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1 **Title Page**

2 Use of tri-axial accelerometers to assess terrestrial mammal behaviour in the wild

3 **Running title**

4 AcTags used to assess terrestrial mammal behaviour

5

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27

28 **Abstract**

29 Tri-axial accelerometer tags provide quantitative data on body movement that can be
30 used to characterise behaviour and understand species ecology in ways that would
31 otherwise be impossible. Using tags on wild terrestrial mammals, especially smaller
32 species, in natural settings has been limited. Poor battery power also reduced the
33 amount of data collected, which limits what can be derived about animal behaviour.
34 Another challenge using wild animals, is acquiring observations of actual behaviours
35 with which to compare tag data and create an adequate training set to reliably identify
36 behavioural states.

37 Brown hares were fitted with accelerometers for five weeks to evaluate their use in
38 collecting detailed behaviour data and activity levels. Collared hares were filmed to
39 associate actual behaviours with tag data. Observed behaviours were classified using
40 Random Forests (ensemble learning method) to create a supervised model and then used
41 to classify hare behaviour from the tags.

42 Increased tag longevity allowed acquisition of large quantities of data from each
43 individual and direct observation of tagged hare's behaviour. Random Forests
44 accurately classified observed behaviours from tag data with an 11 % error rate.

45 Individual accuracy of behaviours varied with running (100 % accuracy), feeding (94.7
46 %) and vigilance (98.3 %) having the highest classification accuracy. Hares spent 46 %
47 of their time being vigilant and 25 % feeding when active.

48 The combination of our tags and Random Forests facilitated large amounts of
49 behavioural data to be collected on animals where observational studies could be
50 limited, or impossible. The same method could be used on a range of terrestrial
51 mammals to create models to investigate behaviour from tag data, to learn more about
52 their behaviour and be used to answer many ecological questions. However, further

53 development of methods for analysing tag data is needed to make the process quicker,
54 simpler and more accurate.

55

56 **Key-words:** 3DA, *Lepus europaeus*, activity, behaviour, random forests, classification,
57 brown hare

58 **Introduction**

59 Understanding animal behaviour typically requires hours of direct observation of
60 individuals in the wild, which is particularly difficult when species are elusive or hard to
61 view. ‘Biologging’ technology, where activity is remotely monitored by accelerometer
62 tags attached to the study animal, has been successfully used to study marine animal
63 behaviour (Wilson *et al.*, 1996; Yoda *et al.*, 1999; Bograd *et al.*, 2010; Gallon *et al.*,
64 2012), but its use on wild terrestrial species has been more limited (Wilson *et al.*, 2008).
65 The availability of mass-produced movement sensors for mobile phones has enabled the
66 development of relatively low cost solutions that allow continuous data collection (Rai
67 *et al.*, 2012). Early studies used only one or two sensors attached to the animal (Yoda *et al.*
68 *et al.*, 2001; Sakamoto *et al.*, 2009), but now three sensors (tri-axial accelerometers) can
69 collect acceleration data along three axes of movement; X, Y and Z, (heave, surge and
70 sway), as well as recording a time stamp (Gjoreski, Gams & Chorbev, 2010), which
71 provides greater detail of temporal patterns in body movement (Bograd *et al.*, 2010).

72

73 Tri-axial accelerometer tags (3DA-Tags) provide quantitative data on body movement
74 which can be used to characterise and quantify behaviour. This data can be used to
75 understand species ecology by linking animal behaviour, movement and activity levels
76 with data on habitat use in ways which would otherwise be impossible (Shepard *et al.*,
77 2008; Gao *et al.*, 2013). A number of machine learning methods have been employed
78 such as linear discriminant analysis, Random Forests and artificial neural networks
79 (Ravi *et al.*, 2005; Gjoreski *et al.*, 2010; Fortmann-Roe *et al.*, 2011; Gao *et al.*, 2013)
80 but there is a lack of standard practice in these analyses. A user friendly standardised
81 method that can be repeated between studies of the same or similar species still requires
82 further development (Campbell *et al.*, 2013; Gao *et al.*, 2013).

83 Many studies of terrestrial species' activity have been conducted on larger mammals
84 such as humans (Ravi *et al.*, 2005; Gjoreski *et al.*, 2010; Gao *et al.*, 2013), or captive
85 and tame animals such as, dogs (*Canis lupus familiaris*), badgers (*Meles meles*) and
86 domestic cats (*Felis catus*) (Campbell *et al.*, 2013; Gao *et al.*, 2013; Watanabe *et al.*,
87 2005). The use of 3DA-Tags on wild mammals, especially on smaller species in natural
88 settings has been limited. A major challenge in using wild animals is acquiring
89 observations of actual behaviours of tagged animals with which to correlate tag data
90 (Gao *et al.*, 2013).

