: a tight fit may help trigger the sensor more easily, thus providing higher activity values. Conversely, a loose collar may slip on the neck and not trigger the activity sensor while the animal is performing certain actions. Consequently, modifications of animal body size may introduce a strong bias, which so far has never been corrected or accounted for. Ungulate body size modifications may be expected as a consequence of weight loss during demanding seasons (Bassano et al., 2003; Rughetti and Festa-Bianchet, 2011) or as a consequence of diseases and poor body condition, while the increase of neck circumference is likely to occur during the rutting season (Lincoln, 2010; Chapman and Chapman, 1997). Thus, finding a method which considers potential variations of collar fit throughout the monitoring period is of utmost importance.

The approach we propose is a revision of the method developed by Gervasi et al. (2006), which enables to analyse the activity of collared mammals, thus overcoming the aforementioned constraints. This method distinguishes between active and inactive behaviours by analysing ARAD to identify a threshold value, with no need of further calibration by using behavioural observation data. Recently, Gervasi et al.'s method was used in the study of activity rhythms of large mammals (Bonnot et al., 2019; de Gabriel Hernando et al., 2020). However, to the best of our knowledge, the validation of the method proposed by Gervasi et al. (2006) by means of direct observations was implemented only on two captive brown bears (*Ursus arctos*). Therefore, before this method can be confidently used for other species, including species whose morphological and behavioural features differ from those of bears, a more robust validation and a larger dataset of direct observations of wild animals are necessary. Gervasi et al. (2006) acknowledged that the tightness of the collar on the animal neck may strongly affect the values recorded by the accelerometer. However, they provided no suggestion to improve their method in the light of this issue. Moreover, they validated it by using data from a short time period (May-June), when the body conditions of the two bears were also not likely to change. By consistently applying the method proposed by Gervasi et al. (2006) biased results may be expected since modifications in collar tightness strongly affect accelerometer data (see Dickinson et al., 2020). For this reason, we proposed to refine the methodology by using ad hoc temporal scale according to the species under analysis. In particular, temporal scales need to be chosen depending on the animal biology and the environmental seasonality, so as to gather intra-individual variations throughout the year.

The aim of this study was to validate Gervasi et al.'s method by making a high number of direct observations of a large dataset of wild collared animals over the year and by adopting different temporal scales. We applied the method to an activity dataset from 26 free-ranging

Alpine ibex (*Capra ibex*, hereinafter referred to as "ibex") fitted with GPS collars equipped with accelerometers. Ibex is a polygynous ungulate that inhabits mountainous environments characterised by marked seasonal changes. This species is characterized by extreme sexual dimorphism (males may be more than 100% larger than females – Loison et al., 1999) and significant body weight variations throughout the year (Giacometti et al., 1997). Moreover, ibex mainly uses open areas (Brivio et al., 2019; Grignolio et al., 2004) and is easy to detect, thus allowing for long observation sessions throughout the year (e.g., Mason et al., 2017; Apollonio et al., 2013). For these reasons, ibex is an ideal case study for testing Gervasi et al.'s methodology by investigating differences among different temporal scales used to distinguish between active and inactive behaviours. We validated the method by comparing the binary behavioural state which we obtained by processing ARAD with direct observation data collected on collared individuals of both sexes. We then evaluated the outcomes of the method at different temporal scales by calculating and analysing the diurnal and nocturnal active time of both males and females throughout the year. We predicted a higher accuracy of the method with the decrease of the temporal scale considered.

Methods

This study complied with all national and regional laws dealing with ethics and animal welfare. Ibex capture and manipulation protocol was approved by the Italian Ministry of Environment (Prot. No. 25114/04).

