

# **The role of personality on spatial behaviour in merino sheep (*Ovis aries*)**

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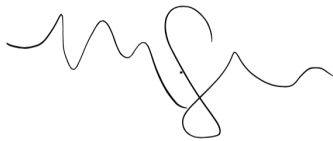
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## **DECLARATION**

I wish to acknowledge the following assistance in the research detailed in this report:

- My supervisors Dr. Stephan Leu and Professor Simon Griffith for their assistance with experimental design, data analysis, data collection, and reading drafts
- Sarah Reid-Andersen, Kati Quiring, Rebeca Violante, and Chi Wei for their help with data collection
- Garry Dowling and Mark for their help with the sheep, including mustering animals in and out of paddocks, providing food, and teaching me about sheep handling

All other research described in this report is my own original work.

A handwritten signature in black ink, appearing to read 'Molly Gilmour', with a stylized, cursive script.

MOLLY GILMOUR

24/10/2018

## **NOTE TO EXAMINERS**

This thesis is written in the form of a journal article from Animal Behaviour except where the journal formatting goes against the guidelines given for the Macquarie University thesis formatting requirements.

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This thesis would not have been completed without the huge help from my supervisors, Stephan Leu and Simon Griffith. The fieldwork would have been impossible without the support of Garry Dowling, station manager at Fowlers Gap, for all his help with the sheep and assistance in the field. Keith Leggett, Vicki Dowling, Mark, and other staff out at Fowlers Gap also made my time out there possible. My field assistants Sarah, Rebecca, and Chi and fellow field buddies Kati and Anika made my fieldwork an amazing time and I wouldn't have been able to do my work without them. Thanks go out to everyone in the Griffith Ecology lab for the support and cheering on I needed, and always helping out whenever I had questions. A special thank you to Theo for helping with statistics, reading drafts, and providing immeasurable emotional support when I needed it. And to Ash, Levin, Stacie, Ali, Cassie, Ko-Huan, Callum, and Paloma for also listening when I needed it. Huge thanks are also owed to my family, especially my Mum, for always encouraging and supporting me. None of this would be possible without them.

## **The role of personality in spatial behaviour of merino sheep (*Ovis aries*)**

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## HIGHLIGHTS

- Studies of animal personality that evaluate traits in controlled settings and assess behaviours of interest in the wild are uncommon
- We use high-resolution measures of animal space use to evaluate fine-detail spatial behaviours in merino sheep (*Ovis aries*)
- We found no relationship between spatial behaviours and personality traits in sheep

## ABSTRACT

Animal personality research has yielded personality-dependent spatial behaviours in many species. However, much of this research is focused on dispersal and foraging patterns. This ignores many other aspects of animal spatial behaviour, such as movement patterns, that occur on a daily basis. Our research investigates travel distances and patterns of paddock exploration in merino sheep to determine if they are influenced by personality traits. We combined assays of two traits, boldness and exploration, quantified in captivity, with high resolution GPS data of free-ranging sheep over three months. We found evidence for boldness and exploration tendency as personality traits, but did not find inter-individual repeatability in distance travelled per day or time taken to explore 3km<sup>2</sup>. Consequently, we found no personality-dependent space use in merino ewes. This expands our understanding of what influences space use in gregarious species, like sheep, and suggest a stronger role of external environment on movement rather than personality.

*Keywords: animal behaviour, animal personality, space use, animal movement, home range*

## INTRODUCTION

The field of animal personality has grown rapidly in the last decade as scientists have become increasingly aware of the adaptive value of consistent inter-individual behavioural differences. Animal personality, also termed behavioural type or temperament in some studies, can potentially explain individual specialization in many space use behaviours (Spiegel, et al., 2017) . Personality has been shown to influence foraging and dispersal in many species, and there is increasing evidence that home ranges and movement distance are personality-dependent (Harrison et al., 2015; Leclerc et al., 2016; Toscano, et al., 2016). The use of space, which can influence habitat selection and choice of foraging patches, affects an animal's access to food, shelter, mates, and inter-individual interactions (e.g. Andreassen & Ims, 1998; Munday, 2001; Reynolds et al., 2012; Street et al., 2016). These interactions can encompass encounters between members of the same or different species, spanning affiliative behaviours within populations and territory defence between individuals, to predator-prey interactions. Thus space use has direct implications on an individual's productivity and fitness. Studying inter-individual variation in spatial behaviours is of crucial importance in the field of animal ecology as they may provide an avenue for species to respond to changing environments.