91

92 We used the 'AcTag' a 3DA based tag similar to one previously used on badgers
93 (Noonan *et al.*, 2014), to quantify brown hare activity by correlating direct observations
94 with recorded accelerometry data. There has been limited direct behavioural observation
95 studies on brown hares in the wild but they were restricted to studying hares in short
96 vegetation at dawn or dusk (Marboutin and Aebischer 1996), or using a feeding station
97 rather than natural settings (Monaghan and Metcalfe 1985). Many studies of hare
98 behaviour have used radio tracking to quantify space use (Tapper & Barnes, 1986; Stott,
99 2003) and make comparisons between day and night, resting and feeding activity levels
100 (Marboutin & Aebischer, 1996; Petrovan, Ward & Wheeler, 2013). Our use of AcTags
101 to collect behavioural data on hares provided a novel opportunity to collect large
102 quantities of behavioural data from each individual hare, particularly at times when
103 visibility was poor due to tall vegetation, or light levels, and gave a detailed insight into
104 their daily activity that was previously not possible. Using this new type of 3DA based
105 tag (AcTag) made it possible to record all three axes of movement for an unprecedented
106 amount of time for 3DA recordings on an animal of this size.

107

108 In this paper we present the first field-scale study of accelerometer-derived behaviour of
109 a medium-sized terrestrial species based entirely on wild individuals. Our work
110 combines field observation with characterisation of individual behaviours and
111 classification of accelerometer data to report novel observations on the behaviour of a
112 species of conservation concern from full 24 hour monitoring using the tags.

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122 **Materials and methods**

123

124 **Capturing and tagging hares**

125 The study site was located in Wykeham, North Yorkshire, UK, (54°12'59.21" N, -
126 0°30'54.05" E) a landscape of lowland mixed arable and pastoral farmland.

127 Five adult hares were captured and AcTags (Biotrack Ltd., Dorset, UK) were attached
128 using collars fixed around the neck of four female hares and one male in August 2012
129 over 2 days. At least 5 people flushed hares into three 6z gauge static nylon long nets
130 (Euroguns, Yorkshire, UK) (Petrovan *et al.*, 2013). To reduce stress each hare was
131 handled and released within 10 minutes of capture. AcTags weighed less than 1 % of
132 the hare's body weight and were fitted using a TW-3 medium mammal cable tie
133 (Biotrack Ltd., Dorset. UK). AcTags integrated a tri-axial accelerometer sensor (3DA),
134 each axis sampling at 16Hz; a 2.4 GHz Zigbee compliant Wi-Fi radio transceiver,
135 capable of transmitting data to a handheld directional antenna and associated base-
136 station, and a microprocessor that stored data losslessly onto 2 GB SD memory card (for
137 full details of the AcTag specification and system see Markham *et al.* (2012)). The
138 AcTags also had a 173 MHz VHF tracking transmitter to allow location of animals
139 using conventional radio tracking equipment. The capturing and tagging of hares were
140 carried out in accordance with the University of Hull's Ethical Committee protocols.

141

142 **Tracking and remote downloading**

143 VHF radio tracking (Telonics TR-4 radio receiver (Telonics Inc, Arizona, USA) and
144 handheld Lintec flexible 3-element Yagi antenna (Biotrack Ltd., Dorset. UK)) was used
145 to locate the tagged hares on a daily basis, and the Wi-Fi antenna was used to download

146 stored data from the AcTags remotely onto the base station once within about 200 m
147 range.

148 Data were collected for up to 5 weeks, although one female hare died 2 weeks after
149 tagging and one collar failed to record any data. Therefore, the analysis was carried out
150 using data from the remaining four hares (Table 2). Data downloaded from the base
151 station were unpacked into a MySQL database and exported as a CSV file.

152

153 **Filming behaviours of tagged hares**

154 Tagged hares were located and filmed in order to characterise behaviours. Hares were
155 filmed over eight evenings using a Sony Handycam Hybrid HDD DCR – SR35 with a
156 40x optical zoom. Hares were identified before filming by homing in with the VHF and
157 Wi-Fi antennae followed by visual confirmation of the tracking collar.

158 Once identified a hare was filmed continuously until either it moved out of sight, or the
159 light levels were too low (as per Monaghan & Metcalfe, 1985). Recordings were made
160 of four hares to collect examples of different hare behaviours, totalling 160 minutes of
161 footage (mean per hare = 53.33 minutes, SD = 20.82 minutes). Individual periods of
162 behaviours were logged with start and finish times in order to align them with output
163 from AcTags.

164

165

166 **Data analysis**

167 **Classification of known behaviours**

168 The 3DA data were synchronised with the filmed behaviours using clear behavioural
169 transitions (e.g. from resting to moving) to precisely align video footage with the AcTag
170 timestamp. The 3DA data were then coded with a behaviour type (Table 1). Nine
171 behaviours were identified from the video footage of the hares and ‘matched’ with the
172 corresponding 3DA data recorded for those hares (Fig. 1): 1 = Resting; 2 = Running; 3
173 = Vigilance; 4 = Feeding; 5 = Scratching; 6 = Licking; 7 = Shaking; 8 = Hopping; 9 =
174 Stretching

175

176 A total of 573 ‘bouts’ of behaviour were used to create a classification model for these
177 behaviours. For each bout of known behaviour a series of summary statistics were
178 calculated (mean, standard deviation, minimum, maximum, kurtosis and skewness for
179 each axis respectively, Table 2) and used to train a Random Forest model (an ensemble
180 learning method for classification) (Breiman & Cutler, 2001; Lush *et al.*, 2015). The use
181 of classification trees has been found to be the most accurate for classifying behaviours
182 from accelerometer data, with accuracy results of 84 % using decision trees (Ravi *et al.*,
183 2005) and 85 % using Random Forests (Gjoreski *et al.*, 2010; Fortmann-Roe *et al.*,
184 2011).

