

1

2 **University of Exeter's Institutional Repository, ORE**

3 <https://ore.exeter.ac.uk/repository/>

4

5 **Article version:** POST-PRINT

6 **Author(s):** Jorge A. Vázquez Diosdado^{1,#a,¶}, Zoe E. Barker², Holly R. Hodges², Jonathan R.
7 Amory², Darren P. Croft³, Nick J. Bell^{4,#b}, Edward A. Codling^{1,*},¶

8 **Article title:** Space-use patterns highlight behavioural differences linked to lameness, parity, and days
9 in milk in barn-housed dairy cows

10 **Originally published in:** PLOS ONE

11 **Link to published article (if available):**

12 **Publisher statement:** This is an Author's Original Manuscript of an article submitted for consideration
13 in PLOS ONE

14

15

16

17

18

19

20

21

22 **Usage guidelines**

23 Before reusing this item please check the rights under which it has been made available. Some
24 items are restricted to non-commercial use. **Please cite the published version where applicable.**

Further information about usage policies can be found at:

<http://as.exeter.ac.uk/library/resources/openaccess/ore/orepolicies/>

25 **Space-use patterns highlight behavioural differences**
26 **linked to lameness, parity, and days in milk in barn-**
27 **housed dairy cows**

28
29 Jorge A. Vázquez Diosdado^{1,#a,¶}, Zoe E. Barker², Holly R. Hodges², Jonathan R. Amory²,
30 Darren P. Croft³, Nick J. Bell^{4,#b}, Edward A. Codling^{1,*},¶

31
32 ¹ Department of Mathematical Sciences, University of Essex, Colchester, Essex, UK.

33 ² Writtle University College, Chelmsford, Essex, UK.

34 ³ Centre for Research in Animal Behaviour, College of Life and Environmental Sciences,
35 University of Exeter, Exeter, Devon, UK.

36 ⁴ Royal Veterinary College, Hatfield, Hertfordshire, UK.

37 ^{#a} Current Address: School of Veterinary Medicine and Science, University of Nottingham,
38 Sutton Bonington Campus, Leicestershire, UK.

39 ^{#b} Current Address: Bos International Ltd, Wimborne, Dorset, UK.

40
41 *Corresponding author: ecodling@essex.ac.uk

42 ¶These authors contributed equally to this work.

43
44 **Abstract**

45 Lameness is a key health and welfare issue affecting commercial herds of dairy cattle, with
46 potentially significant economic impacts due to the expense of treatment and lost milk
47 production. Existing lameness detection methods can be time-intensive, and under-detection

48 remains a significant problem leading to delayed or missed treatment. Hence, there is a need
49 for automated monitoring systems that can quickly and accurately detect lameness in individual
50 cows within commercial dairy herds. Recent advances in sensor tracking technology have made
51 it possible to observe the movement, behaviour and space-use of a range of animal species over
52 extended time-scales. However, little is known about how observed movement behaviour and
53 space-use patterns in individual dairy cattle relate to lameness, or to other possible confounding
54 factors such as parity or number of days in milk. In this cross-sectional study, ten lame and ten
55 non-lame barn-housed dairy cows were classified through mobility scoring and subsequently
56 tracked using a wireless local positioning system. Nearly 900,000 spatial locations were
57 recorded in total, allowing a range of movement and space-use measures to be determined for
58 each individual cow. Using linear models, we highlight where lameness, parity, and the number
59 of days in milk have a significant effect on the observed space-use patterns. Non-lame cows
60 spent more time, and had higher site fidelity (on a day-to-day basis they were more likely to
61 revisit areas they had visited previously), in the feeding area. Non-lame cows also had a larger
62 full range size within the barn. In contrast, lame cows spent more time, and had a higher site-
63 fidelity, in the cubicle (resting) areas of the barn than non-lame cows. Higher parity cows were
64 found to spend more time in the right-hand-side area of the barn, closer to the passageway to
65 the milking parlour. The number of days in milk was found to positively affect the core range
66 size, but with a negative interaction effect with lameness. Using a simple predictive model, we
67 demonstrate how it is possible to accurately determine the lameness status of all individual
68 cows within the study using only two observed space-use measures, the proportion of time
69 spent in the feeding area and the full range size. Our findings suggest that differences in
70 individual movement and space-use behaviour could be used as indicators of health status for
71 automated monitoring within a Precision Livestock Farming approach, potentially leading to

72 faster diagnosis and treatment, and improved animal welfare for dairy cattle and other managed
73 animal species.

74

75 **Introduction**

76 Globally, lameness is one of the key health and welfare issues that affects intensive
77 dairy farms, particularly for herds that are housed indoors permanently or semi-permanently
78 [1–3]. In the UK alone, the estimated cost to the dairy industry of treatment, lost milk yield,
79 and lost fertility is over £128 million per annum [4]. Prompt treatment of lameness can reduce
80 severity and the number of required treatments [5], hence reducing financial costs and the
81 duration and impact of pain for the individual animal. However, early detection of lameness
82 remains a problem as many farmers may underestimate the prevalence of lameness within their
83 herd [2], identify and treat cows later than might be optimal [5], or time constraints may mean
84 they are unable to undertake time- and labour-intensive mobility monitoring [6]. Increasing
85 intensification of farming practices means that these detection issues are likely to become even
86 more problematic in larger dairy herds. Hence, there is a need for systems which can
87 automatically detect lameness at an early stage without the need for time-consuming mobility
88 observations of individual animals. Recent attempts to use automated systems to detect
89 lameness have relied upon the identification of abnormal gait using load cells, pressure
90 sensitive mats, computer vision or accelerometers [7,8], but the uptake of such technology on
91 farms has been limited due to both costs and practical effectiveness in the working farm
92 environment. More generally, within Precision Livestock Farming approaches [9], a range of
93 behavioural measures have been suggested as potential indicators of health status and disease
94 for monitoring managed animal species. Lameness is known to cause pain and walking
95 difficulty in affected cows [10,11], and this may influence how they move and use the available
96 space within the barn. However, existing studies that have linked the lameness status of

97 individual dairy cows to their space-use behaviour have been restricted to small spatial scales
98 (i.e. at the level of individual stalls) [12].

99 In the wider movement ecology context, animal movement and space-use behaviour is
100 known to be influenced by landscape characteristics such as the location of water or food
101 resources, habitat type and vegetation cover [13], as well as local topographic features such as
102 the gradient of a hillside [14]. For example, grazing animals are known to move to locations
103 with higher quantities of grass resources or where there is better quality of nutrients [15]. By
104 adapting to their environment, animals can hence visit favourable areas more than others
105 [16,17]. In a limited home range, an animal may repeatedly visit certain locations [18] or
106 actively spend more time in specific areas leading to different levels of space-use intensity. For
107 an individual animal, the level of similarity in its space use at different time points can be
108 calculated and the level of site fidelity quantified [19–22]. In the specific context of pasture-
109 based cattle, [23] showed how spatial overlap between domesticated cattle and wild buffalo
110 was linked to the gradient of available resources, [24] demonstrated how concentrate
111 supplement can modify the feeding behaviour of grazing cows in high mountain pastures, while
112 [25] considered how spatial interactions between cattle and wild boar could potentially
113 facilitate cross-species disease transmission.

114 Understanding how illness or welfare status may affect animal movement behaviour,
115 space-use, and interactions with the local landscape could potentially provide extremely useful
116 insights and indicators for monitoring and managing a range of animal species [9]. Lameness,
117 mastitis and ketosis (metabolic disorder) are all important diseases of dairy cattle that have
118 been shown to affect feeding and lying behaviour [26–32], and in this context, the use of cow-
119 mounted accelerometers to measure cow behaviour is well established [8,33–35]. However,
120 despite these extensive studies highlighting the links between disease and dairy cow behaviour,
121 an automated method for disease detection based on behavioural observations is still lacking.

122 A major issue with any automated approach is the complex interplay between health status and
123 other potential confounding factors such as age, parity, or stage of lactation [36,37], that lead
124 to individual behavioural differences. A recent study investigated a range of possible
125 behavioural indicators of health status in dairy cattle including lying, locomotion, feeding and
126 rumination activities, in addition to brush and concentrate feeder visits and milking order [29].
127 Although there were differences between lame and non-lame cows, [29] also reported a high
128 variability across individual animals and predictor variables overlapped between these groups.

129 The use of spatial tracking systems for monitoring dairy cattle is less well developed
130 than accelerometer-based systems, but they have the potential to provide additional important
131 behavioural information about movement and space-use in individual animals. With pasture-
132 based animals, tracking is possible with standard Global Positioning Systems (GPS) [38,39],
133 but for indoor barn-housed dairy cows alternative systems are needed. Real-Time Location
134 Systems (RTLS) are a recent new development in the application of radio frequency technology
135 with great potential for use in livestock agriculture. They have been tested and validated for
136 indoor spatial tracking of dairy cows [28,40–42], and have subsequently been used to predict
137 time budgets of behavioural activities [43], to determine the probability of cattle undertaking
138 feeding or drinking [44], or to detect behavioural changes related to oestrus [45]. However, to
139 date there have been no studies that have reported how differences in space-use behaviour
140 within a commercial barn may be directly linked to the lameness status of individual dairy
141 cows.

142 In this paper we present results from of an analysis of a tracking data set containing
143 nearly 900,000 recorded spatial locations obtained over five days from a cross-sectional study
144 group of ten lame and ten non-lame barn-housed dairy cows using a wireless positioning
145 system. We determine measures of space-use behaviour within the barn for each cow, and using
146 linear models we demonstrate where lameness status, parity and days in milk have a significant

147 effect on the observed space-use measures. We demonstrate how observable differences in
148 space-use patterns can be used directly within a simple predictive model to accurately
149 determine the lameness status of individual cows. The methodology and approach described
150 within the study could be adapted to study space-use behaviour in other commercially managed
151 or wild animal species.

152

153 **Materials and methods**

154 The study was carried out in strict accordance with the UK Animal Welfare Act (2006). The
155 study was reviewed and approved by the Royal Veterinary College Ethics and Welfare
156 Committee under the unique reference number 2012 1223. The study was non-invasive and the
157 collars used were similar to those in standard industry use. Lame cows were managed according
158 to the farm's animal health plan and all animals were monitored daily whilst in the study in
159 order to identify any potential welfare issues which needed addressing.

160

161 **Data collection**

162 The study was undertaken over 5 successive days in January 2014 on a commercial
163 dairy farm in Essex, UK. A total of 210 Holstein pedigree cows were housed in a rectangular
164 free-stall barn measuring 30m by 60m. The cows were split into high yield (120 cows) and low
165 yield (90 cows) groups, separated by a central feed alley (Fig 1a). The high yield group were
166 housed in the upper part of the barn and had access to 120 free-stalls, and linear feed space of
167 0.43m per cow. The milking parlour and collecting yard were situated in the lower part of the
168 barn, with a connecting return passage positioned on the right-hand side of the barn (Fig 1a).
169 All cows were fed a commercial total mixed ration (TMR) and milking took place three times
170 a day (05:00hrs, 13:00hrs, 21:00hrs).