### *Animal personality*

Animal personality traits have been identified across many taxa, including humans and other mammals, insects, reptiles, birds, and amphibians (Bell, et al., 2009; Dall & Griffith, 2014; Dingemanse & Réale, 2005; Stamps & Groothuis, 2010). The field of animal behaviour has often focused on testing the presence of the main traits identified in human psychology in non-human primates and, more recently, other species. Boldness-shyness was one of the first personality traits identified in non-human animals (Sloan Wilson, et al., 1994) and has since been found in a large range of other species, along with exploration tendency, activity, aggressiveness, and sociability . Personality traits are commonly measured on a gradient scale, e.g. the boldness-shyness axis. Studies on personality have revealed highly repeatable personality traits not only in merino sheep (Brown et al., 2016; Dwyer & Lawrence, 2000; Hauschildt & Gerken, 2015; Michelena, Sibbald, et al., 2009; Sibbald, et al., 2009), but other livestock animals (Cafe et al., 2011; Curley, et al., 2006; Müller & von Keyserlingk, 2006; Petherick, et al., 2009). This matches evidence in wildlife showing consistent individual variation in personality traits (Dingemanse &

Réale, 2005; Stamps & Groothuis, 2010). An issue in animal personality studies is that scientists can a) use different tests to describe the same trait between studies, or b) use the same, or similar, test to describe different traits. Often two different measures for the “same” personality trait are not always highly correlated - suggesting that they are, in fact, measuring different behaviours (Carter, et al., 2012). Therefore it is important to design tests of personality carefully and be cautious about over-interpretation of traits without validating what they are measuring. When investigating whether certain behaviours, for instance home range size, are personality dependent, recent literature has highlighted the importance of identifying and quantifying personality types that are independent of the behaviour of interest (Spiegel et al., 2017). This may be achieved by conducting personality tests under controlled conditions. Spiegel et al (2017) argue that many personality measures, e.g. exploration, activity, flight initiation distance, inherently involve movement. When studying spatial behaviour it can be difficult to untangle movement patterns recorded during the study and the type of movement measured as a personality trait. Thus, it is important to assure that measured traits are independent of each other. Doing this ensures measures of personality and measures of movement or space use behaviour are not influenced by an additional trait, e.g. activity, that may influence behaviours concurrently (Spiegel et al., 2017).

### *Personality-dependent behaviours*

To understand why and how evolution favours the maintenance of consistent individual differences, studies have investigated the relationship between personality and life history traits in a broad range of animal taxa (Biro & Stamps, 2008). Traits such as boldness, aggressiveness, and activity have been shown to strongly influence individual productivity in various species (Biro & Stamps, 2008). Research in chacma baboons (*Papio ursinus*) has found that the position on the boldness-shyness axis conditioned an individual's foraging strategy when presented with unreliable patch information (Carter, et al., 2013). Similarly, foraging decisions in birds (e.g. barnacle geese (*Branta leucopsis*), great tits) (*Parus major*) are also affected by personality traits, with position on the bold-shy axis reflecting either scrounger or producer strategies (Kурvers, et al., 2010; van Overveld & Matthysen, 2010), and their spatial position in group foraging situations (Aplin, et al, 2014). The volume of food, as well as rate of food intake, has been linked to personality traits in animals including roe deer (*Capreolus capreolus*) and blue tits (*Cyanistes*

*caeruleus*) (Bergvall, et al., 2011; Serrano-Davies, et al., 2017). Foraging success in sticklebacks (*Gasterosteidae*) has been shown to be strongly correlated with position along the boldness-shyness axis, where bolder individuals were more likely to outcompete their conspecifics for access to resources (Jolles, et al., 2016; Ward, et al., 2004) and eat more food overall regardless of body size (Jolles et al., 2016). Additionally, individuals who were willing to take more risks, identified during tests of boldness, also had greater foraging success in larger groups (Ioannou & Dall, 2016). Similarly in schooling fish, a sociability-exploratory behavioural type was linked to greater foraging success for both individuals and the group (Jolles, et al., 2017). The composition of a group can also affect the foraging success of all individuals. In guppies (*Poecilia reticulata*), shoals consisting of a mix of bold and shy individuals had greater foraging success than non-heterogonous groups (Dyer, et al., 2009). Fast-exploring blue tits (*C. caeruleus*) were also seen to occupy different habitats to slow-explorers, leading researchers to wonder if the relationship between habitat selection, food intake, and personality was causative (and if so, in what direction) or the result of traits being acted upon by the same selective pressure (Bergvall et al., 2011). The differential use of habitats by different personality types is also seen in squirrels (*Tamiascurus hudsonicus*) (Boon,e et al., 2008) and chipmunks (*Tamias sibiricus*) (Boyer, et al., 2010), where bold squirrels occupy a larger number of habitats than shy ones. Segregation in habitat by personality type is also seen in sea anemones (*Condylactis gigantea*) (Hensley, et al., 2012) and bluebirds (*Sialia mexicana*) (Duckworth, 2006).

