'The Effects of Uncertainty on Movement and Space-use in Sheep'

by

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DECLARATION

I declare that this thesis is a record of original work and contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text.

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Signature

Sarah Bartsch

31/05/2022

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ABSTRACT

Within the growing field of movement ecology, the way animals respond to uncertainty caused by changing environments is of great interest. Our changing climate and associated diminishing resources could challenge specific animal communities. Food resource locations across the landscape could become less predictable, and animals must adjust their foraging behaviour when responding to these changes. However, how animals react to this uncertainty remains unclear. Here I studied the movement behaviour of Merino sheep situated in a drought-impacted region of arid New South Wales. GPS tracking of 50 individuals recorded individual locations every 15 seconds during daylight hours. Movements within a period where the sheep had gained little environmental information and were more uncertain of the type and distribution of available environmental resources were compared with a subsequent period where resources were relocated. Still, despite this, the animals had gained higher overall knowledge of resource locations throughout the second period. During the period of uncertainty, individuals were found to have slower walking speeds, travelled shorter distances per day and were generally less displaced from their daily starting location. The sheep also had smaller home ranges and more severe turn angles during periods where their knowledge of the environment was limited. This study shows that individuals experiencing higher levels of uncertainty use a 'win-stay' foraging strategy, whereas as more high-value resources are discovered, a 'win-shift' strategy is adopted. This study demonstrates that arid zone, free-ranging ungulates have the capability to quickly adjust their movement strategy to enhance efficiency in changed conditions as they gain environmental information. These findings may facilitate the study of the effects of uncertainty and impacts of environmental changes on foraging strategies in wild ungulate populations.

INTRODUCTION

Environmental knowledge is vital information that an animal needs to gather for successful and efficient foraging. Sheep use a combination of acquired information such as experiences, sensory cues, or navigational mechanisms to create spatial memories that make movement and travel between resources more efficient (Edwards et al., 1996; Lee et al., 2006). When an animal has no or limited knowledge about its environment, i.e., when uncertainty is high, the animal can make less informed movement decisions, which can result in energetically costly movement patterns. In the context of foraging, this may ultimately lead to the animal using foraging strategies that are not optimal, with a lower likelihood of resource encounters. Drought, increased temperatures, or other environmental events can cause changes to the availability and distribution of food which could be detrimental unless the animal can use appropriate strategies to gather new information. These habitat changes can force animals to travel further, either by embarking on foraging trips or through migration (Kefi et al., 2007; Papageorgiou et al., 2021). Ultimately, difficulty in locating resources could lead to increased mortalities and potentially species extinctions (Foley et al., 2008; Paniw et al., 2019; Trisos et al., 2020; Urban, 2015). In this project, I aim to examine whether and how movement and space use patterns change when the uncertainty of resource locations and distribution increases.

Most animal species move through space to locate food. However, an animal's movements can be constrained or altered by movement barriers, such as habitat fragmentation or uncertainty about where to find resources. (Armansin et al., 2020; Nathan et al., 2008). This uncertainty arises when the animal possesses limited or no information about the environment, which is needed to make a decision. The way animals respond behaviourally to the uncertainty caused by a changing environment can determine how effectively the animal can locate crucial resources (Cunningham et al., 2015; Dall et al., 2005; Fagan et al., 2013;

Herzing et al., 2017). For example, elephants that responded to drought by travelling further for food had increased fitness through higher calf survival rates (Foley et al., 2008).

One way of acquiring environmental information in response to uncertainty is through search behaviour, which can be identified by the characteristic of movement patterns. The purpose of these movement patterns is usually to collect information or relocate to a new locality (Bartumeus et al., 2016). Individuals change their movement characteristics when they are initially unaware of the location of their goal but then transition to a more efficient strategy to locate the desired resource (Krakauer and Rodrı́guez-Gironés, 1995; Rook et al., 2005). For example, a slow local search, with short steps and many turns, is best used whilst gaining enough information to decide on whether to leave an area; once the decision has been made to leave, it is best to use faster, long, direct movements to find food which is further away (Bartumeus et al., 2005; Moorter et al., 2013; Venter et al., 2017). The need to travel further due to uncertain environments could be more important in sparse landscapes, i.e., areas in which vegetative patches are less numerous. A study by Moorter et al. (2013) found that moose inhabiting sparse and heterogeneous landscapes were more likely to travel further after a period of environmental change leading to reductions in resource availability.

In addition to environmental events, inter or intra-species competition can influence changes in movement behaviour (Barta and Giraldeau, 1998). For example, competition for high-value food often results in increased travel to alternative, or more distant food sources, which can increase travel distances and displacement. Displacement through competition is more likely when food sources are rare (Herfindal et al., 2019; Wignall et al., 2020); this probably often arises due to social conflict (Michelena et al., 2009).

All movements, travel paths and exploration, whether locally or across a landscape additively create an animal's home range. The home range represents a territory and use of space containing the resources critical to the animal (Senft et al., 1987). If the resource needs of an individual increase, the home range size can increase (Foley et al., 2008; Larter and Gates, 1990; Papageorgiou et al., 2021; Ullmann et al., 2018). For example, vulturine guineafowl increased their ranging distances after periods of drought to support their population (Papageorgiou et al., 2021). Thus, as guineafowl resources became more unreliable or uncertain, the home range size probably increased due to an extended exploration of the environment to meet individual needs and reduce competition with conspecifics.