171 To explore the effect of lameness, and possible confounding factors such as parity and
172 days in milk, on cow space-use and behaviour, a cross-sectional study design was used. Prior
173 to the study, all cows in the high yield group were locomotion scored at the exit to the milking
174 parlour using the 4-point AHDB Dairy Mobility Score [46] by ZB (where 0 = sound and 3 =
175 severely lame), and re-scored in the main barn by HH the following day. Cows which were
176 known to have had a health incident in the previous three months, including foot lesions and
177 mastitis treatments, were excluded. Two study groups (10 lame cows and 10 non-lame cows)
178 were selected based on their mobility scores, and to match yield and parity where possible (S1
179 Table). It should be noted that only cows with a mobility score of 2 ('lame') were included in
180 the lame group; score 3 cows ('severely lame') were not included due to a low number of cows
181 with this score within the herd, and for ethical reasons (the selected cows would not be treated
182 until the end of the study). Selection of the cows was made without any prior knowledge of
183 their space-use behaviour. Individual parity ranged from 1 to 6 years (mean = 3.25, s.d = 1.44),
184 and for the current parturition period, days in milk (DIM) ranged from 44 to 220 (mean = 125,
185 s.d. = 51.3, and mean daily milk yield (in litres) ranged from 28.7 to 58.4 (mean = 42.5, s.d. =
186 6.88), see S1 Table. At the end of the study period all cows were clinically inspected for
187 lameness and foot trimming was carried out where appropriate.

188 The selected cows were fitted with wireless sensors (Ominsense Series 500 Cluster
189 Geolocation System [28,35,47,48]; www.omnisense.co.uk/), to track spatial location in the
190 upper area of the barn. The Series 500 sensors form a RTLS wireless network able to compute
191 relative spatial locations in (x, y, z) coordinates of each individual sensor within the system
192 using the arrival time of periodic messages sent from each node to its neighbours to triangulate
193 distances (note that in this study, cows were restricted to a single elevation, so only the (x, y)
194 coordinates were used). Thirteen sensors were attached to known fixed positions around the
195 barn and a further eight were positioned within the adjacent collecting yard and milking parlour

196 to improve network coverage and triangulation measurements (Fig 1a). Validation of sensor
197 precision and accuracy within this specific barn environment has been reported previously in
198 [28]. The sensors were found to perform well for spatial tracking of individual cows, although
199 performance was slightly worse than the commercially advertised specification (95% of
200 measurements within 2 m of ground truth; Omnisense Ltd.), which is likely due to metal
201 features within the barn environment disrupting the sensor signals [28]. The sensors were
202 mounted on cows using a neck collar that incorporates a counterweight to keep the sensor in a
203 stable position at the top of the neck [28,35].

204 Location data were collected continuously for 24 hours per day over the 5 days of the
205 study using a 0.125Hz sample rate, leading to a theoretical maximum of 54,000 location data
206 points being collected per cow over the duration of the study. However, location data during
207 the three daily milking events, each lasting approximately 90 minutes when the cows left the
208 upper barn area, were excluded as cow movement and space-use behaviour was constrained by
209 human interventions at these times. In addition, some further minor data loss occurred when
210 sensors occasionally suffered battery failure before being replaced, or when sensor error
211 seemingly placed a cow outside the barn (any such coordinates were removed from the
212 analysis). In total, 876,621 location data points (81% of the theoretical maximum) were
213 collected in the upper barn area and used in the following data analysis. The mean number of
214 location data points collected per day across all cows was 8767 (median = 8930), and the
215 minimum average number of data points collected for a single cow over the 5 days of the study
216 was 8175 data points per day.

217 The sensor recorded raw location data were smoothed to remove outliers using a simple
218 moving average (SMA) over a two-minute moving window (i.e. 15 data points at the 0.125Hz
219 sampling rate; Fig 1b). Basic movement and space-use measures calculated directly from the

220 smoothed sensor location data include the total distance moved per hour, and the mean x and
221 mean y locations.

222 A basic analysis of this data set was described in [28], where spatial location data were
223 used alongside accelerometer data in a decision tree algorithm to classify cow behaviour as
224 either ‘feeding’, ‘non-feeding’, or ‘out of the pen for milking’. Differences in the daily activity
225 budgets between lame and non-lame cows were highlighted, with lame cows spending
226 significantly less time feeding. However, [28] only considered daily behavioural time budgets
227 and did not directly consider differences in space-use measures or site fidelity between the lame
228 and non-lame groups as we do in more detail here.

229

230 **Figure 1. Schematic map of barn and examples of cow movement trajectory and space-**
231 **use intensity.** (a) Schematic map of barn indicating features and areas of interest. Fixed sensors
232 were positioned on the barn walls to aid tracking of mobile cow-mounted sensors. Areas C_1 ,
233 C_2 and C_3 are zones defined to correspond to the three main cubicle blocks in the upper barn
234 area (C_T is the total cubicle area corresponding to the union of C_1 , C_2 and C_3); area F
235 corresponds to the feeding zone and includes space either side of the feed barrier; area P is a
236 passageway allowing access from the upper barn area to the collecting yard and milking
237 parlour. (b) Example of a cow trajectory (cow 1078, day 5) produced by smoothing the raw
238 sensor-collected data using a simple moving average over a 15 time-step (2 minute) moving
239 window. (c) Example space-use intensity plot (cow 1078, day 5) produced by overlaying a
240 1.5m^2 square grid onto the map of the barn and counting the cells in which trajectory points are
241 found. Darker colours correspond to higher space-use intensity. The 95% and 50% isopleths
242 are respectively indicated by the dashed and solid contour lines. Note that the plot shows space-
243 use data from the full barn for illustrative purposes; results in the main paper are for location
244 data from the upper barn only, see Fig 2.

245

246 **Space-use intensity and the utility distribution**

247 Animal space use intensity can be quantified from location data using a utility
248 distribution (UD) for each individual animal [49–51]. In many movement data sets, spatial
249 locations are only recorded at low temporal sampling resolutions or there may be missing data,
250 and a range of methods have been developed to estimate the UD in such cases [52]. These
251 include kernel density estimation [50,53], the Brownian bridge movement model (BBMM)
252 [15,54,55], step-selection analysis [56], and state space models [57]. However, since our location
253 data are collected at high temporal sampling resolution (0.125Hz) with very few missing data
254 points, and we calculate the UD on a daily basis over a confined spatial area, a simple cell-
255 counting method is much more computationally efficient and will give similar results [52,58].

256 To determine the daily UD for each individual cow in our data set we overlay a virtual
257 40 x 13 square grid of 1.5m x 1.5m (= 2.25m²) cells onto the upper barn area ($0 \leq x \leq 60$, and
258 $10 \leq y \leq 30$ in Fig 1a). The cell size is chosen to be slightly larger than the known sensor
259 precision and to roughly correspond to the area that can be occupied by a single cow. For each
260 cow, each of the smoothed (x, y) coordinate locations in the upper barn area are assigned to the
261 relevant grid cell and the count for that cell is increased by one. Any coordinate locations lying
262 outside the upper barn area are removed (corresponding to milking periods or when sensor
263 error resulted in a location outside the barn). The final daily UD is then rescaled to form a
264 discrete probability distribution that sums to 1, by dividing all individual cell counts by the
265 total cell count across all cells (Fig 1c).

266 To explore relative space use intensity we use the UD to determine the mean daily
267 proportion of time spent in the upper barn area in specific biologically relevant areas of interest
268 (see Fig 1a): feeding area (F: $0 \leq x \leq 53$, $10 \leq y \leq 20$); full cubicle area (C_T: $0 \leq x \leq 60$, $20 \leq y$
269 ≤ 30); right-hand cubicle area (C₁: $40 \leq x \leq 60$, $20 \leq y \leq 30$); central cubicle area (C₂: $20 \leq x \leq$

270 40, $20 \leq y \leq 30$); and left-hand cubicle area (C_3 : $0 \leq x \leq 20$, $20 \leq y \leq 30$). The feeding area, F,
271 is defined on either side of the physical feed barrier marked in Fig 1a, and does not span the
272 entire width of the barn. A small area on the right-hand side of the barn, marked as P on Fig 1a
273 (P: $53 \leq x \leq 60$, $10 \leq y \leq 20$), serves as a passage and return to the milking parlour. The cubicle
274 areas include fixed cubicle blocks, where cows are able to lie down in individual cubicles
275 (stalls), as well as interconnecting passageways (Fig 1a).

276 In animal home range analysis, the 50% isopleth (the contour line which can be drawn
277 on the UD corresponding to the highest density cells that cumulatively account for 50% of the
278 total observed density) is often considered as the ‘core’ home range of the animal as it contains
279 those cells where the animal spends the most amount of time [59–63]. Similarly, the 95%
280 isopleth is considered to be the ‘full’ or largest extent of the home range; cells lying outside
281 the 95% isopleth are usually assumed to correspond to noise in the data or to areas only very
282 infrequently visited [59–63]. For our location data, we truncate and rescale the UD at both the
283 95% isopleth (full range) and 50% isopleth (core range) levels (Fig 1c; Fig 2). We determine
284 the mean daily size of the full and core ranges for each cow, measured in terms of the number
285 of virtual cells lying inside the relevant isopleth level.

286

287 **Site fidelity**

288 By comparing the level of overlap or similarity of UDs at different time-points it is
289 possible to determine how the level of consistency of space-use, or site fidelity, of an animal
290 may change over time [19–21]. Assuming two different discrete UDs that have both been
291 rescaled as probability distributions, the Bhattacharyya coefficient (or Bhattacharyya's affinity)
292 is a simple way to compare the level of similarity or overlap of the UDs [59,64,65]:

$$293 \quad O_{t_1 t_2} = \sum_{q \in Q} \sqrt{U_{t_1}(q) \cdot U_{t_2}(q)}, \quad (1)$$

294 where q represents each discrete cell in the spatial grid and $U_{t_i}(q)$ is the probability mass for
295 that cell at time t_i . The Bhattacharyya coefficient ranges from 0 (no overlap) to 1 (full overlap).
296 We calculate the Bhattacharyya coefficient for each cow using the UD across the full upper
297 barn areas compared across successive days within the study. The space-use similarity score of
298 smaller UDs corresponding to site fidelity in the feeding area (F) only, and the cubicle area
299 (C_T) only, are also calculated.

300 We determine an overall measure of the similarity score of corresponding UDs over the
301 5 days of the study (i.e. an overall measure of site fidelity) for each cow by determining the
302 average Bhattacharyya coefficient calculated from each pair of consecutive days:

$$303 \quad \bar{O} = \frac{1}{4} \sum_{i=1}^4 O_{t_i t_{i+1}} \quad (2)$$

304 To check the robustness of results to the averaging procedure used, we also considered two
305 further approaches: averaging the Bhattacharyya coefficient over all possible combinations of
306 pairs of days within the study (10 possible unique pairs in total), and a similar approach but
307 where each pair of days is weighted according to the metric distance between the days before
308 taking the average. However, site-fidelity results were very similar using all three approaches
309 and hence we only report results from the simplest method here.