Different habitats may be favoured by different personality traits, resulting from several factors, or combinations of such factors. Social interactions, mediated by personality type, can lead to different spatial patterns of individuals within a group or environment. There is evidence for positive and negative personality assortment across species. This may result from finer-scale social structuring among personality traits. In sticklebacks (*Gasterosteus aculeatus*), bold individuals have less social interactions, but among more conspecifics, than their shyer counterparts (Pike, et al., 2008). Conversely, in guppies (*P. reticulata*), bold fish had less social connections and their connections were weaker than those of shy individuals (Croft et al., 2009). Less social guppies were also more likely to become leaders as a result of their tendency to be positioned at the front or edges of a group (Jolles et al., 2017). Consistent individual differences in willingness to associate with conspecifics, measured by sociability, have been demonstrated in

lizards (Cote & Clobert, 2007). Baboons (*Papio hamadryas*) also show sociability personality traits, affecting the numbers of bonds females form with conspecifics (Seyfarth, et al., 2014). (Seyfarth, et al., 2014). Similarly in great tits, personality type influences the temporal stability of an individual's social connections (Aplin, et al, 2013). Personality traits can also influence dominance hierarchies (Colléter & Brown, 2011; David, Auclair, & Cézilly, 2011; Fox, et al., 2009), group size (Michelena et al., 2009), leadership patterns (Harcourt, et al., and even an individual's tendency to use social information (Kurvers, et al., 2010). Therefore personality traits may be more beneficial in different habitats due to personality-mediated interactions.

Habitat selection may also occur due to the behaviours the habitats themselves allow – for example, risk-averse or shy individuals may prefer habitats with more shelter (e.g. Brown, et al., 2005; Wilson & McLaughlin, 2007). Differences in habitat choice may also be driven, in part, by other behaviours that can also be driven by personality. For example, personality-dependent dispersal may influence the types of habitat/s an individual is present in. Personality-dependent dispersal is found across many species (for a review see: Cote, et al., 2010), including great tits (*Parus major*) (but only certain measures of dispersal) (Quinn, et al., 2011), mosquitofish (*Gambusia affinis*) (Cote, et al., 2010), and mice (Krackow, 2003). Boldness and dispersal are linked in the Trinidad killifish (*Rivulus hartii*), where bolder individuals travel further distances (Fraser, et al., 2001). More often, however, dispersal tendency and distance of dispersal has been linked to exploration measured in captive assays (Dingemanse, et al., 2003).

Personality traits that influence dispersal can also affect an individual's settlement into a population as well. For example, aggression can both enhance (Aragón, et al., 2006; Duckworth, 2008; Duckworth & Badyaev, 2007) or decrease (Aragón et al., 2006; Griesser, et al., 2008) an individual's chances of successful integration into a new group. An individual's ability to enter into a population and form connections with other individuals may have implications for its mating success, proportion of antagonistic interactions, or predation risk, which can affect the fitness and survival of individuals (Bowler & Benton, 2005). This may explain why personality traits appear adaptive in some situations, but not others.

### *Personality and life history*

It has been hypothesized that all individuals exhibit a “pace of life” that explains variation in behaviours across a lifetime (Réale et al., 2010). Pace of life syndromes (POLS) state that individuals will perform different behaviours depending on their level of investment in reproduction or survival (e.g. “live fast die young”) (Réale et al., 2010). The POLS hypothesis predicts the maintenance of personality traits among individuals due to trade-offs between risk-taking, survival, and reproductive success (Réale et al., 2010). Many species exhibit inter-individual differences in reproductive fitness, survival, and general life history. Consistent individual differences in growth rates, metabolism, and food consumption have been observed across species. For some animals the rates of acquisition and use of resources, as well as changes in body size and body weight, remain consistent - or within a consistent range - over time. This suggests they may be constrained by internal mechanisms that govern their metabolism and potentially their behaviour (Biro & Stamps, 2008). Indeed, there is growing evidence for personality being part of pace of life syndromes (Hall et al., 2015).