The body of literature in the growing discipline of movement ecology often features field studies tracking movement in relation to environmental events; however, few models involve large herbivores in controlled settings. Using Merino sheep (*Ovis aries*) as a subject, the purpose of this experiment was to record how animals modify their behaviour after environmental change and determine specifically how the internal state of uncertainty impacts animal movements directly. I predicted that animals would travel faster and further during periods of uncertainty to increase the chances of finding food that is further away and to reduce conspecific competition. I expected that longer travel distances would also result in an increase in home range size. Additionally, I hypothesised that the daily displacement of the sheep would increase. If animals move longer distances and have larger home range sizes, it is conceivable that they do not return to the same locations at night where they started the day. This would lead to larger displacement measures. Furthermore, I expected to see more tortuous walking paths with more severe turn angles during periods when the sheep are sampling the environment to gain information.

The ability to respond appropriately to variable environments with uncertain resource distributions or locations can be advantageous for a species during environmental change. Unfortunately, our knowledge of animal movement behaviour in response to uncertainty due to variable environments is limited (Bartumeus et al., 2016). However, it is crucial to understand how individuals and ultimately, species can cope with the changing environments, for example, due to climate change or habitat loss (Gross, 2018). Furthermore, early detection of movement behaviours that indicate uncertainty may help us identify environmental stressors that could impact vulnerable wild animal populations and determine if animals can appropriately adjust their behaviour quickly enough to persist through those changes.

MATERIALS AND METHODS

Study Site

The study was conducted at Fowler's Gap Arid Zone Research Station, New South Wales, Australia (31°05′S, 141°43′E). The study area was a 6 x 1 kilometre paddock with a water trough located at one corner and is characterised as arid chenopod shrubland, with predominantly *Maireana* spp., Fowler's Gap, and the study paddock had been affected by severe drought over consecutive years, with little grass growing (Fig. 1).

Fig. 1 A group of sheep feeding at one of the food locations in the experiment (photo by S.T. Leu).

Animals

I observed fifty 2-year-old non-pregnant ewes in the experiment. Each individual was fitted with a global positioning system (GPS) collar weighing 700g (MobileAction GPS, i-gotU GT-120, and Core Electronics battery CE04381). All GPS collars were removed at the end of the project, and the sheep were released back into the paddock. The GPS collars recorded the location of each sheep every 15 seconds for 16 hours during daylight hours throughout the study, between 4:30 and 20:30 Australian Central Standard Time. The collars were synchronised to enable all sheep locations to be recorded simultaneously.

All procedures in this experiment were approved by the University of New South Wales Animal Care and Ethics Committee and Macquarie University Animal Ethics Committee.

GPS Data Processing

The data processing and analysis were done as part of this honours project, using R (v4.1.2; R Development Core Team, 2021). I used the data processing methods described in Leu et al. (2021). In short, first, I removed GPS locations if they were recorded with less than three satellites, fell outside the paddock boundaries, or exceeded the animal's maximum movement speed or turn angle during the 15-second interval. I used the function 'vmask' from the R package 'argosfilter' to process the data as described above. The filter uses two previous and two following locations to calculate and remove locations that would require speeds in excess of 5.34 kilometres per hour (Manning et al., 2014) and turn angles in excess of 120 degrees (Bjørneraas et al., 2010). The 15-second location recordings can vary by a few seconds among GPS units. To account for this, I interpolated the locations of all sheep such that they perfectly fit 15-second intervals. I used the function 'na.approx' from the R package 'zoo' to interpolate the data. The interpolation process assumes straight and constant movement, which has no to minimal effect given the short recording interval. The function can also fill in missing location data using the known locations before and after the gap. However, if more than two consecutive locations were missing, representing a gap of more than 30 seconds, I did not estimate those locations to avoid generating data that may deviate too greatly from the empirical location (Leu et al., 2021).

Experimental Design

Eight food locations within the study area were randomly selected but also met the following criteria: more than 200 metres from the fence line, at least 1500 metres from the water trough (located in the Northwest corner of the paddock), and at least 400 metres apart. Two bales of lucerne hay (approximately weighing twenty kilograms each) were placed at each of those eight locations (Fig 1). The sheep were released into the paddock near the water trough, where an extra two bales of lucerne had been placed. The data until the next morning was excluded from the analysis to allow the animals to adjust after being handled.

The experimental design (Fig 2) had four periods; each period consisted of three days. The lucerne bales were replenished twice, between the first and second periods and the third and fourth periods. Replenishment commenced whilst the animals were sighted at the water trough and not within view of the food patches.

The experiment also included an event (between periods 2 and 3) where all remaining food was collected whilst the animals were at the water trough. Eight new randomised locations were selected using the criteria listed above. The new location was at least 400 metres away from the previous site, and the new patches were once again stocked with two bales of lucerne. I excluded all days of replenishment or relocation of food patches from the analysis.

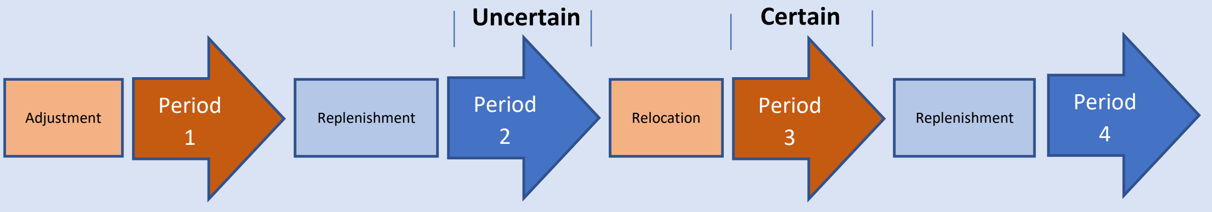

Fig. 2 Experimental design. Period 2 represents the 'uncertain' period, Period 3 represents the 'certain' period

Movement and Space Use Measures

I calculated the distances between all successive coordinate positions using the R package 'moveHMM', 'prepData' function. I used this information to measure the speed (distance travelled per 15 seconds), and the total distance travelled per day. I determined the net displacement by measuring the distance between the first and last observation recorded per day per individual using the R package 'geosphere', 'distGeo' function.

