

Bio-logging reveals heritable patterns of natural behaviours in sheep

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ABSTRACT

The measurement of behaviour in extensively managed livestock for the assessment of welfare remains a challenge. Bio-logging devices offer the opportunity to collect continuous behavioural data over long periods while animals are in their normal physical environment. Using collar-measured acceleration from 84 ewes over 28 days in a commercial flock, we built two-component daily phenotypic profiles with data-driven analysis techniques not reliant on human observations. Our analysis demonstrates the moderate repeatability of both components $(0.58 \pm 0.06 \text{ and } 0.53 \pm 0.05)$, the heritability of one component (0.53 ± 0.15) , and environmental associations with wind chill index (-0.63 ± 0.13) , and day length (-0.66 ± 0.19) . We discuss these results in relation to previous work, showing that our methods of measurement and analysis are capable of revealing the daily patterns of behaviour in sheep and how these are influenced by the physical environment and genetics. This approach can be generalised to assess behavioural phenotypes and the determinants of behaviour in other breeds or species.

Section: RESEARCH PAPER

Keywords: welfare, sheep, behaviour, continuous measurement, accelerometers, data-driven, bio-logging, compositional analysis, linear mixed-effects models, heritability

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1. INTRODUCTION

The ability for individuals to express natural patterns of behaviour is one of the five freedoms of animal welfare [1], [2]. In extensively managed livestock, such as sheep, it could be assumed that animals have the space to behave naturally without hindrance [3], but in fact, there are still behavioural constraints from the physical environment and management techniques [4]. A further challenge in extensive management systems is the ability to reliably measure the full range of behaviours that an animal might need to express. Without these measures, it is not possible to characterise behavioural patterns or shifts in those patterns that could indicate welfare states, changes in welfare, or changes in the managed environment from which welfare changes may result. Many aspects of animal welfare can be assessed with discrete observations of the environment (access to water, food, or shelter) and the animals themselves (freedom from pain, discomfort, disease, or distress). In livestock, these observations are highly effective and efficient at a typical granularity of every 24 hours (as often required by regulation). In contrast, assessing behavioural dimensions of animal welfare

requires different approaches. Behaviours change at every moment of the day in response to a wide range of varying external and internal stimuli, with the presence of a human observer being an important influence [5].

Continuous measurement with bio-logging devices allows the passive collection of data over long periods while animals are in their normal physical environment subject to their normal management regime. A range of sensors have been used successfully in sheep behavioural research, for example, GPS for absolute location [6] and Bluetooth proximity for social contact [7]. In particular, small accelerometers that measure relative movement, and posture with long battery lives have proved to be a practical and accurate method of identifying many physical behaviours in sheep [8], [9]. However, the quantification of physical behaviours in sheep is currently largely dependent on many small-scale studies with different breeds and methods, reliant on time-consuming and subjective human observations. There are opportunities for data-driven approaches to create more replicable and generalisable methods and results that can be applied to large numbers of animals outside research contexts.

In this study, we analysed collar-mounted accelerometer data from 84 pedigree-recorded ewes over two 14-day periods alongside detailed information about their environmental conditions. Data-driven analysis approaches were used to identify sequences of distinct behavioural events expressed by individuals without relying on observer-based classification models. The patterning of daily behaviour was characterised using compositional analysis to create phenotypic profiles. Linear mixed-effects models were then fitted to the data to investigate associations with the managed and natural aspects of their environment. Finally, detailed pedigree information was integrated into linear mixed-effects models, allowing us to determine the heritability of the behavioural traits detected.

The aim of our study was to assess how the patterns of behaviour in extensively managed sheep are influenced by natural environmental conditions, management approaches, and individual preferences. The repeatability and heritability of the derived behavioural phenotypes provide an indication of an individual's ability to express natural patterns of behaviour. A further objective was to establish a repeatable, objective, data-driven approach to the extraction of distinct behavioural events from acceleration measured on a collar.

Our hypothesis was that data-driven, event-based analysis of continuous bio-logging sensor data can reflect the underlying behaviour of animals with repeatable daily phenotypic profiles; that these phenotypic profiles are dependent on environmental conditions; and that the phenotypic profiles are heritable.

2. METHODS

All data were collected under ethics approval from the University of Exeter (eCLESPsy000541).

2.1. Data collection

Data were collected on a commercial sheep-breeding farm during the summer of 2018 in the South West of England near Exeter at an elevation of 240 m above sea level and a latitude of 51° 56' N. A total of 84 pregnant ewes were assessed in two separate deployments, each lasting 2 weeks. The sheep were pedigree, performance-recorded Poll Dorsets. The first deployment started at the beginning of July and the second at the beginning of August. Pedigree information, collected on breeding farms for over 20 years, was accessed through the UK's Agriculture and Horticulture Development Board.