310

311 **Statistical analysis of space-use**

312 Although our main interest in this study is to explore behavioural differences between
313 lame and non-lame cows, it is important to also consider potential confounding factors. Hence
314 in the statistical analysis we consider three predictor variables: ‘lameness’ (L , assigned to a
315 binary variable with 1 as lame and 0 as non-lame), ‘parity’ (P), and ‘days in milk’ (D , calculated
316 over the current parturition only), see S1 Table. We also considered mean daily yield as a
317 predictor variable but preliminary investigations showed that this had no effect and hence was
318 not included in the subsequent analysis. As data were collected continuously over the 5 days

319 of the study for all cows, with no specific management interventions on any days, we do not
320 include ‘day’ as a predictor variable in our analysis (S2 File highlights no clear trends or
321 differences by day between the lame and non-lame groups for any of the basic space-use
322 measures considered). Similarly, as the study only lasts for 5 days, we do not have a long
323 enough time period of data to consider changes in lameness status (or parity or DIM) during
324 the study (although this may be possible in much longer studies).

325 In total, sixteen different space-use and site-fidelity dependent variables, S_1 to S_{16} , were
326 considered: S_1 : mean distance moved per hour; S_2 : mean x coordinate; S_3 : mean y coordinate;
327 S_4 : proportion of time spent in the feeding area (F); S_5 : proportion of time spent in the full
328 cubicle area (C_T); $S_6 - S_8$: proportion of time spent in each of the specific cubicle areas (C_1 , C_2 ,
329 C_3 considered separately); S_9 : mean size (in virtual cells) of the daily ‘full’ range
330 (corresponding to the 95% isopleth of the UD); S_{10} : mean size (in virtual cells) of the daily
331 ‘core’ range (corresponding to the 50% isopleth of the UD); $S_{11} - S_{16}$: site fidelity determined
332 for each of three areas (full upper barn area, feeding area (F) only, and cubicle area (C_T) only)
333 for two different isopleth levels (full range = 95%; core range = 50%).

334 Statistical analysis was undertaken using model selection based on a multivariate linear
335 (regression) model with the three predictor variables (lameness, L ; parity, P ; days in milk, D).
336 Linear models corresponding to all possible combinations of the predictor variables and their
337 interaction terms were fitted to each of the individual space-use measures, S_1 to S_{16} in turn:

$$338 \quad S_i = \alpha_0 + \alpha_1 L + \alpha_2 P + \alpha_3 D + \text{interaction effects}, \quad (3)$$

339 where α_n are regression coefficients to be determined (α_0 is the intercept). For each linear
340 model, the Akaike Information Criterion (AICc; corrected for small sample sizes) was used to
341 select the best relative fitting model for that space-use measure [66] (the lowest AICc score
342 corresponds to the best fitting model). For the best fitting linear model, the F -statistic and
343 associated p -value are then used to determine whether the model is a significantly better fit (at

344 the 5% level) to the data than an intercept-only model (which does not include any of the
345 predictor variables). Subsequently, the individual p -values corresponding to each regression
346 coefficient, α_j , are used to determine the significance (at the 5% level) of each predictor
347 variable (and any interaction effects) within the linear model.

348 For the multivariate linear regression model to be valid the following assumptions must
349 hold [67]. Firstly, there must be a linear relationship between the predictor variables and the
350 dependent variables (we assume this implicitly during the analysis, and also check by
351 examining the data visually in the output plots). Secondly, there must be no multicollinearity
352 between the predictor variables. To test this, Variance Inflation Factor (VIF) scores were
353 calculated for each predictor variable ($L_{VIF} = 1.465776$, $D_{VIF} = 1.0714$, $P_{VIF} = 1.3877$), and
354 since no scores were higher than the threshold score of $VIF > 10$, we conclude that there is not
355 a high level of multicollinearity between our predictor variables [68]. Thirdly, the model
356 residuals must be normally distributed; and finally, there must be no heteroscedasticity within
357 the data [67]. For each fitted linear model, we test the residuals for normality using the Shapiro-
358 Wilks test (S-W; 5% significance level) and for heteroscedasticity using the non-constant
359 variance test (NCV; 5% significance level). Regression and model fitting were undertaken
360 using the ‘glm’ and ‘AICc’ functions in R [69].

361

362 **Predictive model for lameness**

363 To explore the potential predictive capability of the observed dependent variables to
364 correctly classify lameness in individual cows we also consider a generalised linear regression
365 model with logit link function of the form:

$$366 \quad \log\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 S_1 + \dots + \beta_n S_n \quad (4),$$

367 where β_n are regression coefficients to be determined (β_0 is the intercept), S_i are the
368 corresponding values of the observed dependent variables in the previous analysis, and p
369 represents the estimated probability from the model that a cow is classified as lame. To avoid
370 over-fitting the predictive model, we restrict the model selection choice to those dependent
371 variables, S_i , where one or more of the predictor variables were found to be significant in the
372 previous analysis. As above, we determine the best relative fitting model using model selection
373 via the Akaike Information Criterion score, AICc (corrected for small sample sizes) [66].
374 Regression and model fitting were undertaken using the ‘glm’ and ‘AICc’ functions in R [69].

375

376 **Results**

377 **Space-use intensity and other basic space-use measures**

378 Fig 2 shows illustrative daily space-use intensity UD_s in the upper barn area for a single
379 lame cow (cow 1078; Fig 2a-e) and a single non-lame cow (cow 2179; Fig 2f-j) over the 5 days
380 of the study (individual plots for all cows and all days of the study are shown in S1 File). Fig
381 2k illustrates the aggregated space-use intensity UD for all 20 cows over all 5 days of the study
382 and highlights areas of higher space-use intensity (i.e. inside the 50% isopleth) corresponding
383 to the cubicle and feeding areas, with lower space-use intensity in the corridors and
384 passageways.

385

386 **Figure 2. Space use intensity plots illustrating typical utility distributions over the five**
387 **days of the trial.** Plots are shown for (a-e) a single lame cow (cow 1078), and (f-j) a single
388 non-lame cow (cow 2179), for each of the five days of the study. The space-use intensity UD
389 is calculated by overlaying a 1.5m x 1.5m square grid (40 x 13 cells) onto the upper barn area
390 only and counting the cells in which the smoothed trajectory points for each cow occur for each

391 day of the trial. Darker colours correspond to higher space-use intensity. The 95% and 50%
392 isopleths (corresponding to the full and core ranges for movement within the upper barn area
393 only) are respectively indicated by the dashed and solid contour lines. (k) Space use intensity
394 plot calculated in the same manner as above but using the aggregated data from all 20 cows
395 over all 5 days of the study.

396

397 Full results for each basic space-use measure (S_1 to S_{10}) at the level of each individual
398 cow are given in S2 Table and are shown as individual data points in Fig 3. Model selection
399 and subsequent analysis revealed that the predictor variables (lameness, parity, and days in
400 milk) had statistically significant effects on a number of the space-use measures (Table 1).
401 Lameness was found to have a significant negative effect on the proportion of time spent in the
402 feeding area (S_4 , $p = 0.004$; Fig 3d), and conversely, had a significant positive effect on the
403 proportion of time spent in the full cubicles area (S_5 , $p = 0.011$; Fig 3e). It should be noted
404 however, that heteroscedasticity was found to be present in the residuals for this latter result
405 (non-lame cows had significantly higher variance) and hence the result should be treated with
406 caution. A weak positive effect of lameness on the mean y coordinate (S_3 , $p = 0.08$, Fig 3c) is
407 consistent with these results given the relative location of the cubicle and feeding areas (Fig 1).
408 Lameness was also found to have a significant negative effect on the full range size (95%
409 isopleth), with non-lame cows having a larger number of cells in their full range (S_9 , $p = 0.029$;
410 Fig 3i).

411 Parity was found to have a significant positive effect on the proportion of time spent in
412 the right-hand cubicles, C_1 (S_6 , $p < 0.001$; Fig 3f), and a significant negative effect on the
413 proportion of time spent in the left-hand cubicles, C_3 (S_8 , $p = 0.006$; Fig 3h). Given the relative
414 locations of these cubicle zones (Fig 1), these results are entirely consistent with the fact that

415 parity also had a significant positive effect on mean x location (S_2 , $p < 0.001$; Fig 3b); higher
416 parity cows consistently spent more time in the area to the right-hand side of the upper barn.

417 Days in milk was found to have a significant negative effect on the proportion of time
418 spent in the right-hand cubicles, C_1 (S_6 , $p = 0.038$), although this effect was not as strong as the
419 (positive) effect of parity within the same linear model (Fig 3f). Days in milk was also found
420 to have a significant positive effect on the core (50% isopleth) range size, (S_6 , $p = 0.002$),
421 although there was also a significant negative interaction effect with lameness ($p = 0.008$), see
422 Fig 3j. This latter result can be interpreted as days in milk having a (strong) positive effect on
423 core range size for non-lame cows and a (weaker) negative effect on core range size for lame
424 cows (see respectively the green and red dashed lines in Fig 3j). However, this somewhat
425 contradicts the finding that lameness (considered on its own within the same linear model) has
426 a weak positive effect on core range size ($p = 0.063$). A complicated model interaction effect
427 such as this should be interpreted with caution given the small sample size within our study.

428 None of the predictor variables were found to have any significant effects on the mean
429 hourly walking distance (S_7 , Fig 3a), or the proportion of time spent in the central cubicle area,
430 C_2 (S_7 , Fig 3g).

431

432 **Figure 3. Plots showing relationship between significant predictor variables (lameness;**
433 **parity; days in milk, DIM) and basic space-use measures.** Data for each basic space-use
434 measure, S_1 to S_{10} , are shown in plots (a) to (j) respectively, and are plotted against the most
435 significant predictor variable determined from the model selection procedure (Table 1). Where
436 none of the predictor variables are significant (at the 5% level) for a given model, the data is
437 plotted for the lame and non-lame groups (a, c, g). Where appropriate, boxplots (with median
438 line) are used to show the spread of the data for each level of the predictor variable (a – i).
439 Individual data points are calculated as a mean average across all five days of the trial for each

440 cow (S2 Table). Lameness cows are plotted as filled triangles and non-lameness cows as filled circles;
441 the colours used to indicate each data point are fixed for each cow and are consistent across all
442 plots (see legend). Where the best fitting linear model includes only a single predictor variable,
443 the fitted regression line is shown as a dashed black line (b, d, e, h, i). In (f) the best fitting
444 linear model includes both parity and DIM terms (Table 1); a regression line fitted only to the
445 parity variable (the most significant predictor) is shown as a blue dashed line for illustrative
446 purposes only. In (j), the best fitting linear model includes lameness, DIM, and an interaction
447 term; regression lines fitted only to the DIM variable are shown for the lameness group (red dashed
448 line) and non-lameness group (green dashed line) to illustrate the negative interaction of lameness
449 with DIM.