I split the data into 3-day temporal periods reflecting the study design. The first period allowed the animals to adjust to the new paddock and become familiar with the food locations. I compared the animal's behaviour during the second period with the third period (before and after the relocation of the food). I considered a patch to be discovered if a sheep had been within a 20-metre distance of the food location and used the R package 'geosphere', 'distGeo' function to calculate this. Using the number of patches discovered as a proxy for uncertainty, the third period reflected a time when sheep had greater environmental knowledge compared to the second period. This contrasted our initial expectations based on the experimental design and the relocation of the resources to new locations. However, the sheep were fast to discover those new locations and hence period 2 represented greater uncertainty and period 3 more certainty (Fig 2).

I built the linear mixed-effects models using the R Package' lme4' function 'lmer' to firstly perform a linear mixed-effects analysis of the relationship between the day within each period and the mean step length, total distance travelled, displacement, home range and turn angles (Example 1). And secondly, the relationship between patch discovery and the above dependent variables (Example 2). Satterthwaite's method was used for the t-tests. P-values for the fixed effects were obtained using Satterthwaite estimation of degrees of freedom, obtained from the 'lmerTest' R package. Visual inspection of residuals using the 'Performance' R package revealed that the data fulfilled the assumptions of homoscedasticity and normality.

Example 1: Linear mixed model for uncertain and certain periods

Dependent variable (e.g. Mean step length) ~ Independent variable 1 (Day) * Independent variable 2 (Period) + (Random group intercept (animal identifier))

Example 2: Linear mixed model for patch discovery

Dependent vaiable (eg. Mean step length) ~ Independent variable 1 (no. patches discovered per day) + Independent variable 2 (Period) + (Random group intercept (animal identifier))

RESULTS

Analysis of movement paths

The total dataset comprised of 2,916,901 GPS locations after processing. During periods of uncertainty, I found that mean step length was significantly lower than the period with greater uncertainty (3.335 metres per 15 seconds) when compared to the period with more certainty (4.703 metres per 15 seconds), (Fig. 3A, estimate = -1.6830, SE = 0.0930, t = -18.091, p = <0.001). Correspondingly, daily distance travelled was also lower; 12.751 kilometres per day travelled during the uncertain period, compared to 17.697 kilmometres travelled during the certain period (Fig. 3B, estimate = -5.8097, SE = 0.3583, t = -16.216, p = <0.001). The average net displacement for individuals in the uncertain period was also significantly lower at 0.988 kilometres, when compared to displacement in the certain period; 1.573 kilometres (Fig. 3C, estimate = -0.5092, SE = 0.1444, t = -3.526, p = <0.001). Uncertainty of resource locations also had a significant relationship with decreased use of space (home range size), ranging form 1.257 kilometres squared during the uncertain period to 2.621 km2 in the certain period. (Fig. 3D, estimate = -2.1150, SE = 0.1150, t = -18.396, p = <0.001). Additionally, there were higher measures of turn angles for individuals in the uncertain period 0.915 radians, when compared to sheep movement behaviour during the certain period: 0.756 radians (Fig. 3E, estimate = 0.1580, SE = 0.0128, t = 12.359, p = <0.001).