2.2. Sensors

At the beginning of the first deployment, the ewes were weighed and had GENEActiv tri-axial accelerometers (Activinsights Ltd, Kimbolton, UK) fitted on a neck collar. As well as measuring raw acceleration, with sampling set to 50 Hz, the GENEActiv units recorded near-body temperature and ambient light levels. Each GENEActiv device was fixed to a standard plastic sheep collar (Kvikk) with an adhesive-backed hook'n'loop fastener and then further secured with electrical tape. The gold contact pins were orientated towards the tail (y-axis) and the collar was free to rotate around the sheep's neck (x and z axes). The total collar mass was approximately 100 g and so below the 5 % of body mass limit for attached bio-logging sensors [10]. At the end of each 2-week deployment, the collars were removed, and raw data was extracted using GENEActiv PC software v2.6.

An internet-enabled weather station (Davis Vantage Connect) recorded weather and environmental conditions on the farm every 15 minutes during the second deployment.

2.3. Data analysis

All data analyses were completed in R [11]. The tri-axial 50 Hz accelerometer output was processed using the R packages GENEAread, to extract the data, and GENEAclassify, to create a contiguous stream of distinct behavioural events. The GENEAclassify package combines the acceleration outputs to create elevation (y-axis) and rotation (x and z axes) signals. It then utilises the Pruned Exact Linear Time (PELT) changepoint detection method [12] within the Changepoint R package to identify changes in the acceleration signals and characterise the variable-length segments between them. The elevation signal is independent of collar rotation and, in this study, we downsampled this to 1 Hz for each day before finding changepoints using the mean and variance.

The PELT algorithm requires a penalty value to be selected for changepoint analysis with a higher value identifying fewer changepoints and, therefore, segments in a given time period. Over-segmentation of the data risks returning multiple, sequential behavioural events of the same type while undersegmentation risks combining different behaviours into the same event. In both cases, the probability of adjacent events having different characteristics is reduced. This reduction of difference can be measured as the entropy or information content of the event sequence [13], [14]. To choose an optimal penalty value, we analysed a random day from each animal for changepoints to create a sequence of mean absolute gravity-subjected acceleration values (a measure of activity intensity) at different penalty values. An entropy value for each sequence was calculated using the TSEntropies R package and we selected the penalty value with the highest mean sequence entropy (a value of 450).

Once daily sequences of variable-length events had been created for each animal, we classified each event by the mean and variance of the elevation signal with a rudimentary clustering approach. These two signal measures can be directly translated as the average neck elevation of the ewe and the amount of neck movement. We identified local minima in the distributions of each of these measures and used them as thresholds to develop a 2-dimensional clustering of all physical behavioural events into a small number of behavioural states. Clusters that represented less than 1 % of the total were combined with the nearest logical neighbouring cluster.

We then combined the total time in each behavioural state for each animal into daily summaries. These aggregated data are compositional in nature, so closure normalisation followed by an isometric log ratio (ILR) transform was completed to move the data from simplex to real space [15].

Finally, we applied principal component analysis (PCA) with oblique rotation and Kaiser normalisation to the ILR-transformed daily summaries, extracting two principal components whose scores represent the daily phenotypic profile for each animal.

The local weather measurements taken on the farm throughout deployment 2 were used to calculate daily measures of rainfall, temperature-humidity index (THI), and wind chill index (WCI) [16]. The daylight hours were calculated from the latitude and time of year. As weather measurements were only available for deployment 2, all subsequent analysis is performed on PC scores from deployment 2 only.

We implemented repeated-measures animal models using a residual maximum likelihood (REML) approach (R package ASReml-R) to estimate the repeatability, narrow-sense heritability, and permanent environment effects of the daily phenotypic profiles [17]. Repeatability (R) is defined as the

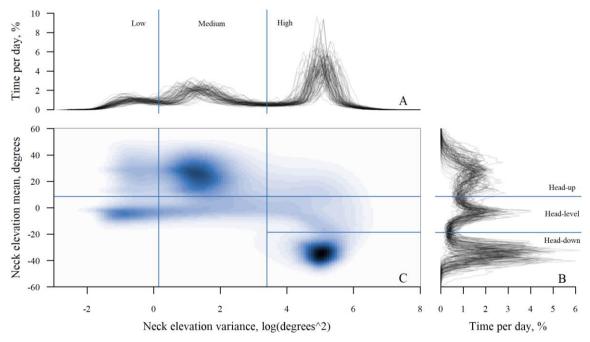


Figure 1. Individual animal distributions of neck elevation variance (A), mean (B) by duration, and resulting heatmap (C) with category thresholds.

proportion of phenotypic variance (V_P) explained by amongindividual variance V_{ind} and can be interpreted as a measure of the consistency of phenotypes [18]. Repeatability sets the upper limit for heritability. We portioned the among-individual variance into the additive genetic variation (V_a) and non-additive additive contributions referred to as permanent environment effects (V_{Pc}) . We then calculated the heritability (h^2) , defined as the proportion of phenotypic variance (V_P) explained by the additive genetic component.