Study area

The study took place in the Levionaz Valley in North-Western Italy, a steep glacial valley in the middle of the Gran Paradiso National Park (GPNP: 45°35′ N, 7°12′ E). The study area, 1700 ha ranging from 1650 to 3300 m a.s.l., is characterised by alpine meadows (mainly *Festuca* and *Poa* spp.), wood patches of larch (*Larix decidua*), rock cliffs, moraines, and glaciers (Grignolio et al., 2018, 2003). The local climate is moist continental mid-latitude, with dry winter and snowfall mostly occurring from November to April. The warmest period generally occurs from June to September. Ibex are captured by chemical immobilisation every year by park wardens and veterinarians, as part of the GPNP conservation programs. At capture, ibex are aged by counting horn annuli (von Hardenberg et al., 2004) and marked (colour-coded ear tags and/or collars) for individual identification (see Brivio et al., 2015 for further details). In order not to jeopardise the uniformity of results, when fitting ibex with collars, we are extremely careful to fasten the collars to a uniform extent among individuals, and not too tight so as to ensure the animals' welfare. Indeed, inappropriate collar fitting was seen to be deleterious for the health of marked animals (Krausman et al., 2004).

Data collection of telemetry data

From May 2013 to October 2019, we fitted 18 male and 8 female ibex with GPS radio collars (GPS PRO Light collar, Vectronic Aerospace GmbH, Germany), equipped with a dual-axis motion sensor (i.e., accelerometer). The accelerometer measures simultaneously along 2 orthogonal directions the changes in acceleration associated with the actual motion experienced by the collar. On the X-axis, the accelerometer was sensitive to acceleration events with forward/backward direction/axes, while, on the Y-axis, it recorded acceleration events with a sideward and rotary direction. The accelerometer had a dynamic range from -2g to +2g and measured activity as the change of static acceleration (gravity) and dynamic acceleration (collar) with a frequency of 4 Hz. Motion data from accelerometers, i.e. activity values, were calculated as the difference between consecutive measurements, averaged over a time interval of 4 minutes and given within a relative range between 0 (no difference between consecutive data) and 255 (difference of -2g/+2g), with the associated date and time. The activity value measured by the sensor depends directly on individual movements, but it can also be indirectly affected by several factors. Among them, a crucial role is played by collar tightness, which depends on the neck size

of the individual and, therefore, can be different for each ibex and even for the same individual at different times (Dickinson et al., 2020). We did not analyse data collected during the first 2 days after capture in consideration of a previous study that showed alterations in ibex behavioural patterns during the first 48 hours following capture (Brivio et al., 2015).

Active and inactive behaviour distinction from telemetry data

To distinguish between active and inactive behaviours by using collar ARAD we employed the individual-based method proposed by Gervasi et al. (2006). For each collared ibex, we calculated the overall activity for any point in time as the sum of the activity values recorded by the accelerometer in the collar along the two orthogonal directions (X axis + Y axis). We then grouped its range (0–510) into 51 activity classes of 10 units and produced the frequency histograms to determine whether its distribution was bimodal. Whenever histograms had a bimodal distribution, we defined the threshold value as the mean value of the activity class with the lowest frequency in the range between the 2 peaks of the frequency distribution (see Fig.1 as an example). Activity values lower than the threshold value were considered inactive, whereas those higher than or equal to it were considered active. Unlike Gervasi et al. (2006), who used the whole dataset to define the threshold value for each individual, we repeated the same procedure at finer temporal scales, since we expected changes in ARAD values related to changes in collar tightness, which in turn depended on the varying neck size of individuals. In fact, both their body and neck size may change considerably throughout the year. Consequently, for each ibex, we grouped collar ARAD over several time windows, namely for each year, semester, season, two-month period, and month of data collection. The definition of the different temporal scales considered the biological cycle of ibex and the phenological cycle of the Alpine environment. We defined the semesters (from 1 April to 30 September and from 1 October to 31 March), the seasons (spring: 1 March–31 May, summer: 1 June–31 August, autumn: 1 September–30 November, winter: 1 December–28 February) and the two-month periods (1 December–31 January, 1 February–31 March, 1 April–31 May, etc.). By using this classification, we ensure the inclusion of the mating season (December-January) and the birth period (June-July, as indicated by Apollonio et al., 2013) within a single semester/season/two-month period. For each temporal scale, we plotted the frequency distribution of all activity classes to determine whether it was bimodal so as to find the corresponding threshold value as described above. Whenever the frequency distribution was not bimodal, we adopted a new approach of analysis by extending the reference period and adding 15-day time spans before and after the starting and ending dates, until we found a bimodal distribution frequency.