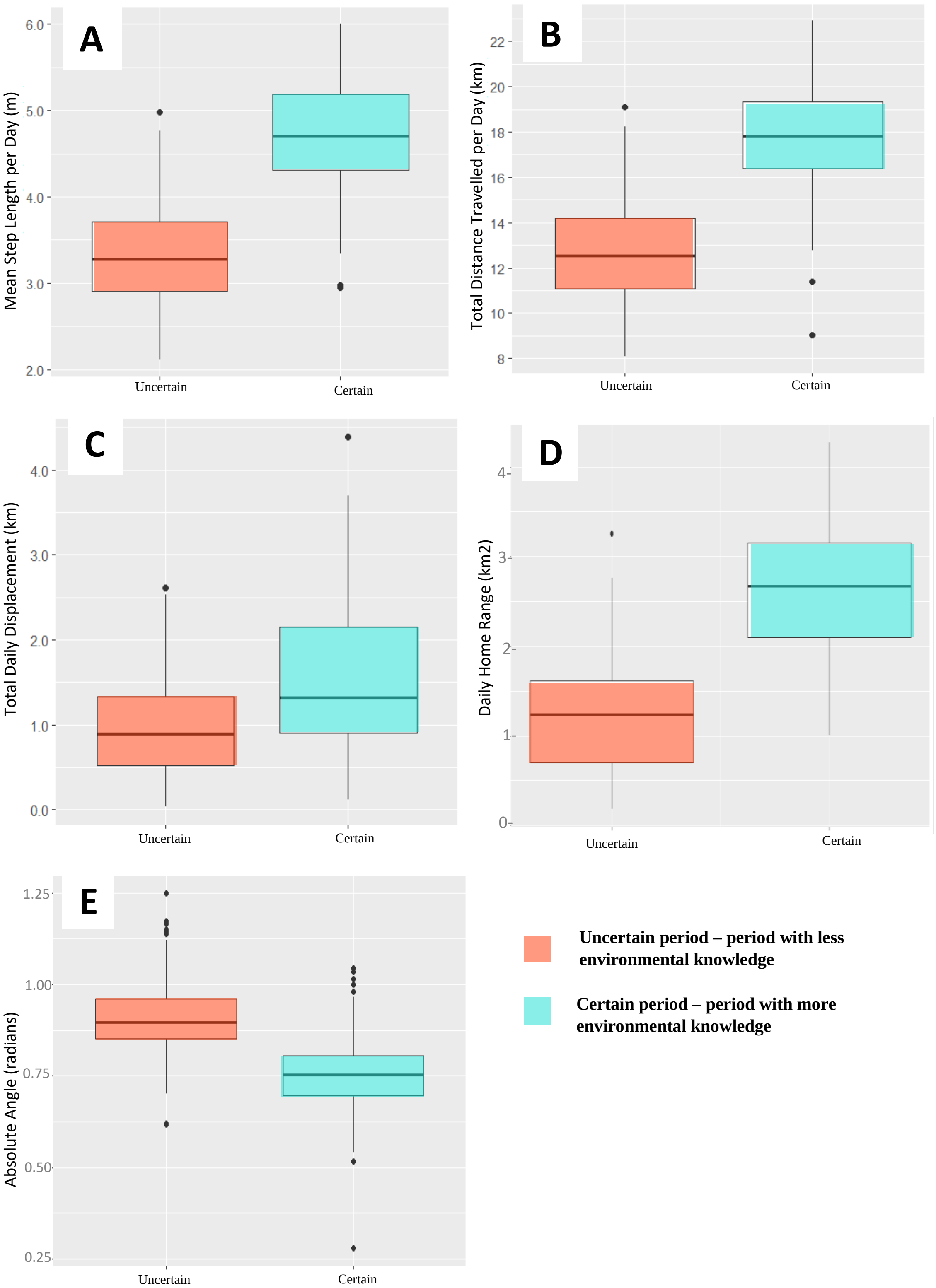

Fig. 3 Sheep movement characteristics differ in response to different levels of certainty. Two study periods were included in the analysis, each comprising of 3 days, classified as *uncertain* and *certain*. Figures show for each movement behaviour in the *uncertain* period: **A** lower mean step length (equivalent to speed in metres per 15 seconds), **B** shorter travel distances, **C** less daily displacement, **D** smaller mean home ranges **E** more turn angles

The number of patches discovered varied between the comparison periods. By the end of the 'uncertain' period (period 2), fewer patches had been found than within the 'certain' period (period 3), wherein more overall patches had been discovered. Looking into the effect of uncertainty more directly, I found that the movement behaviour corresponded with the number of patches encountered. Therefore, to analyse the effect of patch discovery on movement behaviour, I included all four periods (Table 1).

Table 1. Cumulative number of patches discovered throughout the study, out of 8 possible patch locations.

Period 1	Day 1:	**2** patches discovered
	Day 2:	**2** patches discovered
	Day 3:	**2** patches discovered
Period 2	Day 1:	**2** patches discovered
	Day 2:	**3** patches discovered
	Day 3:	**5** patches discovered
Period 3	Day 1:	**7** patches discovered
	Day 2:	**7** patches discovered
	Day 3:	**7** patches discovered
Period 4	Day 1:	**7** patches discovered
	Day 2:	**7** patches discovered
	Day 3:	**8** patches discovered

The mean speed and total distances travelled increased as the number of patches encountered increased (Fig 4A, Model summary presented in Supplementary Table 1; Fig 4B, Supplementary Table 2). Displacement varied depending on the number of patches found, generally increasing, except in the instance of the third patch being discovered, which corresponded with a decrease in displacement (Fig 4C, Supplementary Table 3). Home range size generally increased as the number of patches increased, except after patch 3 discovery, which saw a significant decrease in displacement (Fig 4D, Supplementary Table 4). Turn angles decreased as the number of patches discovered increased (Fig 4E, Supplementary Table 5).

Posthoc tests were used to determine whether our measures of movement behaviour and space use changed significantly with each additional patch discovered (Supplementary Table 6). Corresponding changes were generally observed. In some cases, although the estimate steadily changed, the change was too incremental to be statistically significant when only one further patch was encountered. However, the changes were always significant when the difference was greater than one patch (e.g., 5 patches versus 3 patches). There was one instance where the total daily displacement decreased significantly from 2 to 3 patches discovered but continued to increase after. It is possible that the discovery of the new patch was highly valued at this point (due to depletion of the other two well-used patches), and some sheep may have spent more time there, effectively reducing overall displacement.