185

186 R (version 3.0.1, R Core Team 2013) was used to run the Random Forest model using
187 the ‘randomForest’ package (Liaw & Wiener, 2002) and the graphical user interface,
188 RATTLE (R Analytical Tool To Learn Easily, Williams 2011). The model was created
189 by randomly selecting 75 % of the data and validated using the remaining 25 %

190 (Fielding, 2007). The behaviour code was set as the target variable, 500 trees were
191 'grown' with 4 variables at each split at the node of the trees; the model is not usually
192 sensitive to changes to these variables (Liaw & Wiener, 2002). An importance graph
193 was also produced to see which variables were the most important in classifying
194 behaviours (Fig. 2).

195

196 **Supervised Classification using Random Forest**

197 The full 3DA datasets for all four hares were split into 5 second windows using R (Rai
198 *et al.* 2012). Summary statistics were calculated for each 5 second window for each hare
199 using R and the package "plyr" (Wickham, 2011). Condensing the data into windows
200 and converting the raw data into a set of behaviours has been found to be more robust
201 and have greater classification accuracy than using the raw data (Gjoreski *et al.*, 2010;
202 Rai *et al.*, 2012).

203

204 A total of 18 attributes were calculated per 5 second window of the three axes (X, Y, Z)
205 (Nathan *et al.*, 2012). The summarised dataset was then run through the Random Forest
206 model created using known behaviours, and a behaviour class was allocated to each 5
207 second window by supervised classification using Random Forests.

208

209 Data were then coded by time of day i.e. dawn, day, dusk and night, to capture changes
210 in daylight hours and to assess if behaviour changed at different times of the day.
211 Sunrise and sunset times for that period were used with an hour either side to denote
212 dawn or dusk (Petrovan *et al.*, 2013). To account for the difference in amount of overall
213 time between the times of day, (i.e. day time = 10 hours compared to dawn which was

214 only 2 hours long), the mean proportion of time was calculated for each behaviour and
215 time of day. Proportion data were logit transformed to meet the assumptions of
216 homogeneity and normality. An ANOVA was performed in SPSS (IBM version 19) to
217 test if there were any differences in behaviours at different times of day and to calculate
218 average activity levels during the day. For the ANOVA analysis, resting and crouching
219 were combined to create the variable “resting” and licking, scratching and shaking were
220 combined to create a new variable called “grooming”. To assess active and non-active
221 periods the variables resting, vigilance and crouching were combined to denote
222 ‘inactive’ and running, feeding, licking, shaking and scratching were combined to
223 denote ‘active’.

224

225 The number of daylight hours reduced from 14.34 hours to 12.17 hours over the course
226 of the AcTag data collection. To assess if this had an effect on hare behaviour the data
227 were split into periods of 12.5 – 13.5 daylight hours and 13.5 – 14.5 daylight hours. A
228 two-way ANOVA was performed to test if the amount of daylight hours affected
229 behaviour at different times of the day.

230 **Results**

231 Nearly 500 million 3DA data points were recorded from all tagged hares (Table 3).

232

233 **Classification of behaviours**

234 The Random Forest model created using the training data had an error rate of 10.47 %.

235 The model classified running, feeding and vigilance behaviours well, but this was not

236 the case for licking, hopping and stretching (Table 4). The other behaviours of resting,

237 scratching and shaking were moderately well classified. The variable importance graph

238 showed that the mean, standard deviation, minimum and maximum, in particular of the

239 Z and Y axis, were more important in the classification of behaviours than other

240 components of parameter estimates (Fig. 2).

241 Model validation of the test data used on the trained model, correctly classified (true

242 positives) in 89 % of cases with the remaining 11 % incorrectly classified (false

243 positives).

244

245 **Daily activity and behaviours**

246 The mean proportion of time hares spent running, feeding and grooming was

247 significantly different between different times of the day (Table 5). However, the

248 proportion of time spent resting or being vigilant was not.

249

250 Post hoc Tukey tests revealed that hares spent a greater mean proportion of time

251 running during dawn and dusk compared to during the day or night (Fig. 3). Hares spent

252 significantly less time feeding during the day compared to all other times of the day

253 (Fig. 3). Hares also spent significantly more time grooming during dawn and dusk times
254 compared to during the day and night (Fig. 3).

255

256 Combining the behaviours into active and inactive behaviours and comparing between
257 different parts of the day (dawn, day, dusk and night) showed that hares spent the
258 majority of their time being inactive, this included resting and sitting/crouched
259 behaviour (Fig. 4). Hares were more inactive during the day (one hour after sunrise to
260 one hour before sunset) ($t = 16.123$, $df = 3$, $P = 0.001$) and the most active at night ($t =$
261 5.963 , $df = 3$, $P = 0.009$).

262

263 **Changes to daylight hours**

264 Hares' behaviour significantly changed when daylight hours per day increased (Table
265 6). When daylight hours increased hares rested less and were more vigilant (Fig. 5),
266 however the amount of time running, feeding or grooming did not change significantly.
267 The only behaviour that was significantly different depending on time of day was
268 running ($F = 9.595$, $df = 3,138$, $P = 0.001$); the other behaviours had no significant
269 interaction between daylight hours and time of day. Hares increased the percentage of
270 time they spent running at dawn, dusk and during the night when daylight hours reduced
271 but decreased during the day (Fig. 6).