Observational data

We carried out direct observations of collared ibex, which were equipped with coloured collars for individual identification from long distances, concomitantly with collar measurements. Females were observed from June to October 2014, while males were observed during two distinct periods: from May 2015 to January 2016 and from November 2017 to April 2018. Observations were conducted with the Focal Animal Sampling method (Altmann, 1974) by means of binoculars and spotting scopes from such a distance (at least 200 meters) that ibex behaviour would not be influenced by the presence of the observers. The focal individual was observed continuously for at least 1 hour, during which we recorded its behaviour and the time of changes in the behavioural states that were maintained for at least 1 min. We uniformly distributed the observation times over the daylight hours and among collared ibex.

Each focal individual observation was sequenced in the same 4-minute periods used by the activity sensor in the GPS collars to record the activity values. Then, each 4-minute sequence was classified as either inactive when the ibex spent ⩾75% of the observed time sleeping, resting, and standing or active when the ibex was feeding, grooming,
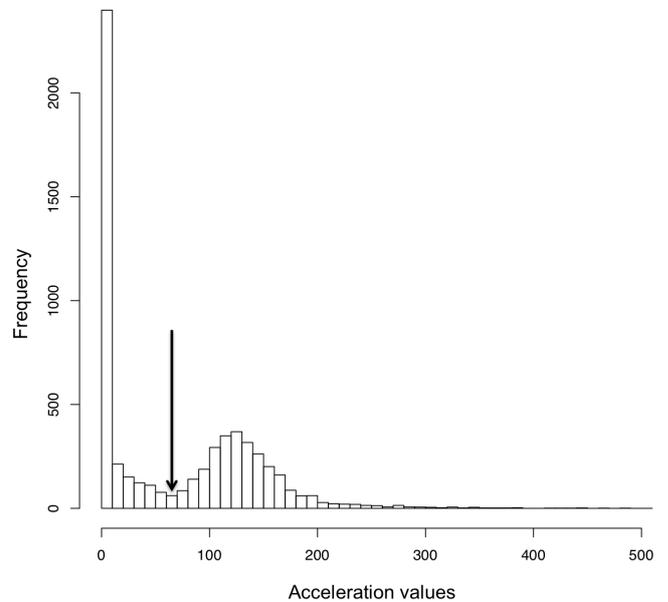
Figure 1 – Frequency distribution of activity classes recorded over a month (July 2013) on a male Alpine ibex (ID 12228) fitted with GPS collar and a dual-axis motion sensor in the Gran Paradiso National Park (Italy). The distribution shows the typical pattern in which the data fall into two clusters; the cluster on the left includes data logged when the animal was standing still or lying down ("inactivity"), while the cluster on the right includes data logged when the animal was grazing, walking, or running ("activity"). The arrow indicates the threshold value used to classify the active/inactive status (see text for more details).

interacting, or moving for ⩾75% of the observed time. All 4-minute periods in which ibex spent <75% in either active or inactive behavioural state were discarded from the subsequent analysis.

Validation

We compared the binary behavioural state (active-inactive) obtained from the observational data with those provided by the dual-axis motion sensor categorised by using the threshold procedure to test their correspondence and validate the threshold values obtained at the different temporal scales considered. To calculate the 95% confidence interval (CI) for the correspondence values, we applied a non-parametric bootstrap with replacement (1000 iterations) on the data for each temporal scale considered, i.e. year, semester, season, two-month period, and month. The bootstrap procedure and the confidence interval calculation were implemented by using the `boot` package (Canty and Ripley, 2017) in R (version 3.0.2; R Core Team, 2016).

Annual trends of diurnal and nocturnal active time

For each ibex, all ARAD recorded by the collars and the corresponding binary behavioural state (active-inactive) obtained from the dual-axis motion sensor by means of the threshold values were classified as either diurnal or nocturnal according to the recording date and time and the corresponding sunrise and sunset times (obtained from the National Oceanic & Atmospheric Administration https://www.noaa.gov/): activity values recorded between sunrise and sunset of day i fell into the diurnal activity subset of day i, while those recorded between sunset of day i and sunrise of day $i+1$ fell into the nocturnal activity subset of day i. After splitting activity data into the two subsets (diurnal and nocturnal), we transformed the binary behavioural state (active-inactive) into: i) proportion of active time during daylight hours (Diurnal Active Time, DAT) and ii) proportion of active time during nocturnal hours (Nocturnal Active Time, NAT), for each day of data collection and each collared ibex. DAT and NAT were calculated as the number of activity values classified as active divided by the total number of activity values during daylight and nocturnal hours, respectively. In order to examine the patterns of active time variations throughout the year, we fitted Generalized Additive Mixed Models (GAMMs) by using DAT and NAT as response variables and Julian date as predictor variable. The Julian date was modelled as a cyclic cubic regression spline in or-