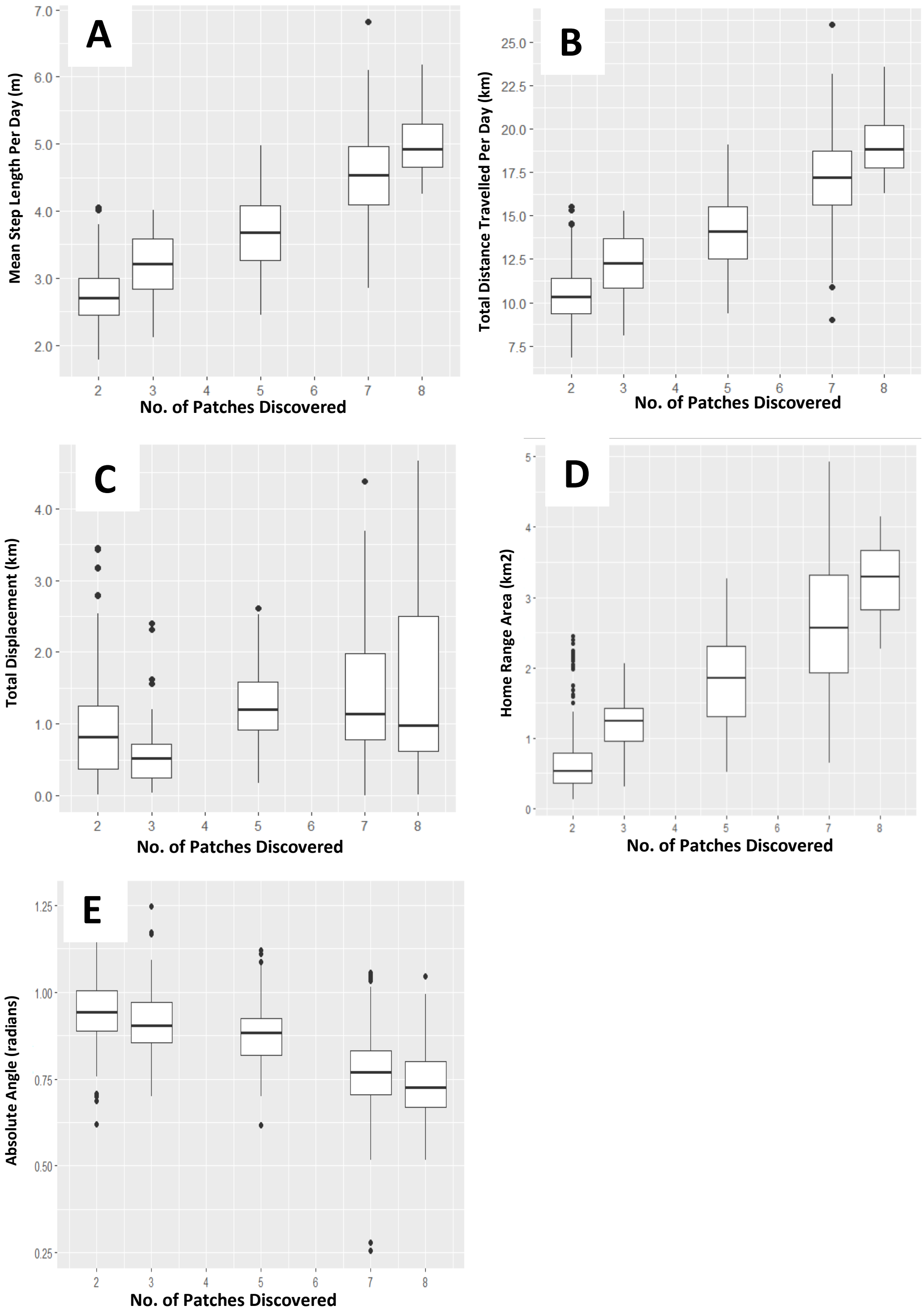

Fig. 4 Sheep movement characteristics differ in response to the number of food patches discovered. Eight resource locations were included in the analysis. Figures show that with lower numbers of patches discovered **A** the mean step length is smaller (step length = speed, here shown in metres per 15 seconds), **B** total daily distances travelled were lower, **C** varying significant differences in daily displacement, **D** smaller mean home range **E** higher severity of turn angles.

DISCUSSION

Bartumeus et al. (2016) discussed associations between different search strategies and how they relate to various stages of uncertainty across local environments and landscapes. The differences between these search strategies can be observed through movement behaviour. Initial explorative behaviours can be labelled as uncertainty, which could be described as investigative movements used by the animal to select the most efficient subsequent system of movements (Bartumeus et al., 2016; Bracis et al., 2015). Information gathering or exploration is a process of learning which results in changes to behaviour and foraging decisions as the individual gains experience (Krakauer and Rodríguez-Gironés, 1995).

In this study, I observed that the level of uncertainty about resource locations significantly affected individual movement and space use behaviours. This was demonstrated by carrying out two different tests: Comparing the 'certain' period to the 'uncertain' period and also examining the effects of the number of patches discovered. Contrary to my prediction, sheep travelled more slowly and shorter distances per day during periods of uncertainty. A potential explanation for this finding is that sheep spent more time in the local area of patches they initially discovered (Dumont and Petit, 1998). It is conceivable that during the latter part of the experiment, when more and more patches were discovered, and hence uncertainty decreased, the sheep continued to move between known food locations thereby travelling longer distances per day (Bracis et al., 2015).

As sheep moved between patches that had already been discovered, they travelled more quickly; potentially indicating that they anticipated the goal (Halsey, 2016). Venter et al. (2017) observed that ungulates moved with longer step lengths, i.e., faster speeds, towards non-visible patches, implying that some other environmental information, such as scent, may have driven the quicker movement rate. Therefore, sheep may move between patches already discovered, know the goal, and hence move more quickly. Finding a familiar type of resource uses different movement strategies compared to detecting an unpredictable resource, i.e., search characteristics are dependent on knowledge of resource type or distribution (Bartumeus et al., 2005; Sulikowski and Burke, 2011). During the more certain period, the sheep quickly found new resource locations. Therefore, it is likely that within the more certain period, the sheep had the experience that faster movements and longer foraging trips increased the likelihood of patch discovery. I found evidence that individuals also generally had less displacement (distance between rest areas from one day to the next) during periods of heightened environmental uncertainty.