450

451 **Table 1. Results of model selection for multivariate linear regression models using the predictor variables (lameness, parity and days in**
 452 **milk) for each of the space-use measures considered within the study.**

Space-use measure	Best fitting linear model	AICc score	<i>F</i> -statistic (<i>p</i> -value)	Regression coefficient values (<i>p</i> -values)	Summary & notes
S_1 : mean distance moved per hour	$S_1 = \alpha_0$ (Intercept only)	154.66	n/a	$\alpha_0 = 114.49$	No significance.
S_2 : mean <i>x</i> coordinate	$S_2 = \alpha_0 + \alpha_2 P$	120.42	$F = 20.36$ ($p < 0.001$)	$\alpha_0 = 18.91$ $\alpha_2 = 2.997$ ($p < 0.001$)	<i>P</i> has a significant positive effect on S_2 .
S_3 : mean <i>y</i> coordinate	$S_3 = \alpha_0 + \alpha_1 L$	60.45	$F = 3.44$ ($p = 0.08$)	$\alpha_0 = 22.90$ $\alpha_1 = 0.795$ ($p = 0.08$)	(<i>L</i> has a weak positive effect on S_3).
S_4 : proportion of time spent in the feeding area (F)	$S_4 = \alpha_0 + \alpha_1 L$	-64.59	$F = 10.85$ ($p = 0.004$)	$\alpha_0 = 0.324$ $\alpha_1 = -0.062$ ($p = 0.004$)	<i>L</i> has a significant negative effect on S_4 .
S_5 : proportion of time spent in the full cubicle area (C_T)	$S_5 = \alpha_0 + \alpha_1 L$	-62.88	$F = 8.13$ ($p = 0.011$)	$\alpha_0 = 0.666$ $\alpha_1 = 0.056$ ($p = 0.011$)	<i>L</i> has a significant positive effect on S_5 . Heteroscedasticity present (NCV: $p = 0.024$; non-lame cows have higher variance, see Fig 3e).
S_6 : proportion of time spent in right cubicles (zone C_1)	$S_6 = \alpha_0 + \alpha_2 P + \alpha_3 D$	-21.32	$F = 10.82$ ($p < 0.001$)	$\alpha_0 = 0.189$ $\alpha_2 = 0.073$ ($p < 0.001$) $\alpha_3 = -0.001$ ($p = 0.038$)	<i>P</i> has a significant positive effect on S_6 . <i>D</i> has a significant negative effect on S_6 .

S_7 : proportion of time spent in central cubicles (zone C ₂)	$S_7 = \alpha_0$ (Intercept only)	-11.43	n/a	$\alpha_0 = 0.400$	No significance.
S_8 : proportion of time spent in left cubicles (zone C ₃)	$S_8 = \alpha_0 + \alpha_2 P$	-16.30	$F = 9.65$ ($p = 0.006$)	$\alpha_0 = 0.537$ $\alpha_2 = -0.068$ ($p = 0.006$)	P has a significant negative effect on S_8 .
S_9 : full range size (95% UD isopleth)	$S_9 = \alpha_0 + \alpha_1 L$	170.28	$F = 5.66$ ($p = 0.029$)	$\alpha_0 = 150.84$ $\alpha_1 = -15.88$ ($p = 0.029$)	L has a significant negative effect on S_9 .
S_{10} : core range size (50% UD isopleth)	$S_{10} = \alpha_0 + \alpha_1 L + \alpha_3 D$ $+ \alpha_4 L:D$	106.12	$F = 7.24$ ($p = 0.003$)	$\alpha_0 = 11.531$ $\alpha_1 = 6.855$ ($p = 0.063$) $\alpha_3 = 0.02$ ($p = 0.002$) $\alpha_4 = -0.076$ ($p = 0.008$)	(L has a weak positive effect on S_{10}). D has a significant positive effect on S_{10} . Significant negative interaction effect between L and D .
S_{11} : site fidelity (full upper barn & full range)	$S_{11} = \alpha_0$ (Intercept only)	-40.81	n/a	$\alpha_0 = 0.472$	No significance. Outlier cow (2596) removed to ensure normality of residuals ($n = 19$).
S_{12} : site fidelity (feeding area & full range).	$S_{12} = \alpha_0 + \alpha_1 L + \alpha_3 D$	-42.69	$F = 3.995$ ($p = 0.039$)	$\alpha_0 = 0.688$ $\alpha_1 = -0.077$ ($p = 0.025$) $\alpha_3 = -0.0006$ ($p = 0.060$)	L has a significant negative effect on S_{12} . (D has a weak negative effect on S_{12}). Outlier cow (2596) removed to ensure normality of residuals ($n = 19$).

S_{13} : site fidelity (cubicle area & full range)	$S_{13} = \alpha_0 + \alpha_1 L$	-28.26	$F = 4.99$ ($p = 0.039$)	$\alpha_0 = 0.355$ $\alpha_1 = 0.102$ ($p = 0.039$)	L has a significant positive effect on S_{13} . Outlier cow (2596) removed to ensure normality of residuals ($n = 19$).
S_{14} : site fidelity (full upper barn & core range)	$S_{14} = \alpha_0 + \alpha_1 L$	-25.32	$F = 4.64$ ($p = 0.046$)	$\alpha_0 = 0.181$ $\alpha_1 = 0.106$ ($p = 0.046$)	L has a significant positive effect on S_{14} . Outlier cow (2596) removed to ensure normality of residuals ($n = 19$). Heteroscedasticity present (NCV: $p = 0.017$; lame cows have higher variance, see Fig 4d).
S_{15} : site fidelity (feeding area & core range)	$S_{15} = \alpha_0 + \alpha_1 L$	-40.47	$F = 10.69$ ($p = 0.004$)	$\alpha_0 = 0.295$ $\alpha_1 = -0.112$ ($p = 0.004$)	L has a significant negative effect on S_{15} .
S_{16} : site fidelity (cubicle area & core range)	$S_{16} = \alpha_0 + \alpha_1 L$	-34.37	$F = 7.89$ ($p = 0.013$)	$\alpha_0 = 0.133$ $\alpha_1 = 0.106$ ($p = 0.013$)	L has a significant positive effect on S_{16} . Outlier cows (2010 & 2596) removed to ensure normality of residuals ($n = 18$).

453 Results highlighted in bold indicate significance ($p < 0.05$). For all linear models considered, the intercept was always found to be significant
454 and is always included. The Shapiro-Wilks test was used to test the normality of model residuals: for $S_{11} - S_{14}$, a single outlier non-lame cow
455 (2596) was removed to ensure normality; for S_{16} , two outlier cows (2010, lame; 2596, non-lame) were removed to ensure normality. The non-
456 constant variance (NCV) test was used to confirm the absence of heteroscedasticity in the model residuals (results non-significant, except for S_5
457 and S_{14}). AICc = Akaike Information Criterion score, corrected for small sample sizes. L = lameness (1 = lame, 0 = non-lame), P = parity, D =
458 days in milk

459

460 **Site fidelity**

461 In general, site fidelity was higher for the full range (95% isopleth; Figs 4a-c) than for
462 the core range (50% isopleth; Figs 4d-f); see S3 Table for site fidelity statistics for individual
463 cows. Analysis of some site fidelity measures (S_{11} to S_{14}) was strongly affected by a single
464 outlier non-lame cow (2596), which resulted in the fitted model residuals being rejected as
465 normal. Removal of this outlier cow (and also an additional lame outlier cow, 2010, for S_{16}),
466 led to the model residuals being accepted as normal, and results are presented on this basis.
467 Given the reduced sample size, results with outlier(s) removed should be treated with caution.
468 Only the fitted model for S_{15} resulted in normally distributed residuals without removal of
469 outliers.

470

471 **Figure 4. Plots showing relationship between significant predictor variables (lameness;**
472 **parity; days in milk, DIM) and site-fidelity similarity measures.** Data for each site-fidelity
473 similarity measure, S_{11} to S_{16} , are shown in plots (a) to (f) respectively, and are plotted against
474 lameness status (which is the most significant predictor variable determined from the model
475 selection procedure (Table 1), in all cases except (a), where no predictor variable is significant).
476 Boxplots are used to show the spread of the data for the non-lame and lame groups, and
477 individual data points are calculated as a mean average across all five days of the trial for each
478 cow (S3 Table). Lame cows are plotted as filled triangles and non-lame cows as filled circles;
479 the colours used to indicate each data point are fixed for each cow and are consistent across all
480 plots (see legend). In (c-f), where the best fitting linear model includes only a single predictor
481 variable, the fitted regression line is shown as a dashed black line. In (b) the best fitting linear
482 model includes both lameness and DIM terms (Table 1); a regression line fitted only to the
483 lameness variable (the most significant predictor) is shown as a blue dashed line for illustrative

484 purposes only. In (a-d) and (f) the outlier cows (2596 and 2010) are marked with a black ring.
485 Outlier cows were not included in the data for the purposes of model fitting (except for (e),
486 where no outlier cows were removed from the data).

487

488 Lameness was the only predictor variable to have a significant effect on site fidelity
489 (although days in milk had a weak negative effect on S_{12}). Lame cows had significantly higher
490 site fidelity than non-lame cows in the full cubicle area at both the full range (S_{13} , $p = 0.039$;
491 Fig 4c) and core range (S_{16} , $p = 0.013$; Fig 4f), and also for the full upper barn area at the core
492 range (S_{14} , $p = 0.046$; Fig 4d). However, heteroscedasticity was present in the residuals for this
493 latter result (lame cows had significantly higher variance in site fidelity). Non-lame cows had
494 significantly higher site fidelity than lame cows in the feeding area at both the full range (S_{12} ,
495 $p = 0.025$; Fig 4b) and core range (S_{15} , $p = 0.004$; Fig 4e). It should be noted that this latter
496 result is the only fitted model that satisfies the assumption of residual normality without
497 removing outliers from the data, and hence can be considered more robust.

498

499 **Predictive model for lameness**

500 Table 2 illustrates that the predictive model structure with the lowest AIC score, and
501 hence the best relative fitting model (accounting for model complexity), is of the form

$$502 \quad \log\left(\frac{p}{1-p}\right) = \beta_0 + \beta_4 S_4 + \beta_9 S_9 \quad (5),$$

503 where S_4 is the proportion of time spent in the feeding area, F, and S_9 is the number of cells in
504 the full range (95% isopleth). This model correctly predicts the lameness status of 18 out of the
505 20 cows within the study (S4 Table). Other model structures that include one or more of the
506 mean x coordinate (S_2), the proportion of time spent in the full cubicle area (S_5), or the site
507 fidelity in the feeding area (core range, S_{15}), are also able to correctly identify the lameness
508 status of at least 18 out of the 20 cows, although these models have a worse AICc score due to

509 having more complex structures with additional parameters. Across all the best-fitting models
 510 in Table 2, cow 2153 (non-lame) is always incorrectly classified as lame. However,
 511 investigation of the health records for this cow revealed that it may have been misclassified by
 512 the expert observers at the start of the study (see Discussion), and hence the models are all
 513 essentially correct in this case.