Personality-linked POLS may be explained by state-behaviour feedbacks (Sih et al., 2015). For example, personality traits may mediate an individual's willingness to sample new foraging patches (Kурvers, et al., 2010). This behaviour may be positively or negatively reinforced, where either only individuals in good condition are able to take the risk of incorrect sampling when searching for food (positive reinforcement) or individuals in bad condition are forced to sample for food in order to gain some energy (Sih et al., 2015). Given the different intrinsic and extrinsic selection pressures on different species, and even populations, it is likely that state-behaviour feedbacks on personality vary between groups. This may be why we see many disparate results between studies, or even different personality-survival relationships within populations under different environmental conditions (Dingemanse, et al., 2004). Thus, consistent inter-individual differences in behaviour can be reinforced by environmental conditions as well as an individual's motivations for survival and reproductive success.

### *Movement and space use*

Environmental conditions affect animal space use and movement behaviour through biotic and abiotic influences. As individuals have different needs, this creates variation in spatial behaviours within species and populations as well as between them. While this variation can be partially explained by the adaptive benefits of switching strategies to maximize resource use, it may also possibly be accounted for by natural variation present in a population. For example, individual foraging strategies have been classified into two categories: “active searchers” or “sit and wait” foragers (Huey & Pianka, 1981). These two descriptors vary greatly in the amount of movement involved: “active searchers” foragers move relatively frequently to find food patches (e.g. any sort of grazing animal or a predator that chases its prey), while “sit and wait” foraging requires little movement and instead relies on food arriving to the organism (such as spiders sitting in a web) (Huey & Pianka, 1981). However, species have been seen to switch between strategies (Davies, 1977; Garthe, et al., 2007; McLaughlin & Montgomerie, 1989), indicating variation at the individual level. This variation in foraging strategies is likely the result of individuals within a population presenting different requirements for resource use and specialising in dietary niche within a larger group (Bolnick & Doebeli, 2003; Van Valen, 1965). While external influences of condition-dependent foraging have been studied on a species-wide scale, it is only in the past decade that individual specialisation in foraging behaviour has been assessed (Araújo, et al., 2011; Bolnick & Doebeli, 2003).

Environments can also influence dispersal patterns, and thereby affect the structure of a population (Namba, 1980). Dispersal patterns are often not random and individuals move within fragmented landscapes with direction and purpose rather than in random directions (Conradt, et al., 2003). This is likely the result of a combination of trade-offs between costs of searching, such as mortality and energy expenditure, and the ability of an individual to perceive its environment and the resources within it (Zollner & Lima, 1999). While this suggests different dispersal strategies are more beneficial under different landscapes conditions for organisms as a whole (Zollner & Lima, 1999), individuals respond to environments differently depending on the costs and benefits to their own fitness, and thus dispersal tendency often differs between individuals

(Baguette, et al., 2013). Evidence for inter-individual differences in dispersal has been found in many species, including hormonal differences in winged insects (Zera & Denno, 1997), body condition in flamingos (*Phoenicopterus ruber roseus*) (Barbraud, et al., 2003), and behavioural type in passerine birds (Duckworth & Badyaev, 2007) and lizards (Cote & Clobert, 2007).

The characteristics of home ranges also vary between individuals in many species. Variations have been observed between sexes (Aronsson et al., 2016; Viana et al., 2018), and are influenced by conspecific densities (Aronsson et al., 2016), temperatures (Reed, 2018), and resource availabilities (Beauchamp, et al., 2018; Saïd et al., 2009). In red foxes (*Vulpes vulpes*), landscape characteristics and sex accounted for 50% of the variation in home range sizes (Walton, et al., 2017). Such variation has been linked to endurance capacity (Singleton & Garland, 2018), body size, and reproductive state (Machado, et al., 2017) across several species. A study on roe deer (*Capreolus capreolus*) found that females had distinctly different home ranges sizes, and that home range sizes were altered dependent on the patchiness and quality of resources within an individual's home range, i.e. females increased their home range size when resources were in lower abundance (Saïd et al., 2009). This effect may be influenced by group behaviour or structure, however, as female roe deer are usually only found in small, loosely connected groups (Pays, et al., 2007). For more gregarious species, trade-offs between individual behaviour and group cohesion may influence individual variation in spatial behaviours.