I had predicted that sheep would travel further in the uncertain period in order to explore their habitat more widely while searching for resources. If home ranges are shared among conspecifics, increasing home range size can decrease competition for the resources within the original home range (Herfindal et al., 2019; Michelena et al., 2009; Riotte-Lambert et al., 2015). Increased home ranges have been documented in other species during dry periods or after drought (Foley et al., 2008; Papageorgiou et al., 2021). Contrary to my hypothesis, the study found that the sheep had a smaller overall use of space, resulting in a smaller home range when they had less environmental knowledge. Smaller observed home ranges, however, are consistent with the findings that travel distances and displacement were less. An explanation for this could be the decision-making processes of the sheep, which result in the highest reward. Two alternative strategies exist, 'win-stay and 'win-shift'. In the win-stay strategy, animals return to the patches where they previously found food that is consistently available, whereas in the win-shift strategy, animals avoid those patches. A 'win-stay' strategy was likely to be favoured until previously discovered resources began to diminish (Dumont and Petit, 1998). Depleted resources likely promoted a shift towards a 'win-shift' foraging strategy. Here known resource patches are left because the discovery of new patches is associated with high food rewards (Charnov, 1976). During this study, each new patch discovery would have been an incentive to explore more of the environment in the anticipation of finding a similar reward.

Furthermore, it was likely that the 'win-shift' strategy was favoured but combined partially with a 'win-stay' strategy due to an occurrence of resource replenishment within each period (Reed, 2018). Hence, it is likely that sheep rewarded by discovering new food locations would repeat that behaviour by leaving previously exploited patches to find new patches and also by revisiting previous patches from time to time. This explanation is consistent with my observations of faster movement speeds, increased distances travelled and increased displacement during more certain periods. Together, these behaviours support the conclusion that the sheep predominantly use a 'win-shift' strategy.

As expected, more severe turn angles were associated with the uncertain period, and the turn angles became less severe as the sheep gained environmental knowledge through patch discovery. Initial phases of uncertainty usually result in local area scans that aid the animal in deciding whether to stay in or leave a locality (Bartumeus et al., 2016). Severe reorientation is often the result of randomised movement when faced with extreme uncertainty within a locality (Bartumeus et al., 2005). These substantial directional changes can decrease as environmental experience is acquired and new movement behaviours are adopted to create a more informed, systematic and efficient area scan. Reduced turn angles are also consistent with moving between and revisiting known patches.

No apparent changes in movement behaviour were observed to be directly related to our relocation of food locations because they rapidly found the new locations.

My study shows how environmental uncertainty affects the foraging movement of individuals. Future research could investigate how the selection of search strategy correlates with various levels of environmental knowledge and how those strategies could be used as an identifier of the internal states that might be driving particular movement decisions in wild populations of ungulates. Further, animal movements can result from a wide range of internal factors such as sensory, memory, navigation and social interactions (Evans et al., 2016; Jones et al., 2017; Nathan et al., 2008). Hence, the extent of the influence of social interactions upon animal movement could be of interest, and future research would be beneficial to determine how these social interactions are impacted by uncertainty.

CONCLUSION

This study aimed to determine how uncertainty affects the movement and space use of sheep. I found that the movement behaviours during the uncertain period were consistent with a 'win-stay' search strategy, and as knowledge increased, a 'win-shift' strategy was adopted. During periods where sheep had less information on resource locations, they were observed to have slower speeds, travel shorter distances and were less displaced than during periods with more environmental knowledge. While sheep were experiencing uncertainty, they had a small home range. As knowledge was gathered about resource locations, the home range size increased correspondingly, and travel paths became straighter. This study provides insight into how a free-ranging ungulate behaves whilst experiencing uncertainty and demonstrates that it can adjust its movements and search strategy depending on the knowledge gained.

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Table 1. Mean step length (distance travelled during a fifteen second interval in metres) were recorded for fifty ewes over 12 days. As the number of patches discovered increased, there was also a significant increase in the average step length.

No. Patches	Effect	SE	DF	*t*-Value	*p*-Value
Intercept	2.754	0.052	99.85	53.430	<0.001
3	0.438	0.078	546.00	5.611	<0.001
5	0.940	0.078	546.00	12.046	<0.001
7	1.782	0.047	546.00	38.081	<0.001
8	2.260	0.078	546.00	28.976	<0.001

Table 2. Mean daily distance travelled (kilometres) were recorded for fifty ewes over 12 days. As the number of patches discovered increased, there was also a significant increase in the distance travelled.

No. Patches	Effect	SE	DF	*t*-Value	*p*-Value
Intercept	10.5354	0.1929	101.42	54.629	<0.001
3	1.6753	0.2946	546.00	5.686	<0.001
5	3.5799	0.2946	546.00	12.151	<0.001
7	6.6238	0.1768	546.00	37.471	<0.001
8	8.5985	0.2946	546.00	29.185	<0.001

Table 3. Mean daily displacement (kilometres) were recorded for fifty ewes over 12 days. Compared to the discovery of two patches, discoveries of 3,5,7 and 8 patches had a significant

relationship with the difference in average displacement observed, however discovery of patch 3 saw a decrease in the daily displacement.

No. Patches	Effect	SE	DF	*t*-Value	*p*-Value
Intercept	0.9350	0.0601	243.02	15.555	<0.001
3	-0.3412	0.1261	546.00	-2.705	<0.010
5	0.3375	0.1261	546.00	2.676	<0.010
7	0.4502	0.0757	546.00	5.949	<0.001
8	0.5383	0.1261	546.00	4.268	<0.001

Table 4. Mean home range area (km2) were recorded per number of patches discovered. As the number of patches discovered increased, the home range size also increased.

No. Patches	Effect	SE	DF	*t*-Value	*p*-Value
Intercept	0.6887	0.0472	595.00	14.598	<0.001
3	0.5099	0.1055	595.00	4.834	<0.001
5	1.1020	0.1055	595.00	10.446	<0.001
7	1.9217	0.0633	595.00	30.361	<0.001
8	2.5749	0.1055	595.00	21.408	<0.001

Table 5. Mean absolute turn angles per day (radians) were recorded for fifty ewes over 12 days. Compared to the discovery of two patches, discoveries of 5,7 and 8 patches had a significant relationship with the difference in average turn angles observed.