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279 **Discussion**

280 We were able to classify observed behaviours from the AcTag data with high accuracy
281 (89 %) with only an 11 % error rate using the Random Forests method. This was similar
282 to other studies that used Random Forests to classify behaviours from 3DA data (Rai *et*
283 *al.*, 2012). Tri-axial accelerometers provide the technology to collect behavioural data
284 on animals that otherwise could be hard to view (Shepard *et al.*, 2008; Nathan *et al.*,
285 2012; McClune *et al.*, 2014). However, validation of behaviours inferred from 3DA
286 data has previously been extremely challenging. The individual accuracy of behaviours
287 defined in our random forest model varied, with running (100 % accuracy), feeding
288 (94.7 %) and vigilance (98.3 %) having the highest classification accuracy. However,
289 there were some behaviours that the model failed to classify, such as hopping and
290 licking that had 0 % classification accuracy.

291

292 Differences in classification class errors could be due to the number of examples of that
293 behaviour that were filmed and, therefore, used to model the behaviour, similarities
294 between different behaviours in the 3DA data that could cause error, or there was no
295 clear pattern for those particular behaviours. Classification accuracy has been a common
296 yet often unquantified problem in studies using 3DA technology, and is likely to vary
297 between species. For example, McClune *et al.* (2014) found that walking, trotting and
298 snuffling could not be distinguished from each other for a badger. Whereas, in our study
299 crouching, vigilance and feeding could not be distinguished, as the head and hence the
300 neck was moved whilst in a crouched position during all three behaviours. McClune *et*
301 *al.* (2014) have suggested that optimising the size of the windows and increasing the
302 number of parameters used could aid in increasing classification accuracy. By using
303 windows to condense the data some of the information is lost. Gjoreski *et al.* (2010)

304 reported that micro activities, such as small movements or gestures, could be lost when
305 condensing data to 5 second windows, which nevertheless accurately classified macro
306 level activities such as walking. However, we found that summarising data into 5
307 second windows did reduce the amount of data noise and also reduced the computer
308 power needed to analyse the data.

309

310 Our successful deployment of AcTags on hares, and robust classification of behaviours
311 has allowed us to gain information on hare behaviour which compares with what little
312 existing behavioural data exist from the wild. Our data was also able to compare
313 behaviours and activity levels at different times of day, which was previously not
314 possible using direct observational methods only. Hares spent the majority of their time
315 being inactive, with the least activity during daylight hours, which was expected as they
316 are crepuscular (Hutchings & Harris, 1996). When they were active they spent 46 % of
317 the time being vigilant and 25 % feeding. The main behaviours that changed were
318 feeding and vigilance, suggesting a possible trade-off between the two. There were
319 increases in other active behaviours, such as running and grooming during the hours
320 around dawn and dusk. At these times of day hares leave or return to their forms after
321 resting or feeding (Monaghan & Metcalfe, 1985; Holley, 2001) and it is likely that they
322 spend that time stretching or cleaning following resting or after a night's activity.

323

324 When daylight hours increased there was a significant reduction in time spent resting
325 and feeding and an increase in vigilance. It is possible that the increase in daylight hours
326 affects hares' perception of predation risk or is associated with higher levels of
327 disturbance. Holley (2001) also found that as daylight hours increased hares were more
328 active during daylight hours but could not relate this to reproduction or feeding

329 requirements. In that study hares were active for at least 12 hours, irrespective of
330 number of daylight hours per day (Holley, 2001), so must have been active during
331 daylight hours in the summer months when night time reduced below 12 hours.

332

333 The only behaviours that were affected by the change in daylight hours and the time of
334 day were running and vigilance, which increased at dawn, dusk and night but reduced
335 during the day. This is consistent with the time around dawn and dusk being spent
336 moving between sites, or perhaps interacting with other hares, and being more cautious,
337 as daylight hours increased. This latter observation is also consistent with observations
338 of Monaghan & Metcalfe (1985) that group vigilance did not alter due to light intensity
339 at dawn and dusk. However, in the current study hares did not increase feeding at dawn
340 and dusk, as most feeding activity was carried out at night. Holley (2001) suggested that
341 daylight is an inhibitory factor to hares activity, and that hares are less daylight-shy
342 when they are hungry, and hence search for food. In this study the difference in day
343 length was only 2 hours, but nevertheless was associated with significant changes to
344 behaviour. Data collected over a longer time period may have demonstrated greater
345 behavioural differences with greater differences in daylight hours.

346

347 Due to the small sample size we cannot identify possible differences between individual
348 hares, male or female behaviour or seasonal variability. This would require further
349 development of the tag analysis methods and remote data collection to cope with larger
350 sample sizes, as well as, a reduction in costs of the AcTags to deploy large numbers of
351 tags.