The idea of dietary niche specialization among individuals (van Valen, 1965), can be extended to other behaviours as well, especially those that influence foraging behaviour. Theory predicts that small individual-level interactions will affect the overall group behaviour (Couzin, et al., 2002). The partitioning of individuals into behavioural niches within a group may be influenced by factors including individual physiology and reproductive strategies or status (DeWitt, et al., 1998). Individual variation in movement and spatial behaviour are likely to be affected by an individual's energetic requirements and energy expenditure alongside its reactivity to perceived predation risk or social density. Under the POLS hypothesis we might be able to see inter-individual differences in behaviour correlate with personality traits such as boldness, exploration, or activity. Some research has found relationships between personality traits and



spatial behaviours (Cote & Clobert, 2007; Cote et al., 2010; Harrison et al., 2015; Michelena et al., 2009; Saïd et al., 2009; Spiegel et al., 2017; Walton et al., 2017).

However, with an increasing emphasis on research conducted in wild settings, many studies measure both personality and behaviours of interest in the same environments (Spiegel et al., 2017). Although studies have investigated the relationship between personality traits and subsets of behaviours related to movement ecology, such as dispersal, foraging, and space use, much of this research measures both personality traits and traits of interest in the same environment. For example, activity assesses the amount of movement of an individual; exploration describes how willing an individual is to move within an unfamiliar environment; and boldness looks at how quickly individuals will move when faced with a threat. Therefore it is not surprising to find that these traits correlate with measures of movement in some species. The confounding effect of movement on many animal personality traits makes it difficult to disentangle the relationship between inter-individual behavioural consistency and movement itself. Further research is needed to test movement-independent personality traits against inter-individual variation in movement characteristics in order to untangle the relationship between the two. Manipulative experiments in personality-dependent spatial behaviour research are even less common (but see: Jolles et al., 2016), but are an important step to understand the complex relationship between inter-individual movement variation, personality traits, and the role of environmental heterogeneity.

Personality-dependent movement is particularly interesting for social species, especially highly gregarious animals, that make trade-offs between individual needs with demands of the group and individuals might partition into behaviours. Our research aims to understand the factors influencing individual short-term movement patterns in a highly gregarious mammal, the merino sheep (*Ovis aries*). Sheep (*O. aries*) are a highly gregarious mammal found across the world. Wild sheep inhabit both mountainous and desert habitats (Berger, 2009), highlighting their adaptability. Genetic studies indicate that sheep have been domesticated independently in both Asia and Europe (Hiendleder et al., 2001). This ability to adapt to a range of climates may have played a part in their commercial success, now prevalent, as livestock (*O. aries*), in many different

regions of the globe. Merino sheep are commonly kept as livestock in Australia and are found across the country's climates. In the arid zone, sheep are stocked at low densities to account for the low and variable resources available compared to more fertile areas of the country. Used for wool, meat, and occasionally dairy, sheep are of high economic importance in Australia (Meat and Livestock Australia, 2017). Sheep meat alone contributed \$5.23 billion to Australia's economy in 2017 (Sheep Producers Australia, 2017). Most research in sheep has focused on genetics, breeding, and maternal behaviour (Dwyer & Lawrence, 2000; Hiendleder et al., 2001; Maddox et al., 2001; Maniatis & Pollott, 2003; Purchas et al., 1991), but in recent years attention is being paid to individual characteristics like animal personality. Boldness-shyness and sociability have been identified as personality traits in sheep, with a focus on identifying how these traits affect collective behaviour (Hauschildt & Gerken, 2015; Michelena et al., 2010; Michelena et al., 2009; Sibbald et al., 2009). Behavioural synchronisation in groups is greater when individuals in the group are more gregarious, a trait that remains consistent over time (Hauschildt & Gerken, 2015). Personality traits also affect social foraging and spatial distribution of sheep, with shy individuals forming closer groups, have larger group sizes, and are less likely to split from a group than bold sheep (Michelena et al., 2010, 2009). Additionally, shy sheep are more likely to stop foraging when disturbed and move away from humans (Sibbald et al., 2009). Some research even quantifies maternal behaviour as a personality trait, but only to identify individuals and genes for increased breeding success (Brown et al., 2016; Dwyer & Lawrence, 2000). Other research quantifying personality in domestic species, such as cattle, only link these traits to weight, productivity, and handling temperament, to improve meat quality and housing conditions (Benhajali et al., 2010; Cafe et al., 2011; Curley et al., 2006; Müller & von Keyserlingk, 2006; Petherick et al., 2009). Domestic animals provide a good system with which to study animal behaviour as they can be easily manipulated and study in controlled environments. Although many aspects of sheep life history are chosen by producers, such as breeding pairs, group size, and the selection of certain physical traits like body size and wool production, inter-individual differences are still found in many behaviours. Sheep are an ideal system in which to study the adaptive benefit of personality traits, as they are a highly gregarious species that must maintain high social group cohesion despite not always actively selecting the group into which they are placed. Thus, unable to form groups naturally by age, experience, or body size, for example, the presence of varied personalities within groups may allow individuals to maximize productivity while maintaining high social cohesion. So although the existence of personality traits in

domestic animals is clear, there is little research linking these with individual behaviours relevant to their general ecology.