No. Patches	Effect	SE	DF	*t*-Value	*p*-Value
Intercept	0.9555	0.0129	60.09	73.888	<0.001
3	-0.0274	0.0111	546.00	-2.475	<0.050

5	-0.0706	0.0111	546.00	-6.386	<0.001
7	-0.1821	0.0066	546.00	-27.453	<0.001
8	-0.2170	0.0111	546.00	-19.627	<0.001

Table 6. Post hoc tests on patches discovered and dependent variables. Replicate 1 represents period 1 and 2 prior to relocation of resources, replicate 2 represents period 3 and 4 post relocation of resources. (Note: step length and distance measures are in kilometres, displacement is measured in metres, turn angle is in radians and home range is in square kilometres).

Step length

```
library(emmeans)
emmeans(m3step, pairwise ~ PatchsDisc)
NOTE: A nesting structure was detected in the fitted model:
    PatchsDisc %in% Replicate
$emmeans
 PatchsDisc Replicate  emmean       SE    df lower.CL upper.CL
 2          1         0.00275 5.15e-05  99.8  0.00265  0.00286
 3          1         0.00319 7.94e-05 375.6  0.00304  0.00335
 5          1         0.00369 7.94e-05 375.6  0.00354  0.00385
 7          2         0.00454 4.91e-05  83.1  0.00444  0.00463
 8          2         0.00501 7.94e-05 375.6  0.00486  0.00517


Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95


$contrasts
 contrast                                            estimate       SE  df t.ratio p.value
 PatchsDisc2 Replicate1 - PatchsDisc3 Replicate1 -0.000438 7.80e-05 546  -5.611  <.0001
 PatchsDisc2 Replicate1 - PatchsDisc5 Replicate1 -0.000940 7.80e-05 546 -12.046  <.0001
 PatchsDisc2 Replicate1 - PatchsDisc7 Replicate2 -0.001782 4.68e-05 546 -38.081  <.0001
 PatchsDisc2 Replicate1 - PatchsDisc8 Replicate2 -0.002260 7.80e-05 546 -28.976  <.0001
 PatchsDisc3 Replicate1 - PatchsDisc5 Replicate1 -0.000502 9.87e-05 546  -5.087  <.0001
 PatchsDisc3 Replicate1 - PatchsDisc7 Replicate2 -0.001345 7.64e-05 546 -17.593  <.0001
 PatchsDisc3 Replicate1 - PatchsDisc8 Replicate2 -0.001823 9.87e-05 546 -18.471  <.0001
 PatchsDisc5 Replicate1 - PatchsDisc7 Replicate2 -0.000843 7.64e-05 546 -11.026  <.0001
 PatchsDisc5 Replicate1 - PatchsDisc8 Replicate2 -0.001321 9.87e-05 546 -13.385  <.0001
 PatchsDisc7 Replicate2 - PatchsDisc8 Replicate2 -0.000478 7.64e-05 546  -6.254  <.0001


Degrees-of-freedom method: kenward-roger
P value adjustment: tukey method for comparing a family of 5
estimates
```

Distance

```
emmeans(m3dist, pairwise ~ PatchsDisc)
NOTE: A nesting structure was detected in the fitted model:
    PatchsDisc %in% Replicate
$emmeans
 PatchsDisc Replicate emmean    SE    df lower.CL upper.CL
 2          1           10.5 0.193 101.4     10.2     10.9
 3          1           12.2 0.299 382.9     11.6     12.8
 5          1           14.1 0.299 382.9     13.5     14.7
 7          2           17.2 0.184  84.1     16.8     17.5
 8          2           19.1 0.299 382.9     18.5     19.7


Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95


$contrasts
 contrast                                          estimate    SE  df t.ratio p.value
 PatchsDisc2 Replicate1 - PatchsDisc3 Replicate1    -1.68 0.295 546  -5.686  <.0001
 PatchsDisc2 Replicate1 - PatchsDisc5 Replicate1    -3.58 0.295 546 -12.151  <.0001
 PatchsDisc2 Replicate1 - PatchsDisc7 Replicate2    -6.62 0.177 546 -37.471  <.0001
 PatchsDisc2 Replicate1 - PatchsDisc8 Replicate2    -8.60 0.295 546 -29.185  <.0001
 PatchsDisc3 Replicate1 - PatchsDisc5 Replicate1    -1.90 0.373 546  -5.111  <.0001
 PatchsDisc3 Replicate1 - PatchsDisc7 Replicate2    -4.95 0.289 546 -17.143  <.0001
 PatchsDisc3 Replicate1 - PatchsDisc8 Replicate2    -6.92 0.373 546 -18.577  <.0001
 PatchsDisc5 Replicate1 - PatchsDisc7 Replicate2    -3.04 0.289 546 -10.545  <.0001
 PatchsDisc5 Replicate1 - PatchsDisc8 Replicate2    -5.02 0.373 546 -13.466  <.0001
 PatchsDisc7 Replicate2 - PatchsDisc8 Replicate2    -1.97 0.289 546  -6.841  <.0001


Degrees-of-freedom method: kenward-roger
P value adjustment: tukey method for comparing a family of 5
estimates
```