We also included random intercepts of day and dam as random effects to account for non-independence and tested their significance using log-likelihood ratio tests (with the appropriate degrees of freedom), which compared full models to reduced models with the random effect being tested removed. We assumed twice the absolute difference in model log-likelihoods is distributed as chi-square with 1 degree of freedom, denoted as X^2 . Only significant random effects were retained in the model. We specified the following fixed factors; age in years, body mass, number of daylight hours, total amount of rainfall, WCI, and THI. Statistical significance of fixed effects was assessed using conditional Wald F-tests with Satterthwaite-corrected degrees of freedom; however, all effects were included regardless of significance due to biological relevance.

We used linear mixed-effects modeling (in R package *lme4*) to predict variation in the daily phenotypic profiles as a function of environmental conditions and animal characteristics, always including random intercepts to account for non-independence among repeated measurements from the same animal and among measurements from different animals on the same day. We also included random slope terms for some predictors if this significantly improved the fit of the model. All continuous predictors were converted to z-scores (subtracting the mean and dividing by the standard deviation) prior to analysis, to aid model fitting and comparison between the estimated effects of different predictors. Parameters were estimated using REML and the significance of fixed effects was assessed using likelihood-ratio tests, based on the change in deviance between models that included or omitted that predictor.

3. RESULTS

We retrieved data from all the collars for both deployments with no lost or damaged units to give 2,408 sheep days of data to analyse. The farm raised no welfare concerns associated with the use of collars over extended periods. The mean temperatures during the two deployments were 18 °C and 16 °C respectively.

3.1. Behavioural event detection

A total of 2,239,917 distinct behavioural events were identified for all animals over all days with a mean duration of 93 seconds. We found the distribution of event durations to approximate closely to the log-normal ($\mu = 3.9$, s.e. = 0.0007 & $\sigma = 1.1$, s.e. = 0.0005).

3.2. Daily phenotypic profiles

The distribution of neck elevation variance is shown in Figure 1A, with lower-movement behaviours to the left and active to the right. The distribution shows three peaks, so we selected variance thresholds at 1 and 30 deg² to create three variance categories: Low, Medium, and High.

The distribution of mean neck elevations is shown in Figure 1B, where 0° indicates a level neck position as measured by the collar; positive values indicate higher neck elevations and negative are lower. The distribution again shows three peaks, so we selected thresholds at -18.5° and 8.5° to create three elevation categories: Head-down, Head-level, and Head-up.

Figure 1C shows neck elevation mean and variance combined to create a 2-dimensional cluster map with the threshold limits of each cluster. The Head-down clusters for Low and Medium movement are very lightly populated, so we merged them with the respective Head-level clusters. Table 1 shows the resulting clusters and their descriptive statistics.

We found that the cleanest PCA output (Table 2) was obtained by using the Medium Head-up cluster as the reference for the ILR transform. The two extracted principal components, PC1 and PC2, together captured 64% of the variation in the ILR-

Table 1. Behavioural cluster descriptions.

Behavioural cluster	Time Spent (%)	Mean Event Duration (s.e.)	
Low Head-up	6.5	59 s (0.10)	
Low Head-level	7.8	83 s (0.17)	
Medium Head-up	27.7	77 s (0.10)	
Medium Head-level	11.6	71 s (0.14)	
High Head-up	4.3	39 s (0.10)	
High Head-level	8.8	65 s (0.21)	
High Head-down	33.3	319 s (1.10)	

Table 2. Loadings of principal components of daily time spent in behavioural clusters.

Behavioural cluster	PC1	PC2	
Low Head-up	0.66	0.33	
Low Head-level	-0.07	0.80	
Medium Head-up	ILR reference	ILR reference	
Medium Head-level	-0.92	0.10	
High Head-up	0.66	-0.34	
High Head-level	-0.09	-0.79	
High Head-down	0.77	0.14	

transformed data. Higher daily values of PC1 are driven by more time in Low Head-up, High Head-up and High Head-down and less time in Medium Head-level. Higher daily values of PC2 are driven by more time in Low Head-level and less in High Head-level.