352

353 The benefit of using AcTags was that they provided a continuous log of activity that
354 revealed patterns in hare behaviour that would not otherwise have been recorded. This
355 suggests there could be potential biases in our understanding of hare behaviour from
356 direct observation studies that have primarily been carried out at dawn or dusk. Linking
357 3DA data with location data could provide detailed insight into the interplay of
358 behaviour and habitat use (Bruno *et al.*, 2015). Future developments in tracking
359 technology may permit AcTags with GPS units which are light enough to be deployed
360 on hares and other small mammals and would provide concurrent spatial data to assess
361 habitat-specific behaviour. However, the processing and analysis of the vast amounts of
362 data collected by AcTags, and other 3DA based tags, require significant time and
363 computer processing power. Standardisation of data management and analysis tools
364 would facilitate comparisons between studies, and may allow retrospective re-analysis
365 of previous studies for comparative purposes.

366

367 **Conclusion**

368 Our AcTags enabled us to collect behavioural data on hares for an unprecedented length
369 of time both day and night that has not been done previously. The Random Forest
370 method was highly accurate at classifying behaviours from supervised models using
371 known behaviours. It is clear that this technology could be used to answer many
372 ecological questions, but methods used to analyse the 3DA data need to be developed to
373 make the process quicker, simpler and more accurate. AcTags offer huge possibilities
374 for the study of mammal behaviour, as they are able to collect data when observations
375 are difficult in the wild and over much longer periods. This will help further our
376 knowledge of animal ecology and behaviour immensely and consequently better inform
377 management policies and conservation.

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490 porpoising behaviour of Adelie penguins. *J. Exp. Biol.* **202**, 3121–3126.
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492 **Tables**

493

494 **Table 1: Classification of behaviours of hares**

Behaviour	Description
Vigilant	Either sitting up or in a crouched position, head is raised.
Feeding	Crouched position with head down, biting or chewing, moving head side to side.
Running	Larger movements involving greater distances either within fields, to a new area, or moving into different fields
Hopping	Smaller movements within the same patch, of a few hops usually during feeding
Grooming	Scratching, licking parts of the body or stretching
Resting	Crouched lower to the ground, relaxed rather than alert
Interaction	Chasing another hare/rabbit or being chased

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497 **Table 2: Mean 3-Dimensional acceleration data for x, y and z axis recorded of the**
 498 **nine identified behaviours**

Behaviours	Mean acceleration (m s⁻²) x axis	Mean SD x axis	Mean acceleration (m s⁻²) y axis	Mean SD y axis	Mean acceleration (m s⁻²) z axis	Mean SD z axis
Resting	10.29	1.85	-17.50	2.39	-21.74	1.26
Running	9.78	7.86	-32.45	12.47	5.55	4.32
Vigilance	11.12	0.82	-23.60	2.86	-14.37	3.69
Feeding	8.58	1.56	-29.47	0.91	6.64	4.27
Scratching	5.64	0.66	-22.52	9.07	-10.87	9.05
Licking	9.36	0.26	-26.02	6.82	-1.90	6.38
Shaking	4.77	0.56	-20.90	8.42	-16.04	3.78
Hopping	14.93	3.57	-25.26	1.50	0.22	3.25
Stretching	11.17	2.46	-24.00	1.57	8.00	3.21

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508 **Table 3: Summary of 3-Dimensional Acceleration data collected from each tagged**
509 **hare**

Hare ID	Number of days of data	Number of 3DA data points
3530 (Female)	34	144 413 696
3531 (Male)	33	145 070 848
3532 (Female)	0	Tag failed
3533 (Female)	33	144 651 264
3534 (Female)	12	60 688 256 (Died half way through)

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522 **Table 4: Confusion matrix of the classification of behaviours from the training**
 523 **data.** Predicted behaviours are the rows and actual behaviours are the columns. The
 524 class error indicates how well the behaviour has been classified with 0 representing
 525 definite positive classification and 1 being poor classification. Those shaded grey have
 526 been classified very well.

	Rest	Run	Vigilance	Feed	Scratch	Lick	Shake	Hop	Stretch	Class error	Accuracy %
Resting	7	0	5	2	0	0	0	0	0	0.50	50
Running	0	8	0	0	0	0	0	0	0	0.00	100
Vigilance	0	0	162	8	0	0	1	0	0	0.05	94.7
Feeding	0	0	3	178	0	0	0	0	0	0.02	98.3
Scratching	1	0	2	1	3	0	2	0	0	0.67	33.33
Licking	0	0	1	2	0	0	0	0	0	1.00	0
Shaking	0	0	0	1	4	0	1	0	0	0.83	0
Hopping	0	0	2	5	0	0	1	0	0	1.00	0
Stretching	0	0	1	0	0	0	0	0	0	1.00	0

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535 **Table 5: Analysis of behaviours at different times of the day.**

536 Results of ANOVA using logit-transformed mean proportion of time hare behaviours
537 (resting, running, vigilance, feeding and grooming) were carried out at different times of
538 the day (dawn, day, dusk and night). Values in bold are significant.

	F	df	P
Time of day			
Resting	1.091	3, 138	0.352
Running	21.126	3, 138	0.001
Vigilance	1.470	3, 138	0.222
Feeding	10.068	3, 138	0.001
Grooming	10.995	3, 138	0.001

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549 **Table 6: Analysis of behaviours when day length increases.**

550 Results of ANOVA using logit-transformed mean proportion of time hares carried out
551 behaviours (resting, running, vigilance, feeding and grooming) between different
552 number of daylight hours per day. Significant values are in bold.