der to take into account the circularity of this variable: in so doing, we ensured that the value of the smoother at the far-left point (1 January) was the same as the one at the far-right point (31 December). Ibex identity was used as a random factor to control for repeated measurements of the same individual by fitting it in the GAMMs by using "re" terms and smoother linkage (Wood, 2013). GAMMs were implemented within the mgcv package (version 1.8–10 in R). We repeated the same analysis for each temporal scale considered (year, semester, season, 2 months, and 1 month) in order to evaluate and compare the results obtained from the different temporal frames.

Results

The total number of animal/day accelerometer data recorded by means of the GPS collars was 5478 and 5796 for males and females, respectively. We directly observed 8 collared males and 8 collared females, obtaining a total of 688 and 199 hours of observation for males and females, respectively.

All frequency distribution plots obtained by using the annual, biannual, and seasonal temporal scales were bimodally distributed (see Fig.1 as an example). When using the monthly and bimonthly temporal scale, 3% of the frequency distribution plots did not show a bimodal distribution. In these cases, by enlarging the period of reference of a month (47% of cases, N=8), two months (41% of cases, N=7), and three months (12% of cases, N=2), we obtained a bimodal distribution, thus enabling the calculation of a threshold value for each time interval. The calculated threshold values ranged from 15 to 85 when using the monthly and bimonthly temporal scale, from 15 to 75 when using the seasonal temporal scale, and from 15 to 65 when using the biannual and annual temporal scale.

For all the temporal scales considered, we found a high positive correspondence between the sensor-derived and the activity data observed for each collared ibex. The mean percentage of correct classification was 91.87% (CI: 91.33–92.40), 92.70% (CI: 92.18–93.22), 93.02% (CI: 92.52–93.52), 93.01% (CI: 92.51–93.54), and 92.98% (CI: 92.49–93.48) for the annual, biannual, seasonal, bimonthly, and monthly temporal scales, respectively (see Tab. 1 for more details).

By transforming the sensor-measured activity into proportion of active time, we found that the time ibex spent active was different during daylight and nocturnal hours, with different patterns of variation throughout the year. The annual DAT and NAT patterns estimated by using the threshold values calculated at different temporal scales were similar: the main differences were found when using the annual and the biannual scales for both males and females (Fig.2). Male DAT showed three peaks throughout the year, with the highest one around the 129th–137th day of the year. The lowest DAT peaks occurred around the 75th, 207th, and the 315th day of the year (Fig.2a). Female DAT showed three positive peaks, the highest one occurring slightly earlier than that of males, i.e., around the 123rd day of the year. Likewise, the negative peaks were reached earlier with respect to males, i.e., around the 64th, 182nd, and 312nd day of the year (Fig.2c). Male NAT reached the minimum value around the 54th day of the year and then progressively increased until the 214th day (Fig.2b). After this peak, NAT progressively decreased until reaching another negative peak around the 54th day of the following year. Likewise, the minimum value of female NAT was reached around the 43rd day of the year, while the maximum one was reached the 289th day of the year, i.e., later than males (Fig.2d). Activity pattern predicted by the using the threshold values calculated with the annual temporal scale showed the maximum activity around the 185th day of the year.

Discussion

The methodology proposed to determine activity patterns from values generated by accelerometer sensor in GPS collars provided a reliable identification of the activity status of the individuals monitored. Threshold values generated by analysing sensor data enabled us to distinguish between active and inactive behaviours with a high percentage of correctly classified binary behavioural state (93%). Our results

Table 1 – Correspondence values and their 95% confidence intervals for all the temporal scales considered. Data were analysed both separately for each sex and with the sexes pooled.