3.3. Repeatability and heritability

Table 3 summarises the contribution of additive genetic and non-genetic effects on the daily behavioural variation captured by PC1 and PC2 in deployment 2.

THI was omitted from the final models presented here because of strong collinearity (> 0.9) with WCI. The scores for both components were moderately repeatable (PC1: $R = 0.582 \pm 0.058$; PC2: $R = 0.532 \pm 0.054$).

A portion of PC1 among-individual variance was attributed to non-genetic effects (29.2 % \pm 17.8 % of the total phenotypic variance) and a small portion of the variance was attributed to additive genetic effects ($X^2_1 = 2.2$, p = 0.138) with a heritability estimate of 0.291 \pm 0.200 (although this was non-significant).

For PC2, almost all of the among-individual variance was attributed to an additive genetic effect ($X^2_1 = 16.9$, p < 0.001), with a heritability estimate of 0.532 \pm 0.151.

Table 3. Parameter estimates of additive genetic and non-genetic effects.

	Effect	Estimate	s.e.	X ²₁	р
PC1	Day	0.11	0.05	255.3	< 0.001
	Additive genetic component (Va)	0.24	0.18	2.2	0.138
	Permanent environment effects (Vpe)	0.25	0.14	3.0	0.085
	Among-animal & residual variance (Vr)	0.25	0.01	NA	NA
PC2	Day	0.04	0.02	99.1	< 0.001
	Additive genetic component (Va)	0.35	0.13	16.9	< 0.001
	Permanent environment effects (Vpe)	0.01	0.08	0.02	0.896
	Among-animal & residual variance (Vr)	0.25	0.01	NA	NA

Table 4. Parameter estimates from a linear mixed-effects model of daily phenotype profile measures for deployment 2.

	Fixed effect	Estimate	s.e.	X ² 1	р
PC1	Wind chill index	-0.63	0.13	13.850	< 0.001
	Rainfall	-0.01	0.10	0.021	0.884
	Day length	0.09	0.13	0.008	0.931
	Body mass	-0.08	0.07	1.284	0.257
	Age	-0.06	0.07	0.654	0.378
<u>PC2</u>	Wind chill index	-0.24	0.10	8.296	0.004
	Rainfall	-0.10	0.07	1.500	0.229
	Day length	-0.66	0.19	14.070	< 0.001
	Body mass	-0.04	0.06	0.403	0.526
	Age	0.13	0.06	4.571	0.033

3.4. Environmental and animal effects

Table 4 summarises the estimated effects of each predictor on the daily behavioural variation captured by PC1 and PC2 in deployment 2.

PC1 was most strongly associated with the wind chill index (Figure 2), and its effect varied significantly among individual ewes (random slope term: $X^2_2 = 83.9$, p < 0.001). PC2 was associated most strongly with day length (Figure 3), with this effect varying significantly among individual ewes ($X^2_2 = 61.7$, p < 0.001), and to a lesser extent with WCI and ewe age (driven by an effect in older animals).

4. DISCUSSION

Our results show that we can derive objective and repeatable phenotypic profiles from collar-mounted accelerometer data in sheep without the need for human observations. The

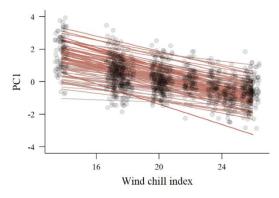


Figure 2. The association of PC1 with WCI during deployment 2.

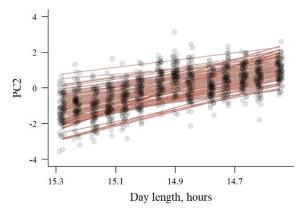


Figure 3. The association of PC2 with day length during deployment 2.

visualisation of raw sensor data clearly demonstrates both variations of movement profiles between animals and consistency in the general patterns of behavioural events with similar neck movements. The clustering of these events supports a data-driven approach to summarising daily physical behaviours. We have found these daily phenotypic profiles to be heritable and influenced by weather and age. The data return rate was excellent and the method of deployment, using easily fitted collars, was of minimum burden to both farm and animals.

The aim of the study was to assess how patterns of behaviour are influenced by environment and individual preference and genetics, rather than validate a specific behavioural prediction model with the inherent challenges of generalisability. Therefore, we did not attempt to validate the objective measurements against field-based observations of physical behaviour. Nonetheless, the results of the physical measurements can be interpreted and compared to previous work.