	F	df	P
Daylight hours			
Resting	16.652	1, 140	0.001
Running	0.720	1, 140	0.401
Vigilance	13.294	1, 140	0.001
Feeding	0.884	1, 140	0.349
Grooming	1.315	1, 140	0.254

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563 **Figures**

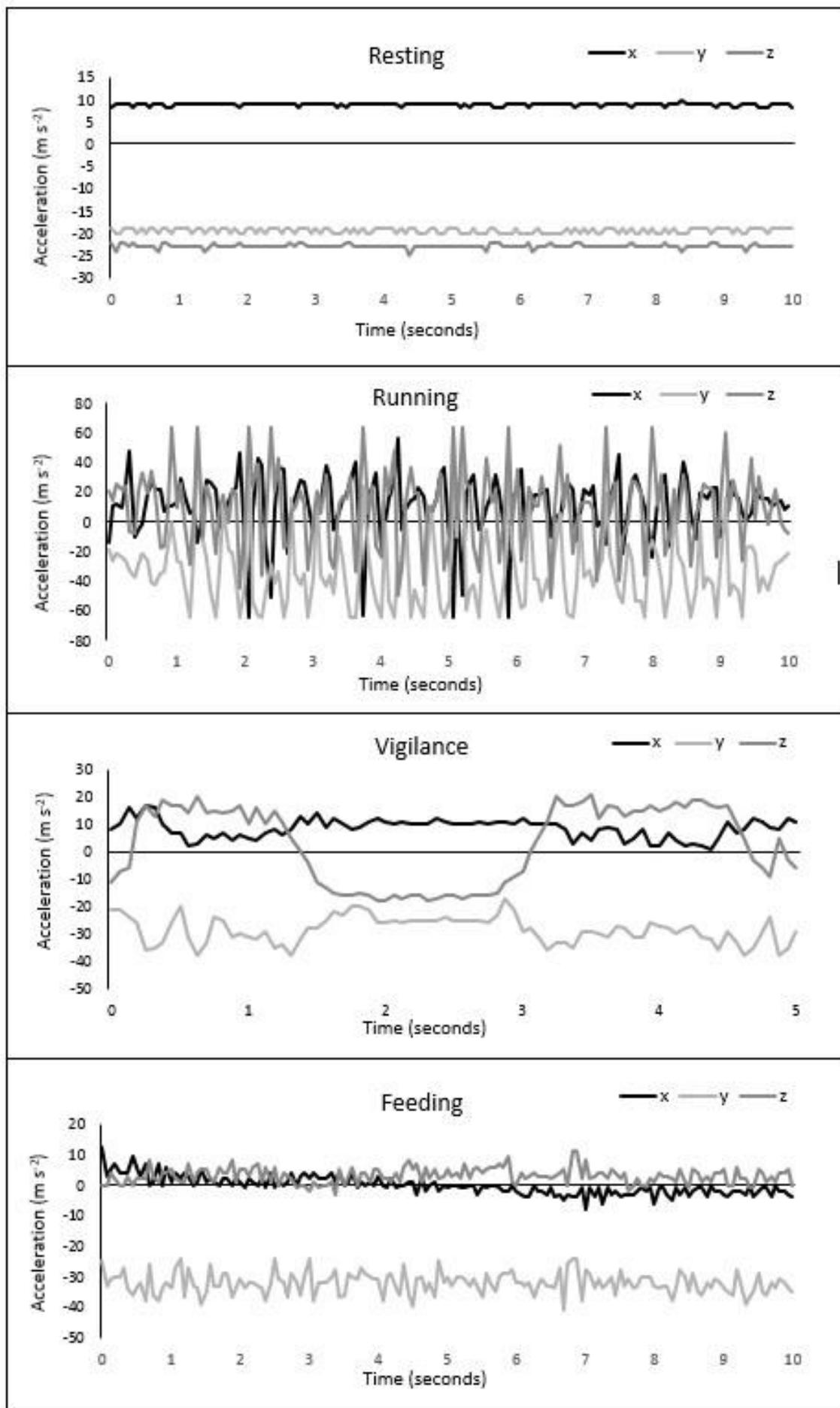
564 **Figure 1: Accelerometer data of four hare behaviours**

565 3-dimensional acceleration data (x, y, z axis) recorded on the tri-axial accelerometer

566 tags as examples of the patterns identified of known behaviours that were recorded from

567 filming the tagged hares.

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571 **Figure 2: Variable importance graph**

572 Variable importance graph of the Random Forest classification model on the 75 % of
573 the data used for model training.