For our study we aimed to investigate the role of personality traits on individual-level spatial behaviours in merino sheep. We quantified two commonly studied personality traits, boldness and exploration, in controlled environments independent of free-ranging behaviour. Using GPS loggers, we tracked individuals in two different habitat complexities and related this to independent-assayed personality traits. We predicted that i) movement behaviour would be a repeatable trait in sheep, with consistent between-individual differences, and as such: ii) bolder and more exploratory individuals would explore their environment faster than less bold or exploratory individuals, and iii) in the same individuals would be faster to explore an open environment than a more heterogeneous environment.

## METHODS

### *Study area and species*

This research was conducted at Fowlers Gap Research Station (31.0872° S, 141.7052° E) in north-western New South Wales in part of Australia's semi-arid zone. Approximately 2000 sheep are run at Fowlers Gap, which covers 39000 hectares in NSW rangelands. The property has existed as a research station since 1966. Above-ground natural water sources are scarce, with the nearest permanent water located in the Darling River, so livestock are provided dams or troughs with constant water from which to drink. The area is subject to patchy and highly localised rainfall, receiving a mean 255.26mm per year (date from 2004 to 2017, Bureau of Meteorology, n.d.). In the year preceding this study, 2017, Fowlers Gap received only 84.4mm of rain. Between years rainfall at Fowlers Gap is highly variable, with the research station experiencing a peak of 526.2mm of rain in 2011, but it's lowest rainfall in 2017. However, rainfall varies even within Fowlers Gap itself – different tanks located around the station have average rainfall ranging from 170.1mm – 243.1mm (Acworth et al, 2016). Such patchy rainfall results in uneven resource distribution, with the dominant vegetation at Fowlers Gap consisting of chenopod and acacia shrublands.

### *Behaviour in yards – personality assessment*

We investigated two commonly described personality traits, boldness and exploration tendency, in this study. 95 merino ewes, without lambs, born in 2016 were haphazardly split into two groups (Group 1, n = 49 and Group 2, n = 46). During the course of the experiment one sheep died and 3 were no longer present in the study group at the end of the experiment. These sheep were assumed to escape the experimental paddock into an adjacent paddock, or to have died and not been found in the paddock. These sheep were not included in the final analysis.