The lack of head-down data points in the low and medium variance categories strongly suggests that these categories are generated by a lying posture. The posture, movement, and time spent (28 %) in the 'medium head-up' cluster indicate this is ruminating, while the low variance clusters represent resting.

We consider the 'high head-down' cluster to be grazing, based on the head-down posture, higher levels of movement, and time spent (33 %). The other high variance clusters are likely to represent behaviours such as walking and running. The roughly even split between high and lower movement behaviours is comparable with other studies [19] as is the time spent resting, runninating, and grazing [20].

In the context of this behavioural interpretation, the ILR transform and principal component analysis holds a 'ruminating' constant. PC1 is then driven by increased grazing and head-up (more alert) postures while PC2 is driven by more time resting and less time in the non-grazing, high variance clusters.

Our estimates of phenotypic profile repeatability were moderate and in the range of previous estimates, with studies on a wide range of behaviours and taxa reporting an average repeatability of 0.37 [21], and studies on sheep behaviour in an arena test reporting R values of 0.10 - 0.71 [5], [22]. Sheep have also been shown to demonstrate repeatable grazing and rumination behaviour [21], [23], [24].

The modelling reveals that PC1 is influenced by both nongenetic effects and slight additive genetic effects and has a strong negative association with wind the chill index. It is likely to be measuring the animals' response to poorer weather as they seek shelter and graze less. Other work has also failed to find a strong genetic component in sheep grazing and ruminating behaviour [24].

We found PC2 to be strongly associated with day length which reduced during the deployments. PC2 also had strong additive genetic effects, indicating it is heritable. Our heritability estimate was relatively high, indicating this could be a useful trait for selective breeding as the response to selection will be relatively fast. Other behavioural traits in sheep have been shown to have a genetic component, with heritability estimates ranging from 0.13 - 0.39 for sheep temperament traits [25]. Heritability estimates for production traits such as growth, carcass, and meat traits are also lower, ranging from 0.04 - 0.42 [26]. Day lengths direct the reproductive cycle and the Poll Dorset sheep in this study have the desirable capability of out-of-season lambing. Other studies [27] have attempted to understand the heritability of this trait and a behavioural perspective may support this work.

Variability in melatonin blood levels in ewes is also under strong genetic influence [28].

Bio-logging enables the measurement of behaviour-based welfare states continuously over long periods of time. While objective measures can only ever be indirect indices of subjective welfare experiences [29], the data-driven framework we have presented here ensures that these measures provide a detailed and accurate reflection of the animal's moment-to-moment experiences. Continuous data are key to capturing the expression of rewarding behaviours and the impact of fluctuating environmental conditions. In addition, chronic and progressive conditions. subclinical disease states, and complex environmental interactions all become more detectable with long-term bio-logging data. The ease of deployment and low-risk nature of a collar measurement system can support wide-scale research and commercial adoption.

A limitation of our study is the simplicity of the clustering approach, which may have inflated the misclassification of behaviour for animals of differing morphologies. Advanced clustering and domain adaptation techniques could improve behaviour assessment accuracy while also improving generalisability across individual animals, breeds, and species.

The framework could be further optimised by including more complex accelerometry features that would reveal other behaviours (e.g. panting) and by including sensor data from other modalities (e.g. proximity tags for recording social contact). The analysis approach could be further extended to examine within-day variation in behavioural patterns such as bout lengths, temporal expression, event sequencing, and fragmentation.

While the removal of observer bias through data-driven analysis is a strength of this work, the addition of observation data with semi-supervised learning techniques, such as label propagation, would deliver better explainability and applicability of the results. An additional limitation is the availability of data from a single deployment. A deeper understanding of the repeatability of phenotypic profiles, genetics, and environmental influences could be gained through the analysis of additional data collected at other times of the year and in a wider range of weather conditions.

5. CONCLUSIONS

Our findings in this study show that daily patterns of behaviour in sheep are influenced by their physical environment and genetics. We achieved these results using easily deployed biologging devices and the data-driven analysis of accelerometer signals.

In the context of animal welfare, our ability to qualify the detailed expression of natural behaviours is relevant for future research. The heritability of behavioural traits may provide opportunities for selection to improve welfare. More broadly, the analysis framework delivers a method for the objective measurement of welfare interventions.

We have also demonstrated a highly generalisable approach to assessing behavioural phenotypic profiles and the determinants of behaviour. This approach is independent of breed or species and does not require human observations.

6. ACKNOWLEDGMENTS

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7. CONFLICTS OF INTEREST

The lead author (J. L.) is Chief Technology Officer of Activinsights, the manufacturer of the GENEActiv accelerometer device used in this study.

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