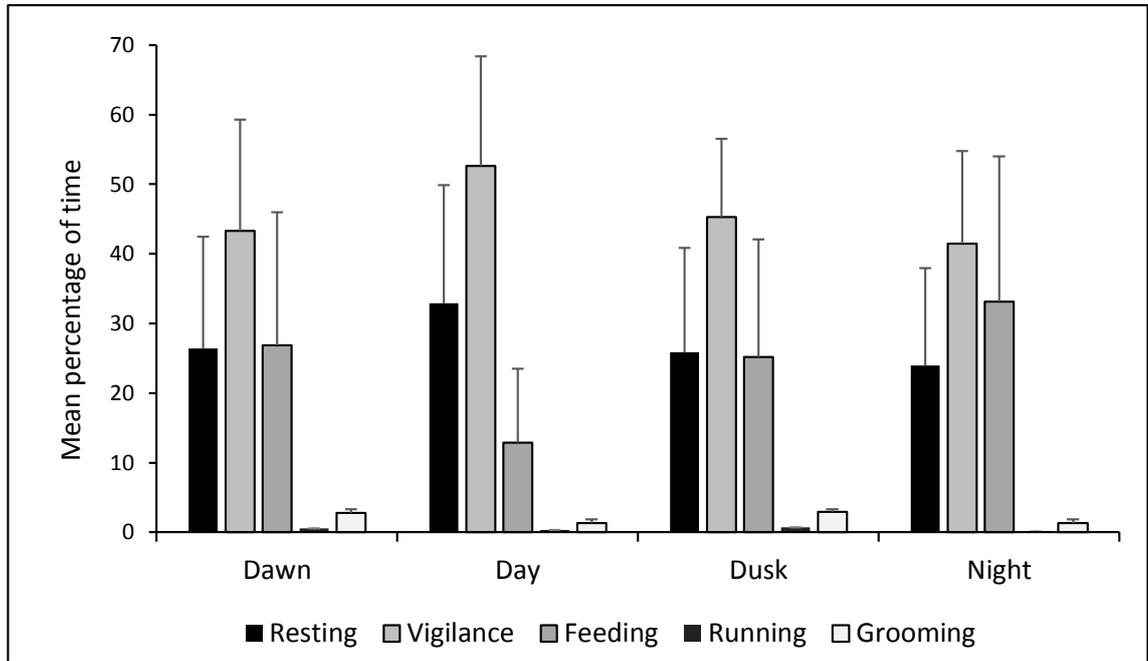


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575 **Figure 3: Hare behaviour at different times of the day**

576 Mean percentage of time hares spent doing behaviours during different times of the day.

577 Error bars are standard deviation.



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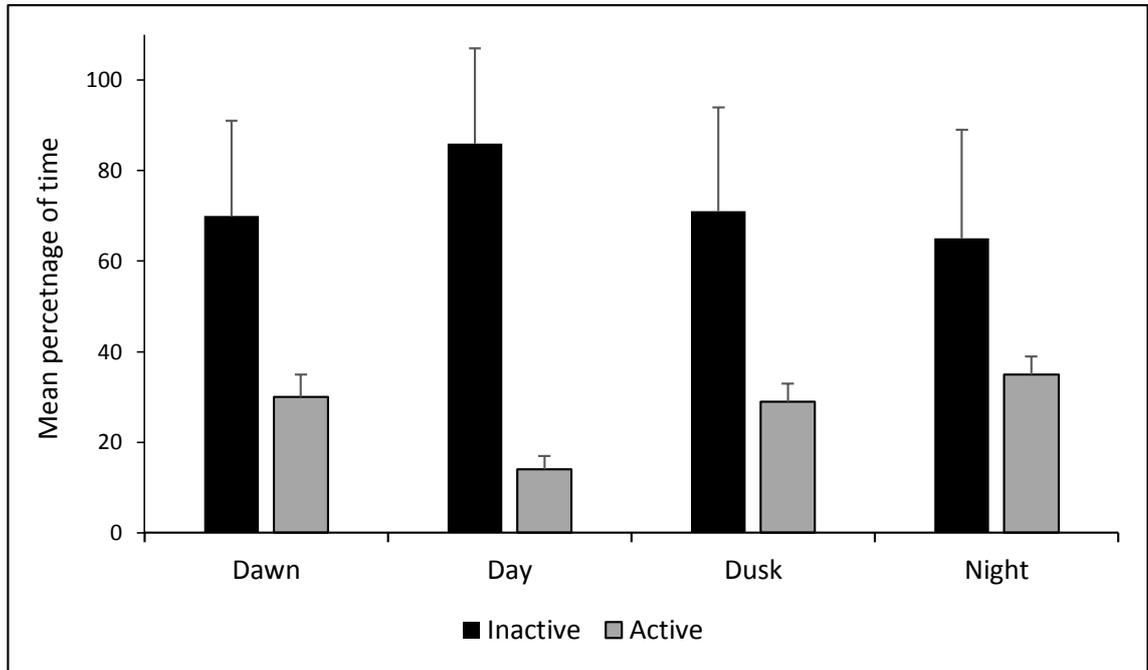
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583 **Figure 4: Hare activity at different times of the day**

584 Mean percentage of time hares spent active and inactive during different times of the
585 day. Error bars are standard deviation.