Temporal scale	Sex	Value	Confidence interval
Months	Males	93.75	93.19–94.29
	Females	90.72	89.57–91.82
	Total	92.98	92.49–93.48
Two months	Males	93.70	93.14–94.23
	Females	90.99	89.89–92.10
	Total	93.01	92.51–93.54
Season	Males	93.73	93.19–94.27
	Females	90.95	89.85–92.04
	Total	93.02	92.52–93.52
Semester	Males	93.46	92.92–94.00
	Females	90.49	89.39–91.65
	Total	92.70	92.18–93.22
Year	Males	92.63	92.05–93.23
	Females	89.63	88.40–90.81
	Total	91.87	91.33–92.40

are consistent with a previous study which tested the methodology on two captive brown bears (Gervasi et al., 2006). The performances of the method can be compared to those obtained in studies conducted on other species by using more complex methods, which reported an overall accuracy ranging from 83% to 92% (Becciolini and Ponzetta, 2018; Signer et al., 2010; Bourgoin et al., 2008; Coulombe et al., 2006; Adrados et al., 2003). Moreover, we highlighted that, by adopting an ad hoc fine temporal scale in data analysis, the approach proposed enables us to take into consideration the influence of individual factor modifications (e.g., body size) on the values recorded by the activity sensor during the monitoring period.

The method proposed is an easy-to-use technique that will greatly benefit researchers and technicians who are using accelerometers to quantify the activity of terrestrial mammals monitored by means of the most common GPS collars. The main advantage of this method is that it does not require any further on-field procedure (e.g., observational data to classify the data from activity sensor) before starting the analysis of activity data. As such, this technique can be implemented for any case study, including the analysis of activity patterns of nocturnal, wide-ranging, and elusive mammals, which are obviously difficult to observe. Moreover, this method overcomes potential biases that may arise from the classification process (i.e., correlation of activity sensor values to behavioural observations). For instance, during