514

515 **Table 2. Best fitting model structures considered for logistic regression predictive model**
 516 **with associated Akaike Information Criterion (AICc) scores (corrected for small sample**
 517 **sizes).**

AICc score	Model structure & regression coefficients	Correct predictions	Incorrectly predicted cow IDS
20.21	$\beta_0 + \beta_4 S_4 + \beta_9 S_9$ $\beta_0 = 25.61, \beta_4 = -39.36, \beta_9 = -0.098$	18/20	2153, 2344
20.27	$\beta_0 + \beta_4 S_4 + \beta_5 S_5 + \beta_9 S_9$ $\beta_0 = 153.29, \beta_4 = -161.70, \beta_5 = -120.02, \beta_9 = -0.158$	18/20	2153, 2344
21.50	$\beta_0 + \beta_4 S_4 + \beta_{15} S_{15}$ $\beta_0 = 12.64, \beta_4 = -23.96, \beta_{15} = -23.46$	18/20	1340, 2153
21.88	$\beta_0 + \beta_2 S_2 + \beta_4 S_4 + \beta_{15} S_{15}$ $\beta_0 = 4.67, \beta_2 = 0.221, \beta_4 = -19.08, \beta_{15} = -24.35$	19/20	2153
21.98	$\beta_0 + \beta_4 S_4 + \beta_9 S_9 + \beta_{15} S_{15}$ $\beta_0 = 24.33, \beta_4 = -30.10, \beta_9 = -0.080, \beta_{15} = -16.62$	18/20	2010, 2153

518 AICc scores are listed in ascending order with lower values corresponding to a better relative
 519 model fit. The model is fitted through a logit link function for the lameness binary variable (0
 520 = non-lame, 1 = lame). All models include an intercept. The dependent variables considered in
 521 the model selection are those found to be significant in the statistical analysis shown in Table
 522 1 and are given by: S_2 : mean x coordinate; S_4 : proportion of time spent in the feeding area (F);
 523 S_5 : proportion of time spent in the full cubicle area (C_T); S_9 : full range size (95% UD isopleth);
 524 S_{15} : site fidelity (feeding area & core range). All other model structures considered had higher
 525 AICc scores (AICc > 22) and are not shown.

526

527 **Discussion**

528 By collecting high resolution spatial location data we have demonstrated in this 5-day
529 cross-sectional study how groups of 10 lame and 10 non-lame cows exhibit a number of
530 statistically significant differences in their movement and space-use behaviour (Table 1),
531 including level of site fidelity, range size, and time spent in specific locations of the barn.
532 Furthermore, we have shown that only two of these space-use measures need to be included
533 within a simple statistical model in order to accurately predict the lameness status of all
534 individual cows within the herd (S4 Table). Lameness is one of the key health and welfare
535 issues affecting dairy cattle globally [3]. Early detection of lameness can reduce animal pain
536 and suffering [5], and also minimise potential costs to farmers [4]. Current lameness detection
537 methods, usually based on expert observations of mobility, can be time-intensive [6] and hence
538 there is a need for novel automated methods of detection. We have demonstrated in this study
539 how a RTLS wireless local positioning system can be used to continuously monitor movement
540 and space-use behaviour at high recording frequency, providing additional sources of
541 behavioural information that cannot be easily collected using other systems based on
542 accelerometers or video [7,8]. This type of RTLS space-use monitoring system could
543 potentially be extended within a Precision Livestock Farming approach [9] to enable automated
544 on-farm prediction of lameness status in individual cows based on space-use and other
545 behavioural differences.

546 Our finding that non-lame cows spend a higher proportion of their time in the feeding
547 area (S_4 , Table 1; Fig 3d), and the equivalent result that lame cows spend more time in the
548 cubicles area (S_5 , Table 1; Fig 3e), is consistent with existing studies on feeding behaviour in
549 dairy cows [26–28,30]. In this study we do not try to distinguish between cows observed in the
550 feeding area that are actually feeding and those that are not feeding. However, this distinction

551 may be possible by combining basic spatial location data with additional accelerometer data
552 on activity [28]. Although we didn't measure feed intake directly in this study, earlier studies
553 have shown that lame cows may eat the same amount but at a faster rate than non-lame cows
554 [26]. This may reflect a reduced time spent at the feed face in order to avoid confrontation and
555 competition from other cows, since lame cows are known to be less likely to start an aggressive
556 interaction [10]. Lame cows may also increase their time spent lying [31] in order to reduce
557 discomfort and pain [1], and this could also explain our observed results.

558 Non-lame cows had significantly higher site fidelity than lame cows in the feeding area
559 (S_{12} and S_{15} , Table 1; Fig 4b,e), and this result holds at the core range even with the outlier cow
560 (2596) included in the analysis. Non-lame cows could be more able, or choosing, to compete
561 for their preferred food locations and consistently revisit these areas, whereas lame cows may
562 be avoiding potential competition and confrontation at the feed face [10]. The spacing of dairy
563 cows at a food trough is known to depend on dominance rank at small group sizes [70], and
564 both dairy cows and buffalo cows are known to show preferences for specific sites within the
565 milking parlour [71,72]. In wild animals, high levels of site fidelity in foraging locations have
566 been observed, albeit with high individual variance related to underlying environmental
567 conditions or prey availability [20]. When the outlier non-lame cow (2596) is removed from
568 the analysis then lame cows are found to have significantly higher site fidelity than non-lame
569 cows in the upper barn area for their core range and also for the cubicles area at both their full
570 range and core range (S_{13} , S_{15} , and S_{16} , Table 1; Fig 4c,e,f). This indicates that lame cows are
571 more likely than non-lame cows to return to the same location within the cubicles area on a
572 day-to-day basis. It should be noted that investigation of farm health records for cow 2596
573 showed no evidence of any serious underlying health issues or related treatments before or after
574 the study period, and with this cow included in the analysis, the results are no longer significant
575 and the linear model is not valid (due to non-normality of residuals). The apparent pattern of

576 higher site fidelity shown in these areas by lame cows (Fig 4) should be investigated further in
577 future studies with larger sample sizes.

578 Non-lame cows had a significantly larger full range size than lame cows (S_9 , Table 1;
579 Fig 3i), even though there was no difference in total walking distance between the two groups
580 (S_{11} , Table 1; Fig 3a). In contrast, the core range size was (weakly) positively influenced by
581 lameness, and by the number of days in milk (S_{10} , Table 1), with a negative interaction term
582 between the two predictor variables (Fig 3j). However, the complexity of this model means it
583 should be treated with some scepticism given the small sample sizes in the study (the complex
584 model structure could potentially be due to the influence of a small number of specific
585 individual cows). Additionally, although the sizes of the full and core ranges for each individual
586 cow are an important measure of how they use the space available within the barn, they may
587 not capture all relevant features of their behaviour; areas visited very infrequently may still be
588 biologically important (e.g. visits to the water trough or brush may be infrequent, but still play
589 an important role in the daily activity of each cow).

590 Parity was found to have a strong effect on the horizontal (mean x) location within the
591 barn (S_2 , $p < 0.001$; Fig 3b), with higher parity cows spending more time in the right-hand
592 cubicles, C_1 (S_6 , $p < 0.001$; Fig 3f), and lower parity cows spending more time in the left-hand
593 cubicles, C_3 (S_8 , $p = 0.006$; Fig 3h). The right-hand side of the barn used in our study
594 corresponds to being close to the passageway to the milking parlour (Fig 1), and hence the
595 difference in horizontal location could be because older and more experienced (higher parity)
596 cows are choosing to stay near the connecting passage to the milking parlour in order to get a
597 better position in the milking queue. Disease status is also known to affect milking order, with
598 lame cows more likely to be found in the last third of the milking [29,73] and taking longer to
599 return from the milking parlour [11]. Similarly, cows suffering from mastitis were found to
600 enter the milking parlour later [74], although the same study reported no effect of age, parity or

601 days in milk on milking order. An alternative interpretation of our results is that when returning
602 from milking, the older higher parity cows in our study are simply not spreading out within the
603 barn as much as younger cows, possibly because they have longer bouts of low activity
604 (standing or lying) and spend less time feeding. For example, previous studies have reported
605 that primiparous (parity 1) cows have significantly more lying bouts of shorter duration when
606 compared to parity 2 and parity 3+ groups [75] and that parity 1 and 2 cows spend more time
607 feeding than parity 3+ cows [76]. Higher parities have also been associated with longer standing
608 times [77]. It is also possible that there is a social aspect to this observed space-use behaviour,
609 with cows of similar parity staying close to each other in different areas of the barn for social
610 reasons. Other potential factors such as localised air quality, temperature, wind, and noise may
611 also influence the preferential use of certain locations within the barn by individual cows, but
612 were variables that were not measured in this study.

613 Days in milk (DIM) was found to have a significant negative effect on the proportion
614 of time spent in the right-hand cubicles, C_1 ($S_6, p = 0.038$) and a significant positive effect on
615 the core (50% isopleth) range size, ($S_6, p = 0.002$) with an associated negative interaction effect
616 with lameness (Fig 3j). Various studies have reported increased lying behaviour with increased
617 DIM [78,79], while increased DIM has also been shown to lead to decreased feeding frequency
618 but increased meal duration and total feeding time [76]. The interplay between DIM, parity and
619 lameness is clearly complex, and further studies are needed to explore how observed space-use
620 behaviour is driven by each of these factors and their potential interactions.

621 Although we have high resolution spatial location data for each individual cow, we also
622 have relatively small sample sizes (10 lame and 10 non-lame cows) and the cross-sectional
623 study ran for only 5 days. Hence, although our results have exciting potential, we are cautious
624 about over-generalisation. In particular, the model parameter values found during the statistical
625 analysis are specific to this study group and barn environment and will almost certainly be

626 different for other cows or other barn locations. We have demonstrated how space-use
627 measures in individual cows are linked to health (lameness) status, parity, and (to a lesser
628 extent) days in milk, but space-use behaviour is also likely to be influenced by management
629 actions, the barn landscape and layout, the frequency of milking and the milking system used
630 (automated v milking parlour), and individual cow age and breed [8]. Similar to [8], as we have
631 undertaken a short-term cross-sectional study using cows with known lameness status, it is not
632 possible to determine from our results how well space-use behavioural indicators may perform
633 in detecting changes in the status of individual cows as they transition from non-lame to lame
634 (and subsequently recover after treatment) over the longer term. Longitudinal studies over an
635 extended time period with larger group sizes would allow us to determine the consistency of
636 any observed space-use differences, as well as what space-use behaviour changes might be
637 detectable at the onset of lameness. By monitoring a full herd across a larger time period it
638 would also be possible to determine more detailed social interactions and spatial dynamics that
639 may influence individual space-use behaviour. In this study, the cows being tracked formed a
640 subset of a much larger herd, and we did not attempt to explore social interactions because of
641 the difficulty in distinguishing between direct and indirect social interactions when many
642 individuals within the full herd are not part of the observed data set. Nevertheless, our results
643 suggesting higher parity cows use different areas of the barn compared to lower parity cows
644 (Figs 3f and 3h) hints at a possible social aspect to their space-use behaviour. More detailed
645 analysis of social behaviour could be undertaken by exploring network features within the herd
646 as a whole [80], or through pairwise analyses of space-use and space-use similarity
647 [23,49,63,64,81].