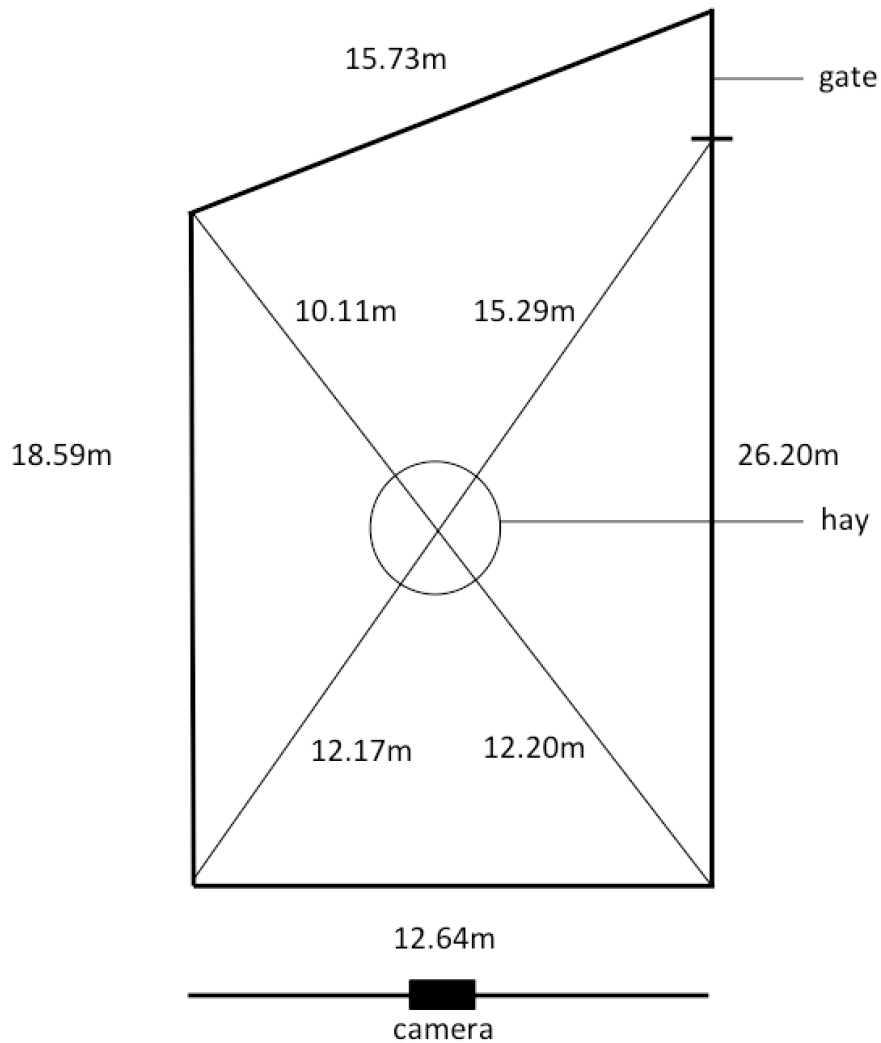
Sheep were kept in holding pens for the duration of the experiment. All sheep were kept on the same feeding schedule of hay during their time in the yards, described below for each experiment. Groups were kept separate from each other. Animals were tested a total of four times across two sessions for each of the two personality types. Tests were conducted in two sessions, 98 days apart in March and repeated again in June 2018. Sheep were tested twice per session, 5 days apart for all tests except for FID for group 2, which was tested 4 days apart due to weather conditions.

### *Measuring flight initiation distance as a proxy for boldness*

We used FID as a measure of boldness. FID is a common measure of boldness in many animal species (e.g. Carter et al., 2012; Godin & Dugatkin, 1996; Petelle et al., 2013; Seltsmann et al., 2012). FID is used to score how close an observer can approach an individual before it ‘flees’. ‘Fleeing’ is defined per species so as to be relevant to its ecology. For our study, an animal was considered to be fleeing when it took two steps away from its original location and was no longer eating. Many factors have been shown to influence FID, and we controlled for them by testing animals in the yards under controlled conditions. Factors including group size (Stankowich, 2008), social conditions (Cooper, 2009), weather (Blumstein & Daniel, 2003), body condition (Seltsmann et al., 2012), observer starting distance (Blumstein, 2003), and habituation (Stankowitch, 2008) have all been shown to influence FID. Sheep had been handled prior to the first tests in each session, but this did not appear to affect habituation of the sheep to researchers.

Animals were then left undisturbed for 3 days before testing began. All sheep were fed two bales of hay per day while being tested for FID.

Tests were conducted in pens (approximately 287.36m<sup>2</sup>, figure 1). The testing arena was an open-air holding pen with a pile of hay placed in the center (figure 1). This was to ensure consistency of location of sheep when beginning approach and that all individuals were performing a similar behaviour (eating at hay) for all FID measures. The gate at the southern end of the pen was covered by shade cloth to hide observers from focal sheep. Each assay was filmed from a birds-eye-view from the northern end of the test arena from a video camera (GoPro Hero 5) was attached to a pole at approximately 4m high.

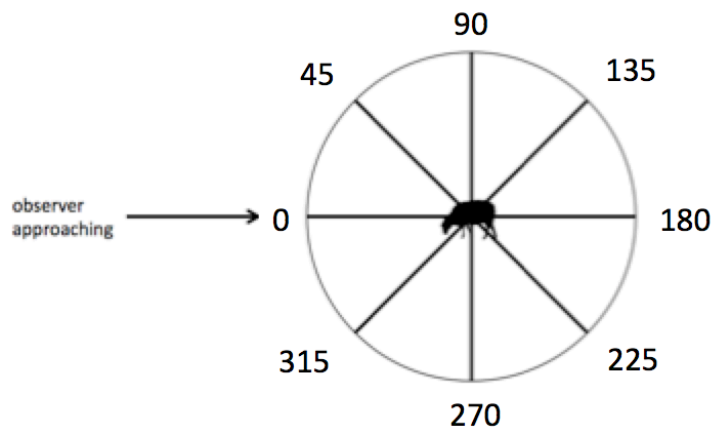


*Figure 1: Experimental set-up for flight initiation distance (FID) tests. Sheep entered into the arena through the gate in the top right. Observers were stationed behind the gate, which was covered by shade cloth to avoid sheep seeing observers during the test.*