this process it was shown that mismatches between collar activity sensor data and direct behavioural observation data may occur on account of failures in the time-keeping mechanisms of the GPS collars, thus resulting in inaccurate classification models (Gaylord and Sanchez, 2014). Furthermore, during the classification process behavioural observations are generally conducted on a restricted number of individuals and then used to infer behaviour from activity sensor output for a larger number of free-living individuals (e.g., Löttker et al., 2009; Bourgoin et al., 2008; Adrados et al., 2003). This may result in biased results, since individual factors (e.g., sex, age, and body size) can affect the amount of movement associated with different behaviours and, therefore, the values recorded by the activity sensor (Löttker et al., 2009; Coulombe et al., 2006; Gervasi et al., 2006). By treating each individual independently, the proposed method is able to account for the influence of individual characteristics on activity sensor data. This issue should not be neglected by researchers: when we used fine temporal scales, we found that monthly threshold values ranged from 15 to 85, thus highlighting a tangible difference in the accelerometer response among individuals and months. For these reasons, we recommend that individual-based methods be always used for classification procedures.
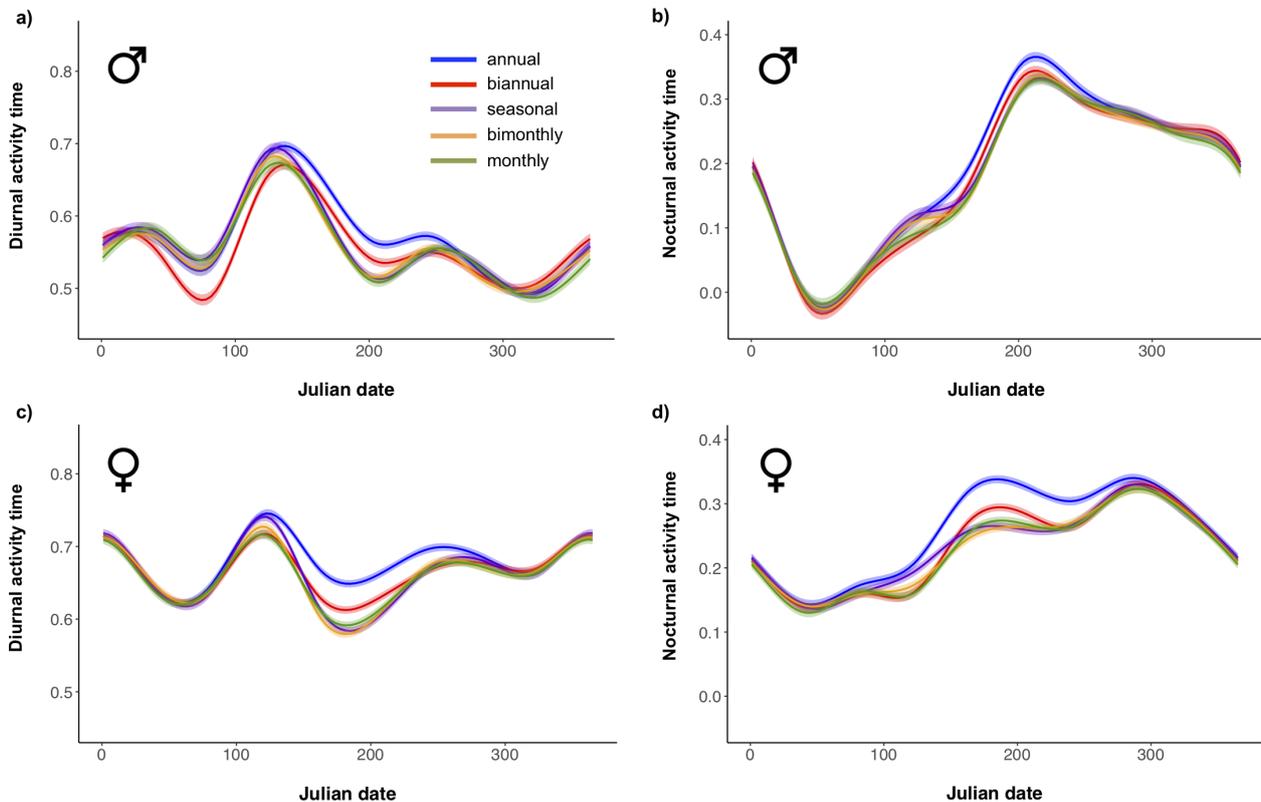
Figure 2 – Values predicted by the Generalised Additive Mixed Models (see the text for more details) of Diurnal Active Time (a-c) and Nocturnal Active Time (b-d) of Alpine ibex in the Gran Paradiso National Park (Italy). The figure shows the effects of the Julian date. In each graph, the coloured lines represent diurnal and nocturnal active time calculated by using threshold values determined at different temporal scales: blue=annual, red=biannual, violet=seasonal, yellow=bimonthly, and green=monthly. The colour-shaded areas are the standard errors estimated by the model.