648 Our aim with the predictive model in Equation (4) is to illustrate the ‘proof of concept’
649 of how observed space-use behavioural data can be used to give an accurate prediction of
650 lameness status in individual cows in this cross-sectional study. As it stands, the model is not

651 directly transferable to other groups of cows or barn locations and would need to be adapted
652 and tested before being used in other farm environments. Nevertheless, it demonstrates the
653 principle of how only a few simple space-use measures could be used to accurately determine
654 lameness status for individual cows within a herd. The best relative fitting model structure only
655 included time spent in the feeding area, and the number of virtual cells in the full range (Table
656 2), demonstrating that as few as two simple space-use measures are needed to give a good
657 description of lameness status in this study group of cows. Such a simple predictive model
658 could potentially be quickly adapted and parameterised for practical on-farm use (assuming the
659 general results hold), unlike more complex predictive models that might require
660 computationally intensive model fitting or continuous re-parametrisation.

661 Out of 20 cows, only one lame cow (2344) and one non-lame cow (2153) were
662 incorrectly classified by the best-fitting predictive model (Table 2, S4 Table). Investigation of
663 the health records of cow 2153 suggests that she was likely to have been misclassified as ‘non-
664 lame’ before the study by the expert observers (through mobility scoring), as lesions with the
665 potential to cause lameness were found on her feet when all cows were inspected at the end of
666 the study period (and hence the model prediction was essentially correct, and was able to detect
667 this earlier misclassification by the expert observers). In March 2014 shortly after our study
668 was completed this cow underwent a series of 11 treatments for mastitis and was eventually
669 culled early. Mastitis is also known to affect dairy cow behaviour, with reduced lying times,
670 reduced feed intake and a reduction in competitive behaviour at the feeder compared to healthy
671 cows [32,82]. No other cows from the non-lame trial group had treatments for any health
672 conditions during the study period (or for at least 3 months after the study had finished).
673 Meanwhile, when inspected at the end of the study period, cow 2344 (lame) was found to be
674 wearing a hoof block, which is fitted to relieve pressure on the affected areas of the hoof, and
675 hence this may have potentially reduced clinical signs and changes in behaviour related to

676 lameness for this cow. No other cows in the lame group had similar treatments during the study
677 period (or for at least 3 months after the study had finished).

678 Increasing demand for animal products and intensification of farming practices in
679 general, means that there is a need for automated behavioural monitoring systems that can act
680 as an ‘early warning’ to detect and predict the health status of managed animals, including
681 dairy cows suffering from lameness and other diseases [7,8,26,83]. Automated lameness
682 detection technology systems have been developed based on the identification of an
683 abnormality of gait or posture [83], using force plate technology [7,84] or kinematics [85].
684 Meanwhile, automated monitoring of feeding behaviour in cattle has relied on electronic feed
685 troughs [27,30]. However, there has not been a widespread uptake of such systems on
686 commercial farms due to the high price, practical limitations such as lack of space, or limited
687 precision of detection [7]. Automated lameness detection systems based on differences in
688 locomotion or activity patterns observed in accelerometer data have been suggested as a lower
689 cost alternative approach [7,8,35]. The results we present here suggest that space-use and site-
690 fidelity measures could be an exciting addition to the suite of behavioural indicators available
691 as part of Precision Livestock Farming approaches for monitoring and detecting diseases such
692 as lameness in cattle and other animals.

693 The use of space-use and site-fidelity measures as health status indicators does not need
694 to be limited to cattle or dairy cows, and similar approaches could also potentially be used with
695 other managed animal species or even wild animals, if similar differences in space-use
696 behaviour linked to health status are found to exist. Little is known about the direct link
697 between space-use behaviour and health in pigs, although there is evidence suggesting that
698 impoverished environments contribute to high levels of boredom and apathy [86]. It should be
699 straightforward to monitor space-use patterns of individual pigs using automated wireless
700 positioning system in a similar manner to what we have done in this study with dairy cows. In

701 the context of broiler chickens, [87] showed how optical flow, a measure of the movement and
702 flow of the flock as a whole through the space within the barn determined by computer vision
703 techniques, could be directly linked to the health and disease status of the flock, illustrating
704 how space-use metrics at the group-level can also be used as indicators for welfare monitoring.
705

706 **Conclusions**

707 We have demonstrated in this study how location tracking data collected from animal-mounted
708 wireless sensors using a Real Time Location System can be processed and analysed to give a
709 suite of space-use behavioural measures. We have used these measures to explore differences
710 in space-use behaviour in two test groups of barn-housed dairy cows in a cross-sectional study
711 design, and found significant differences between lame and non-lame individuals. Non-lame
712 cows had higher site fidelity, and spent more time, in the feeding area, and had a larger range
713 within the barn. In contrast, lame cows spent less time in the feeding area and more time in the
714 cubicle areas of the barn, where they had higher site fidelity. Space-use behaviour was also
715 found to be influenced by parity and days in milk: higher parity cows had a mean location
716 closer to where the connecting passage to the milking parlour is situated, and days in milk was
717 found to influence the core range size. We have demonstrated that only two simple space-use
718 measures, proportion of time spent in the feeding area and full range size, are needed within a
719 simple statistical model in order to accurately predict the lameness status of all individual cows
720 within the herd. The sample size used within this study (10 lame and 10 non-lame cows) was
721 small and hence care should be taken in directly extrapolating our results and conclusions to
722 other studies and contexts. However, the general findings and associated methods for exploring
723 animal space-use could potentially be developed in future studies to form a new set of tools for
724 automated monitoring of dairy cattle, or for monitoring, detecting and predicting health status
725 in other managed or wild animal species.

726

727 **Acknowledgements**

728 We are very grateful to all the farm staff who helped to facilitate this study.

729

730 **References**

- 731 1. Whay HR, Waterman AE, Webster AJ, O'Brien JK. 1998 The influence of lesion type on
732 the duration of hyperalgesia associated with hindlimb lameness in dairy cattle. *Vet. J.*
733 *Lond. Engl.* 1997 **156**, 23–29.
- 734 2. Leach KA, Whay HR, Maggs CM, Barker ZE, Paul ES, Bell AK, Main DCJ. 2010
735 Working towards a reduction in cattle lameness: 1. Understanding barriers to lameness
736 control on dairy farms. *Res. Vet. Sci.* **89**, 311–317. (doi:10.1016/j.rvsc.2010.02.014)
- 737 3. Archer S, Bell N, Huxley J. 2010 Lameness in UK dairy cows: a review of the current
738 status. *In Pract.* **32**, 492–504. (doi:10.1136/inp.c6672)
- 739 4. Willshire JA, Bell NJ. 2009 An economic review of cattle lameness. *Cattle Pract.* **17**,
740 136–141.
- 741 5. Leach KA, Tisdall DA, Bell NJ, Main DCJ, Green LE. 2012 The effects of early treatment
742 for hindlimb lameness in dairy cows on four commercial UK farms. *Vet. J.* **193**, 626–632.
743 (doi:10.1016/j.tvjl.2012.06.043)
- 744 6. Horseman SV, Roe EJ, Huxley JN, Bell NJ, Mason CS, Whay HR. 2014 The use of in-
745 depth interviews to understand the process of treating lame dairy cows from the farmers'
746 perspective. *Anim. Welf.* **23**, 157–169.
- 747 7. Van Nuffel A, Zwervaegher I, Van Weyenberg S, Pastell M, Thorup VM, Bahr C, Sonck
748 B, Saeyns W. 2015 Lameness Detection in Dairy Cows: Part 2. Use of Sensors to
749 Automatically Register Changes in Locomotion or Behavior. *Anim. Open Access J. MDPI*
750 **5**, 861–885. (doi:10.3390/ani5030388)
- 751 8. Beer G, Alsaad M, Starke A, Schuepbach-Regula G, Müller H, Kohler P, Steiner A. 2016
752 Use of Extended Characteristics of Locomotion and Feeding Behavior for Automated
753 Identification of Lame Dairy Cows. *PLoS One* **11**, e0155796.
754 (doi:10.1371/journal.pone.0155796)
- 755 9. Berckmans D. 2014 Precision livestock farming technologies for welfare management in
756 intensive livestock systems. *Rev. Sci. Tech. Int. Off. Epizoot.* **33**, 189–196.
- 757 10. Galindo F, Broom DM. 2002 Effects of lameness of dairy cows. *J. Appl. Anim. Welf.*
758 *Sci. JAAWS* **5**, 193–201. (doi:10.1207/S15327604JAWS0503_03)
- 759 11. Juarez ST, Robinson PH, DePeters EJ, Price EO. 2003 Impact of lameness on
760 behavior and productivity of lactating Holstein cows. *Appl. Anim. Behav. Sci.* **83**, 1–14.
761 (doi:10.1016/S0168-1591(03)00107-2)
- 762 12. Ceballos A, Sanderson D, Rushen J, Weary DM. 2004 Improving stall design: use of
763 3-D kinematics to measure space use by dairy cows when lying down. *J. Dairy Sci.* **87**,
764 2042–2050. (doi:10.3168/jds.S0022-0302(04)70022-3)
- 765 13. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008 A
766 movement ecology paradigm for unifying organismal movement research. *Proc. Natl.*
767 *Acad. Sci.* **105**, 19052–19059. (doi:10.1073/pnas.0800375105)