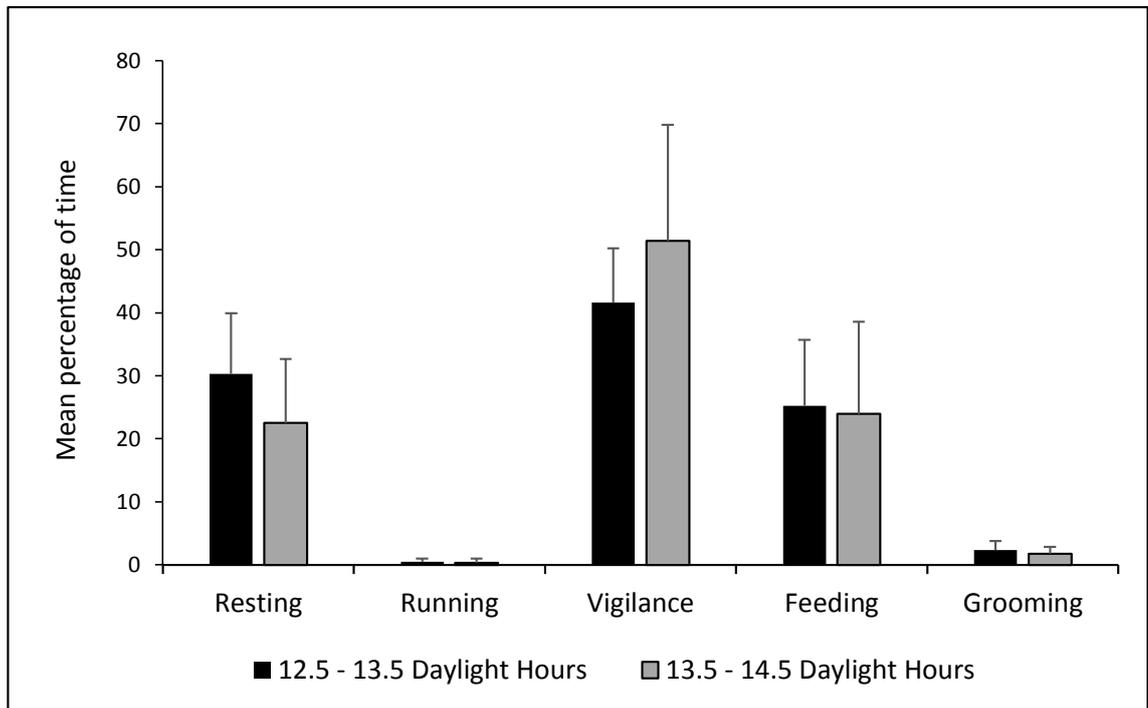
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588 **Figure 5: Hare behaviour when daylight length increases.**

589 Mean percentage of time hares spent doing behaviours between different number of

590 daylight hours. Error bars are standard deviation.

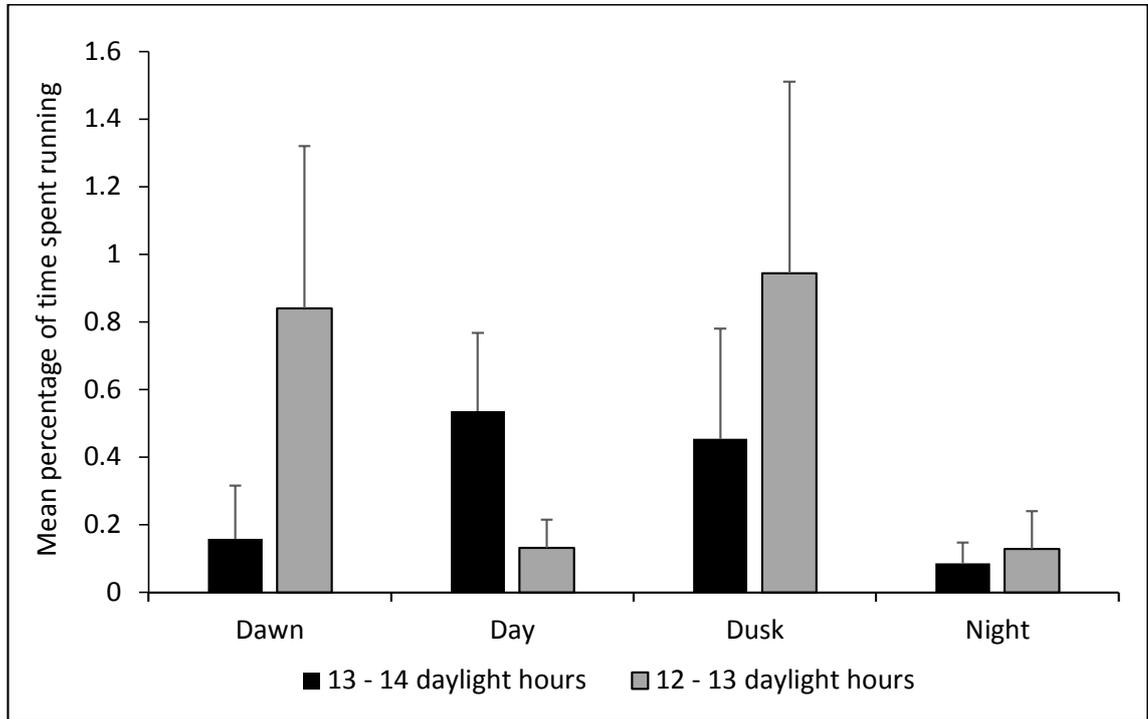


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593 **Figure 6: Hare running behaviour at different times of day and day length**

594 Mean percentage of time hares spent running at different times of the day and between
595 different amounts of daylight hours. Error bars are standard deviation.



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