Displacement

```
emmeans(m3disp, pairwise ~ PatchsDisc)
NOTE: A nesting structure was detected in the fitted model:
    PatchsDisc %in% Replicate
$emmeans
 PatchsDisc Replicate emmean    SE  df lower.CL upper.CL
 2          1            935  60.1 243      817     1053
 3          1            594 114.7 587      369      819
 5          1           1273 114.7 587     1047     1498
 7          2           1385  54.6 179     1278     1493
 8          2           1473 114.7 587     1248     1699


Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95


$contrasts
 contrast                                          estimate    SE  df t.ratio p.value
 PatchsDisc2 Replicate1 - PatchsDisc3 Replicate1    341.2 126.1 546   2.705  0.0544
 PatchsDisc2 Replicate1 - PatchsDisc5 Replicate1   -337.5 126.1 546  -2.676  0.0588
 PatchsDisc2 Replicate1 - PatchsDisc7 Replicate2   -450.2  75.7 546  -5.949  <.0001
 PatchsDisc2 Replicate1 - PatchsDisc8 Replicate2   -538.3 126.1 546  -4.268  0.0002
 PatchsDisc3 Replicate1 - PatchsDisc5 Replicate1   -678.7 159.5 546  -4.255  0.0002
 PatchsDisc3 Replicate1 - PatchsDisc7 Replicate2   -791.3 123.6 546  -6.404  <.0001
 PatchsDisc3 Replicate1 - PatchsDisc8 Replicate2   -879.5 159.5 546  -5.513  <.0001
 PatchsDisc5 Replicate1 - PatchsDisc7 Replicate2   -112.7 123.6 546  -0.912  0.8923
 PatchsDisc5 Replicate1 - PatchsDisc8 Replicate2   -200.8 159.5 546  -1.259  0.7166
 PatchsDisc7 Replicate2 - PatchsDisc8 Replicate2    -88.1 123.6 546  -0.713  0.9534


Degrees-of-freedom method: kenward-roger
```

```
P value adjustment: tukey method for comparing a family of 5
estimates
```

Angles

```
emmeans(m3ang, pairwise ~ PatchsDisc)
NOTE: A nesting structure was detected in the fitted model:
    PatchsDisc %in% Replicate
$emmeans
 PatchsDisc Replicate emmean     SE    df lower.CL upper.CL
 2          1          0.956 0.0129  60.1    0.930    0.981
 3          1          0.928 0.0155 120.6    0.897    0.959
 5          1          0.885 0.0155 120.6    0.854    0.916
 7          2          0.773 0.0127  56.7    0.748    0.799
 8          2          0.739 0.0155 120.6    0.708    0.769


Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95


$contrasts
 contrast                                        estimate      SE  df t.ratio p.value
 PatchsDisc2 Replicate1 - PatchsDisc3 Replicate1   0.0274 0.01106 546   2.475  0.0979
 PatchsDisc2 Replicate1 - PatchsDisc5 Replicate1   0.0706 0.01106 546   6.386  <.0001
 PatchsDisc2 Replicate1 - PatchsDisc7 Replicate2   0.1821 0.00663 546  27.453  <.0001
 PatchsDisc2 Replicate1 - PatchsDisc8 Replicate2   0.2170 0.01106 546  19.627  <.0001
 PatchsDisc3 Replicate1 - PatchsDisc5 Replicate1   0.0432 0.01398 546   3.092  0.0178
 PatchsDisc3 Replicate1 - PatchsDisc7 Replicate2   0.1547 0.01083 546  14.286  <.0001
 PatchsDisc3 Replicate1 - PatchsDisc8 Replicate2   0.1896 0.01398 546  13.560  <.0001
 PatchsDisc5 Replicate1 - PatchsDisc7 Replicate2   0.1115 0.01083 546  10.294  <.0001
 PatchsDisc5 Replicate1 - PatchsDisc8 Replicate2   0.1464 0.01398 546  10.468  <.0001
 PatchsDisc7 Replicate2 - PatchsDisc8 Replicate2   0.0349 0.01083 546   3.221  0.0118


Degrees-of-freedom method: kenward-roger
P value adjustment: tukey method for comparing a family of 5
estimates
```

Home range

```
emmeans(mhr, pairwise ~ nopatches)
NOTE: A nesting structure was detected in the fitted model:
    nopatches %in% Replicate
$emmeans
 nopatches Replicate emmean     SE  df lower.CL upper.CL
 2         1          0.689 0.0472 325    0.596    0.781
 3         1          1.199 0.0944 595    1.013    1.384
 5         1          1.791 0.0944 595    1.605    1.976
 7         2          2.610 0.0422 240    2.527    2.693
 8         2          3.264 0.0944 595    3.078    3.449


Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95


$contrasts
 contrast                                      estimate     SE  df t.ratio p.value
 nopatches2 Replicate1 - nopatches3 Replicate1   -0.510 0.1055 546  -4.834  <.0001
 nopatches2 Replicate1 - nopatches5 Replicate1   -1.102 0.1055 546 -10.446  <.0001
 nopatches2 Replicate1 - nopatches7 Replicate2   -1.922 0.0633 546 -30.361  <.0001
 nopatches2 Replicate1 - nopatches8 Replicate2   -2.575 0.1055 546 -24.408  <.0001
 nopatches3 Replicate1 - nopatches5 Replicate1   -0.592 0.1334 546  -4.437  0.0001
 nopatches3 Replicate1 - nopatches7 Replicate2   -1.412 0.1034 546 -13.659  <.0001
 nopatches3 Replicate1 - nopatches8 Replicate2   -2.065 0.1334 546 -15.475  <.0001
 nopatches5 Replicate1 - nopatches7 Replicate2   -0.820 0.1034 546  -7.931  <.0001
```

```
 nopatches5 Replicate1 - nopatches8 Replicate2   -1.473 0.1334 546 -11.038  <.0001
 nopatches7 Replicate2 - nopatches8 Replicate2   -0.653 0.1034 546  -6.320  <.0001


Degrees-of-freedom method: kenward-roger
P value adjustment: tukey method for comparing a family of 5
estimates
```