- 768 14. Homburger H, Lüscher A, Scherer-Lorenzen M, Schneider MK. 2015 Patterns of
769 livestock activity on heterogeneous subalpine pastures reveal distinct responses to spatial
770 autocorrelation, environment and management. *Mov. Ecol.* **3**, 35. (doi:10.1186/s40462-
771 015-0053-6)
- 772 15. Martin J, Benhamou S, Yoganand K, Owen-Smith N. 2015 Coping with Spatial
773 Heterogeneity and Temporal Variability in Resources and Risks: Adaptive Movement
774 Behaviour by a Large Grazing Herbivore. *PLOS ONE* **10**, e0118461.
775 (doi:10.1371/journal.pone.0118461)
- 776 16. Börger Luca, Dalziel Benjamin D., Fryxell John M. 2008 Are there general
777 mechanisms of animal home range behaviour? A review and prospects for future research.
778 *Ecol. Lett.* **11**, 637–650. (doi:10.1111/j.1461-0248.2008.01182.x)
- 779 17. Riotte-Lambert L, Benhamou S, Chamaillé-Jammes S. 2013 Periodicity analysis of
780 movement recursions. *J. Theor. Biol.* **317**, 238–243. (doi:10.1016/j.jtbi.2012.10.026)
- 781 18. Van Moorter Bram, Visscher Darcy, Benhamou Simon, Börger Luca, Boyce Mark S.,
782 Gaillard Jean-Michel. 2009 Memory keeps you at home: a mechanistic model for home
783 range emergence. *Oikos* **118**, 641–652. (doi:10.1111/j.1600-0706.2008.17003.x)
- 784 19. Martínez-Miranzo B, Banda E, Gardiazábal A, Ferreiro E, Aguirre JI. 2016
785 Differential spatial use and spatial fidelity by breeders in Bonelli's Eagle (<Emphasis
786 Type="Italic">Aquila fasciata</Emphasis>). *J. Ornithol.* **157**, 971–979.
787 (doi:10.1007/s10336-016-1347-1)
- 788 20. Arthur B, Hindell M, Bester M, Trathan P, Jonsen I, Staniland I, Oosthuizen WC,
789 Wege M, Lea M-A. 2015 Return Customers: Foraging Site Fidelity and the Effect of
790 Environmental Variability in Wide-Ranging Antarctic Fur Seals. *PLOS ONE* **10**,
791 e0120888. (doi:10.1371/journal.pone.0120888)
- 792 21. Brough AM, Justin DeRose R, Conner MM, Long JN. 2017 Summer-fall home-range
793 fidelity of female elk in northwestern Colorado: Implications for aspen management. *For.*
794 *Ecol. Manag.* **389**, 220–227. (doi:10.1016/j.foreco.2016.11.034)
- 795 22. Sorensen AA, van Beest FM, Brook RK. 2015 Quantifying overlap in crop selection
796 patterns among three sympatric ungulates in an agricultural landscape. *Basic Appl. Ecol.*
797 **16**, 601–609. (doi:10.1016/j.baae.2015.05.001)
- 798 23. Zengeya FM, Murwira A, Caron A, Cornélis D, Gandiwa P, de Garine-Wichatitsky
799 M. 2015 Spatial overlap between sympatric wild and domestic herbivores links to resource
800 gradients. *Remote Sens. Appl. Soc. Environ.* **2**, 56–65. (doi:10.1016/j.rsase.2015.11.001)
- 801 24. Romanzin A, Corazzin M, Piasentier E, Bovolenta S. 2018 Concentrate Supplement
802 Modifies the Feeding Behavior of Simmental Cows Grazing in Two High Mountain
803 Pastures. *Anim. Open Access J. MDPI* **8**. (doi:10.3390/ani8050076)
- 804 25. Barasona JA, Latham MC, Acevedo P, Armenteros JA, Latham ADM, Gortazar C,
805 Carro F, Sorriquer RC, Vicente J. 2014 Spatiotemporal interactions between wild boar and
806 cattle: implications for cross-species disease transmission. *Vet. Res.* **45**, 122.
807 (doi:10.1186/s13567-014-0122-7)

- 808 26. González LA, Tolkamp BJ, Coffey MP, Ferret A, Kyriazakis I. 2008 Changes in
809 feeding behavior as possible indicators for the automatic monitoring of health disorders in
810 dairy cows. *J. Dairy Sci.* **91**, 1017–1028. (doi:10.3168/jds.2007-0530)
- 811 27. Palmer MA, Law R, O’Connell NE. 2012 Relationships between lameness and
812 feeding behaviour in cubicle-housed Holstein–Friesian dairy cows. *Appl. Anim. Behav.*
813 *Sci.* **140**, 121–127. (doi:10.1016/j.applanim.2012.06.005)
- 814 28. Barker ZE, Vázquez Diosdado JA, Codling EA, Bell NJ, Hodges HR, Croft DP,
815 Amory JR. In press. Use of novel sensors combining local positioning and acceleration to
816 measure feeding behavior differences associated with lameness in dairy cattle. *J. Dairy*
817 *Sci.* **in press**.
- 818 29. Weigele HC, Gygax L, Steiner A, Wechsler B, Burla J-B. 2018 Moderate lameness
819 leads to marked behavioral changes in dairy cows. *J. Dairy Sci.* **101**, 2370–2382.
820 (doi:10.3168/jds.2017-13120)
- 821 30. Norring M, Häggman J, Simojoki H, Tamminen P, Winckler C, Pastell M. 2014 Short
822 communication: Lameness impairs feeding behavior of dairy cows. *J. Dairy Sci.* **97**, 4317–
823 4321. (doi:10.3168/jds.2013-7512)
- 824 31. Blackie N, Amory J, Bleach E, Scaife J. 2011 The effect of lameness on lying
825 behaviour of zero grazed Holstein dairy cattle. *Appl. Anim. Behav. Sci.* **134**, 85–91.
826 (doi:10.1016/j.applanim.2011.08.004)
- 827 32. Medrano-Galarza C, Gibbons J, Wagner S, de Passillé AM, Rushen J. 2012
828 Behavioral changes in dairy cows with mastitis. *J. Dairy Sci.* **95**, 6994–7002.
829 (doi:10.3168/jds.2011-5247)
- 830 33. Martiskainen P, Järvinen M, Skön J-P, Tiirikainen J, Kolehmainen M, Mononen J.
831 2009 Cow behaviour pattern recognition using a three-dimensional accelerometer and
832 support vector machines. *Appl. Anim. Behav. Sci.* **119**, 32–38.
833 (doi:10.1016/j.applanim.2009.03.005)
- 834 34. González LA, Bishop-Hurley GJ, Handcock RN, Crossman C. 2015 Behavioral
835 classification of data from collars containing motion sensors in grazing cattle. *Comput.*
836 *Electron. Agric.* **110**, 91–102. (doi:10.1016/j.compag.2014.10.018)
- 837 35. Vázquez Diosdado JA, Barker ZE, Hodges HR, Amory JR, Croft DP, Bell NJ,
838 Codling EA. 2015 Classification of behaviour in housed dairy cows using an
839 accelerometer-based activity monitoring system. *Anim. Biotelemetry* **3**, 15.
840 (doi:10.1186/s40317-015-0045-8)
- 841 36. DeVries TJ, von Keyserlingk MAG, Weary DM, Beauchemin KA. 2003 Measuring
842 the Feeding Behavior of Lactating Dairy Cows in Early to Peak Lactation. *J. Dairy Sci.* **86**,
843 3354–3361. (doi:10.3168/jds.S0022-0302(03)73938-1)
- 844 37. Azizi O, Kaufmann O, Hasselmann L. 2009 Relationship between feeding behaviour
845 and feed intake of dairy cows depending on their parity and milk yield. *Livest. Sci.* **122**,
846 156–161. (doi:10.1016/j.livsci.2008.08.009)

- 847 38. Williams ML, Mac Parthaláin N, Brewer P, James WPJ, Rose MT. 2016 A novel
848 behavioral model of the pasture-based dairy cow from GPS data using data mining and
849 machine learning techniques. *J. Dairy Sci.* **99**, 2063–2075. (doi:10.3168/jds.2015-10254)
- 850 39. Homburger H, Schneider MK, Hilfiker S, Lüscher A. 2014 Inferring Behavioral
851 States of Grazing Livestock from High-Frequency Position Data Alone. *PLOS ONE* **9**,
852 e114522. (doi:10.1371/journal.pone.0114522)
- 853 40. Gygax L, Neisen G, Bollhalder H. 2007 Accuracy and validation of a radar-based
854 automatic local position measurement system for tracking dairy cows in free-stall barns.
855 *Comput. Electron. Agric.* **56**, 23–33. (doi:10.1016/j.compag.2006.12.004)
- 856 41. Alarifi A, Al-Salman A, Alsaleh M, Alnafessah A, Al-Hadhrami S, Al-Ammar MA,
857 Al-Khalifa HS. 2016 Ultra Wideband Indoor Positioning Technologies: Analysis and
858 Recent Advances. *Sensors* **16**. (doi:10.3390/s16050707)
- 859 42. Tullo E, Fontana I, Gottardo D, Sloth KH, Guarino M. 2016 Technical note:
860 Validation of a commercial system for the continuous and automated monitoring of dairy
861 cow activity. *J. Dairy Sci.* **99**, 7489–7494. (doi:10.3168/jds.2016-11014)
- 862 43. Meunier B, Pradel P, Sloth KH, Cirié C, Delval E, Mialon MM, Veissier I. In press
863 Image analysis to refine measurements of dairy cow behaviour from a real-time location
864 system. *Biosyst. Eng.* (doi:10.1016/j.biosystemseng.2017.08.019)
- 865 44. Shane DD, White BJ, Larson RL, Amrine DE, Kramer JL. 2016 Probabilities of cattle
866 participating in eating and drinking behavior when located at feeding and watering
867 locations by a real time location system. *Comput. Electron. Agric.* **127**, 460–466.
868 (doi:10.1016/j.compag.2016.07.005)
- 869 45. Arcidiacono C, Porto SMC, Mancino M, Cascone G. In press A software tool for the
870 automatic and real-time analysis of cow velocity data in free-stall barns: The case study of
871 oestrus detection from Ultra-Wide-Band data. *Biosyst. Eng.*
872 (doi:10.1016/j.biosystemseng.2017.10.007)
- 873 46. Bell N, Huxley J. 2009 Locomotion, lameness and mobility in dairy cows. *Vet. Rec.*
874 **164**, 726–726. (doi:10.1136/vr.164.23.726)
- 875 47. Spence AJ, Tan H, Wilson A. 2008 Accuracy of the TurfTrax Racing Data System for
876 determination of equine speed and position. *Equine Vet. J.* **40**, 680–683.
- 877 48. Omnisense Ltd. 2013 Series 500 Cluster Geolocation System: System Data Sheet.
- 878 49. Fieberg J, Kochanny CO, Lanham. 2005 Quantifying home-range overlap: the
879 importance of the utilization distribution. *J. Wildl. Manag.* **69**, 1346–1359.
880 (doi:10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2)
- 881 50. Benhamou Simon, Cornélis Daniel. 2010 Incorporating Movement Behavior and
882 Barriers to Improve Kernel Home Range Space Use Estimates. *J. Wildl. Manag.* **74**, 1353–
883 1360. (doi:10.1111/j.1937-2817.2010.tb01257.x)