Among the individual characteristics, the fit of the collar around the neck strongly influences how easily the activity sensor is triggered by animal movements, thus affecting the values recorded by the accelerometer (Dickinson et al., 2020). For example, a tight fit (i.e., when the collar is close-fitting on the animal neck) may help trigger the sensor more easily and provide higher activity values. On the contrary, a loose fit (i.e., when the collar is too large for the animal neck) may allow the collar to slide on the neck rather than trigger the activity sensor during certain behaviours (Coulombe et al., 2006; Dickinson et al., 2020). How tight a collar is fastened can vary depending on how the collar was adjusted on the animal neck during the capture, but it can also change for the same individual on account of variations of its body weight and conditions during the monitoring period. For instance, this may be due to seasonality in capital species and disease. Moreover, season-related environmental effects (e.g., weather conditions, plant phenology) as well as the species-specific habits and biology have to be considered when inferring behaviour in animals, since they may produce significant alterations in the intensity of activity (Becciolini and Ponzetta, 2018). Therefore, researchers should be careful in analysing activity data collected by accelerometers throughout long periods of time as it may be necessary to correct collar ARAD and analyse them at fine temporal scale, chosen depending on the animal biology and the environmental seasonality.

Our approach allows to take into consideration changes related to variation of individual factors, animal biology, and the effect of environmental conditions, by adopting ad hoc temporal scales to generate the threshold values used to distinguish between active and inactive statuses. In testing the methodology on the ibex dataset, we expected its accuracy to increase with the decrease of the temporal scale considered. Contrary to our expectation, the percentage of correct classification in ibex resulted to be slightly dependent on the temporal scale. Only when pooling the accelerometer data of a whole year, the performance of the method significantly decreased. By reducing the temporal resolution from biannual to monthly level, we did not find any significant improvement in the classification procedure. This was likely caused by

the fact that the low percentage of wrong classification (8–9%) might be mostly due to sampling constraints. Mismatches between recording time of the observational data and sensor data may have occurred as a consequence of failures in the time-keeping mechanisms of the GPS collars (Gaylord and Sanchez, 2014). Moreover, it is worth noting that the activity sensor data are averaged over a 4-minute time period, during which an individual can perform different actions and switch from an active to an inactive status. Therefore, we argue that the variability in the accuracy of classification in our test might be mostly due to sampling constraints which overmatched the variability owing to the temporal scale used.

By using the threshold values, we were able to transform the collar ARAD of the accelerometer in proportion of time spent active by each monitored individual. This metric enabled the researchers to investigate the behavioural pattern of ibex throughout the year, taking into account this species' typical annual variation of body mass (i.e., more than 40% from autumn to spring, Giacometti et al., 1997). Predictions of the annual activity pattern of the monitored individuals were quite similar when using threshold values calculated at different temporal scales. However, differences were found when using threshold values calculated by gathering accelerometer data at an annual and biannual level, predicting significantly different peaks of activity throughout the year. Though our results apply to ibex, a similar approach may be applied to other animals in accordance with their biology and annual cycle (e.g., the neck circumference of male red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) increases during the rutting season – Lincoln, 2010; Chapman and Chapman, 1997). We argue that, by adopting ad hoc temporal scales, researchers may be able to better predict the activity patterns of the species studied by taking into consideration fine variations of individual characteristics, thus ensuring an improved understanding of behavioural patterns of the animals monitored.

It is worth noting that the activity sensors (i.e., accelerometers) integrated in GPS collars mostly used in large mammals provide a summary statistic of acceleration, averaged over the duration of a programmed sampling interval. The identification of specific behaviours (e.g., feed-

ing, standing, moving, lying) would require data to be collected with different modalities. Recently, manufacturers of collars provided the opportunity to obtain raw activity data, i.e., each variation in acceleration recorded by each sensor. To do so, collars need to be retrieved by either using the drop-off system or re-capturing the marked animals. By recording the total acceleration on three axes and analysing continuous acceleration data (e.g., by looking for patterns in the waveforms of accelerometers data), the performance of classification may be considerably improved in terms of both percentage of correct classification and number of behavioural categories identified (e.g., Nathan et al., 2012; Shepard et al., 2008). Although this technique may provide deeper insights into animal activity patterns, it requires more complex and time-consuming statistical analyses (e.g., time machine learning techniques), which take several days of computer time.

Conclusions

GPS collars combined with activity sensor (i.e., accelerometer) represent an effective technique to track movements of free-living animals and, at the same time, to infer on their behavioural state. The use of threshold values calculated at a fine temporal scale proved useful to distinguish between active and inactive behaviours so as to transform collar ARAD into biological meaningful variables (i.e., time spent active). The analysis of time spent active instead of collar ARAD is a more correct approach to investigate and compare activity levels of individuals monitored in different study areas where capture and marking activities are performed differently, likely resulting in collars positioned differently on animal necks. Moreover, by transforming collar ARAD into time spent active, it may be possible to compare activity patterns of different species and thus, for instance, analyse prey-predator relationship by looking at the activity of both with the same methodology and a high comparability of results. Furthermore, once defined the individual status from the accelerometer data it may be possible to allocate each GPS location to active or inactive behaviours. This may enable to conduct fine scale resource selection analysis in order to clearly identify habitats selected for resting and performing their activities (see also Adrados et al., 2003). In turn, this may foster the development of more appropriate strategies for species management and conservation. ✍

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Sample size and data collection schedule for accelerometer data and direct observations

Table S2-S6 Results of the Generalised Additive Mixed Models fitted to predict the diurnal active time of male Alpine ibex

Table S7-S11 Results of the Generalised Additive Mixed Models fitted to predict the nocturnal active time of male Alpine ibex

Table S12-S16 Results of the Generalised Additive Mixed Models fitted to predict the diurnal active time of female Alpine ibex

Table S17-S21 Results of the Generalised Additive Mixed Models fitted to predict the nocturnal active time of female Alpine ibex