- 884 51. Benhamou S, Riote-Lambert L. 2012 Beyond the Utilization Distribution: Identifying
885 home range areas that are intensively exploited or repeatedly visited. *Ecol. Model.* **227**,
886 112–116. (doi:10.1016/j.ecolmodel.2011.12.015)
- 887 52. Powell RA. 2000 Animal Home Ranges and Territories and Home Range Estimators.
888 In *Research Techniques in Animal Ecology: Controversies and Consequences* (eds M
889 Pearl, L Boitani, T Fuller), pp. 65–110. Columbia University Press.
- 890 53. Worton B. J. 1989 Kernel Methods for Estimating the Utilization Distribution in
891 Home-Range Studies. *Ecology* **70**, 164–168. (doi:10.2307/1938423)
- 892 54. Horne JS, Garton EO, Krone SM, Lewis JS. 2007 Analyzing animal movements using
893 Brownian bridges. *Ecology* **88**, 2354–2363.
- 894 55. Kranstauber Bart, Kays Roland, LaPoint Scott D., Wikelski Martin, Safi Kamran.
895 2012 A dynamic Brownian bridge movement model to estimate utilization distributions for
896 heterogeneous animal movement. *J. Anim. Ecol.* **81**, 738–746. (doi:10.1111/j.1365-
897 2656.2012.01955.x)
- 898 56. Signer Johannes, Fieberg John, Avgar Tal. 2017 Estimating utilization distributions
899 from fitted step-selection functions. *Ecosphere* **8**, e01771. (doi:10.1002/ecs2.1771)
- 900 57. Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J. 2008 State-
901 space models of individual animal movement. *Trends Ecol. Evol.* **23**, 87–94.
902 (doi:10.1016/j.tree.2007.10.009)
- 903 58. Doncaster CP, Macdonald DW. 1991 Drifting Territoriality in the Red Fox *Vulpes*
904 *vulpes*. *J. Anim. Ecol.* **60**, 423–439. (doi:10.2307/5288)
- 905 59. Clapp JG, Beck JL. 2015 Evaluating distributional shifts in home range estimates.
906 *Ecol. Evol.* **5**, 3869–3878. (doi:10.1002/ece3.1655)
- 907 60. Ostfeld RS. 1986 Territoriality and Mating System of California Voles. *J. Anim. Ecol.*
908 **55**, 691–706. (doi:10.2307/4748)
- 909 61. Heupel MR, Simpfendorfer CA, Hueter RE. 2004 Estimation of Shark Home Ranges
910 using Passive Monitoring Techniques. *Environ. Biol. Fishes* **71**, 135–142.
911 (doi:10.1023/B:EBFI.0000045710.18997.f7)
- 912 62. Kie JG, Matthiopoulos J, Fieberg J, Powell RA, Cagnacci F, Mitchell MS, Gaillard J-
913 M, Moorcroft PR. 2010 The home-range concept: are traditional estimators still relevant
914 with modern telemetry technology? *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 2221–2231.
915 (doi:10.1098/rstb.2010.0093)
- 916 63. Garitano-Zavala A, Chura Z, Cotín J, Ferrer X, Nadal J. 2013 Home range extension
917 and overlap of the Ornate Tinamou (*Nothoprocta ornata*) in an Andean agro-ecosystem.
918 *Wilson J. Ornithol.* **125**, 491–501. (doi:10.1676/12-151.1)
- 919 64. Benhamou S, Valeix M, Chamaillé-Jammes S, Macdonald DW, Loveridge AJ. 2014
920 Movement-based analysis of interactions in African lions. *Anim. Behav.* **90**, 171–180.
921 (doi:10.1016/j.anbehav.2014.01.030)

- 922 65. Bhattacharyya A. 1946 On a Measure of Divergence between Two Multinomial
923 Populations. *Sankhyā Indian J. Stat. 1933-1960* **7**, 401–406.
- 924 66. Burnham KP, Anderson DR. 2002 *Model Selection and Multimodel Inference: A*
925 *Practical Information-Theoretic Approach*. 2nd edn. New York: Springer-Verlag. See
926 //www.springer.com/gb/book/9780387953649.
- 927 67. Myers RH. 1990 *Classical and Modern Regression with Applications*.
928 Duxbury/Thompson Learning.
- 929 68. Hair J, Anderson R, Black B, Babin B. 2016 *Multivariate Data Analysis*. Pearson
930 Higher Ed.
- 931 69. R Core Team. 2017 R: A language and environment for statistical computing.
- 932 70. Manson FJ, Appleby MC. 1990 Spacing of dairy cows at a food trough. *Appl. Anim.*
933 *Behav. Sci.* **26**, 69–81. (doi:10.1016/0168-1591(90)90088-U)
- 934 71. Grasso F, Rosa GD, Napolitano F, Francia AD, Bordi A. 2007 Entrance order and
935 side preference of dairy cows in the milking parlour. *Ital. J. Anim. Sci.* **6**, 187–194.
936 (doi:10.4081/ijas.2007.187)
- 937 72. Polikarpus A, Grasso F, Pacelli C, Napolitano F, Rosa GD. 2014 Milking behaviour
938 of buffalo cows: entrance order and side preference in the milking parlour. *J. Dairy Res.*
939 **81**, 24–29. (doi:10.1017/S0022029913000587)
- 940 73. Main DCJ, Barker ZE, Leach KA, Bell NJ, Whay HR, Browne WJ. 2010 Sampling
941 strategies for monitoring lameness in dairy cattle. *J. Dairy Sci.* **93**, 1970–1978.
942 (doi:10.3168/jds.2009-2500)
- 943 74. Polikarpus A, Kaart T, Mootse H, De Rosa G, Arney D. 2015 Influences of various
944 factors on cows' entrance order into the milking parlour. *Appl. Anim. Behav. Sci.* **166**, 20–
945 24. (doi:10.1016/j.applanim.2015.02.016)
- 946 75. Solano L *et al.* 2016 Associations between lying behavior and lameness in Canadian
947 Holstein-Friesian cows housed in freestall barns. *J. Dairy Sci.* **99**, 2086–2101.
948 (doi:10.3168/jds.2015-10336)
- 949 76. Azizi O, Hasselmann L, Kaufmann O. 2010 Variations in feeding behaviour of high-
950 yielding dairy cows in relation to parity during early to peak lactation. *Arch. Anim. Breed.*
951 **53**, 130–140. (doi:10.5194/aab-53-130-2010)
- 952 77. Deming JA, Bergeron R, Leslie KE, DeVries TJ. 2013 Associations of housing,
953 management, milking activity, and standing and lying behavior of dairy cows milked in
954 automatic systems. *J. Dairy Sci.* **96**, 344–351. (doi:10.3168/jds.2012-5985)
- 955 78. Bewley JM, Boyce RE, Hockin J, Munksgaard L, Eicher SD, Einstein ME, Schutz
956 MM. 2010 Influence of milk yield, stage of lactation, and body condition on dairy cattle
957 lying behaviour measured using an automated activity monitoring sensor. *J. Dairy Res.* **77**,
958 1–6. (doi:10.1017/S0022029909990227)

- 959 79. Maselyne J, Pastell M, Thomsen PT, Thorup VM, Hänninen L, Vangeyte J, Van
960 Nuffel A, Munksgaard L. 2017 Daily lying time, motion index and step frequency in dairy
961 cows change throughout lactation. *Res. Vet. Sci.* **110**, 1–3.
962 (doi:10.1016/j.rvsc.2016.10.003)
- 963 80. Krause J, Krause S, Arlinghaus R, Psorakis I, Roberts S, Rutz C. 2013 Reality mining
964 of animal social systems. *Trends Ecol. Evol.* **28**, 541–551.
965 (doi:10.1016/j.tree.2013.06.002)
- 966 81. Long JA, Webb SL, Nelson TA, Gee KL. 2015 Mapping areas of spatial-temporal
967 overlap from wildlife tracking data. *Mov. Ecol.* **3**. (doi:10.1186/s40462-015-0064-3)
- 968 82. Sepúlveda-Varas P, Proudfoot KL, Weary DM, Keyserlingk MAG von. 2016
969 Changes in behaviour of dairy cows with clinical mastitis. *Appl. Anim. Behav. Sci.* **175**, 8–
970 13. (doi:10.1016/j.applanim.2014.09.022)
- 971 83. Chapinal N, de Passillé AM, Rushen J, Wagner S. 2010 Automated methods for
972 detecting lameness and measuring analgesia in dairy cattle. *J. Dairy Sci.* **93**, 2007–2013.
973 (doi:10.3168/jds.2009-2803)
- 974 84. Ghotoorlar SM, Ghamsari SM, Nowrouzian I, Ghotoorlar SM, Ghidary SS. 2012
975 Lameness scoring system for dairy cows using force plates and artificial intelligence. *Vet.*
976 *Rec.* **170**, 126. (doi:10.1136/vr.100429)
- 977 85. Blackie N, Bleach ECL, Amory JR, Scaife JR. 2013 Associations between
978 locomotion score and kinematic measures in dairy cows with varying hoof lesion types. *J.*
979 *Dairy Sci.* **96**, 3564–3572. (doi:10.3168/jds.2012-5597)
- 980 86. Wood-Gush DGM, Vestergaard K. 1989 Exploratory behavior and the welfare of
981 intensively kept animals. *J. Agric. Ethics* **2**, 161–169. (doi:10.1007/BF01826929)
- 982 87. Dawkins MS, Cain R, Roberts SJ. 2012 Optical flow, flock behaviour and chicken
983 welfare. *Anim. Behav.* **84**, 219–223. (doi:10.1016/j.anbehav.2012.04.036)
- 984

985 **Supporting information**

986 **Table S1. Health and milk production data for cows used within the study.**

987

988 **Table S2. Summary space-use statistics for each cow within the study.**

989

990 **Table S3. Summary site-fidelity statistics for each cow within the study.**

991

992 **Table S4. True and predicted probability of lameness for each cow in the study using best**
993 **relative fitting predictive model.**

994

995 **File S1. Space-use intensity plots for all cows and all study days.** Supplementary file S1
996 contains space-use intensity plots (UDs) for all cows over all five days of the trial. The space-
997 use intensity UD is calculated by overlaying a 1.5m x 1.5m square grid (40 x 13 cells) onto the
998 upper barn area only and counting the cells in which the smoothed trajectory points for each
999 cow occur for each day of the trial. Darker colours correspond to higher space-use intensity.
1000 The 95% and 50% isopleths (corresponding to the full and core ranges for movement within
1001 the upper barn area only) are respectively indicated by the dashed and solid contour lines.

1002

1003 **File S2. Basic space-use measures for each study day.** Supplementary file S2 contains box-
1004 plots showing basic space-use measures by day of the trial. Lame cows are marked using
1005 triangles and non-lame cows are marked using circles. The colours used to indicate each cow
1006 are consistent across all plots. There are no clear trends by day in any of the basic space-use
1007 measures considered.

1008

1009 **File S3. Location data for all cows and study days.** Supplementary file S3 contains the raw
1010 location tracking data for each cow for each day of the study as used in the analysis.