Groups were tested separately. Individuals were selected haphazardly from the tested group and sent into the test arena. The tested group was held inside a closed shed and the other group was moved to a yard out of sight of the testing arena. Hence, no other sheep was visible from the testing arena. This ensured the focal individual was not visually attracted to conspecifics, important for testing FID in gregarious animals, and to control perceived group size (single individuals). Observers waited behind the covered gate, watching the arena through video link to determine when the sheep was in the correct position at the bale of hay. After the individual was eating at the hay for one minute, with its head down, the observer (MEG) entered the arena and

approached at a constant pace (approx. 1m/s) (FID can be affected by approach speed: Cooper, 2006). The same observer conducted all tests and wore neutral clothing for all tests. Some individuals ate at hay but left before one minute had elapsed. When this happened, observer waited until the animal approached the hay again and entered as soon as its head was facing downwards regardless of time spent at hay (26/352 tests). Some individuals never ate at hay, and hence had fewer data points in the analysis. From 378 total tests, 26 were not recorded at the hay (26 individuals).

The observer approached the focal individual and recorded awareness- and flight initiation distances. We defined awareness distance as the distance at which the animal raised its head and observed the approaching observer. Flight initiation distance was defined as the point at which an individual 'fled' from approaching observer. Awareness distance and FID were marked by quietly dropping a plastic cap during the test. Distances between the marker and the location of the sheep at the hay, before fleeing, were measured after the test was complete using a 50m tape measure. As the orientation of the focal animal to the observer differed between tests, we also recorded the 'angle of approach' during a test. Angle of approach, determined visually, was scored in 45-degree segments based on position to observer during approach (figure 2). For example, if observer approached a sheep head-on this was an angle of 0 degrees.



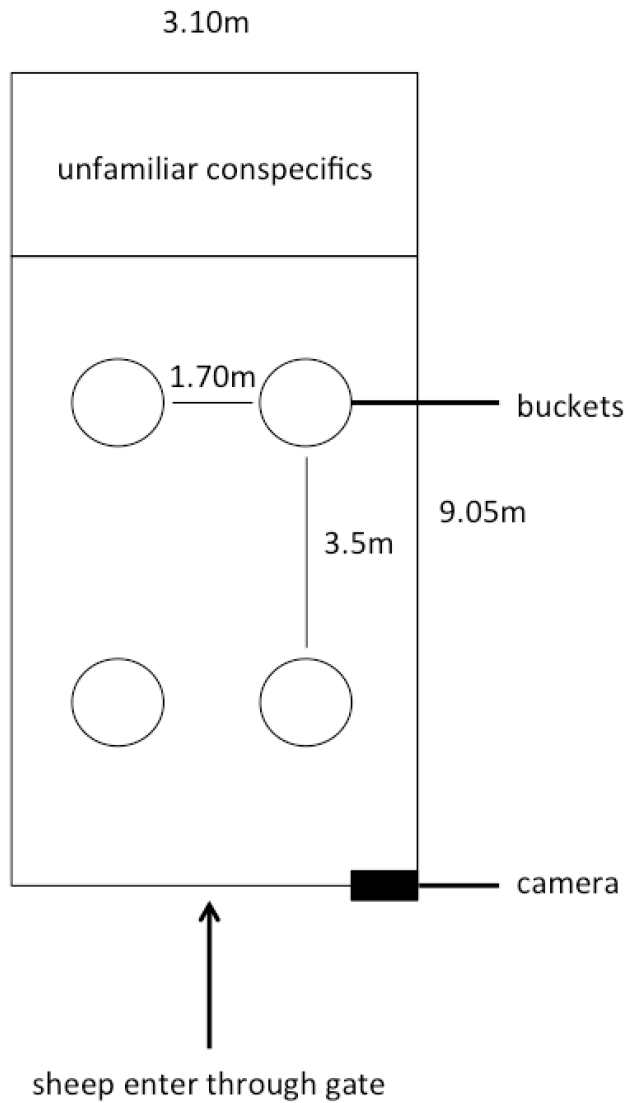
*Figure 2. Angle of approach between observer and sheep. Angle recorded depended on the position of the animal's head.*

### *Measuring exploration tendency*

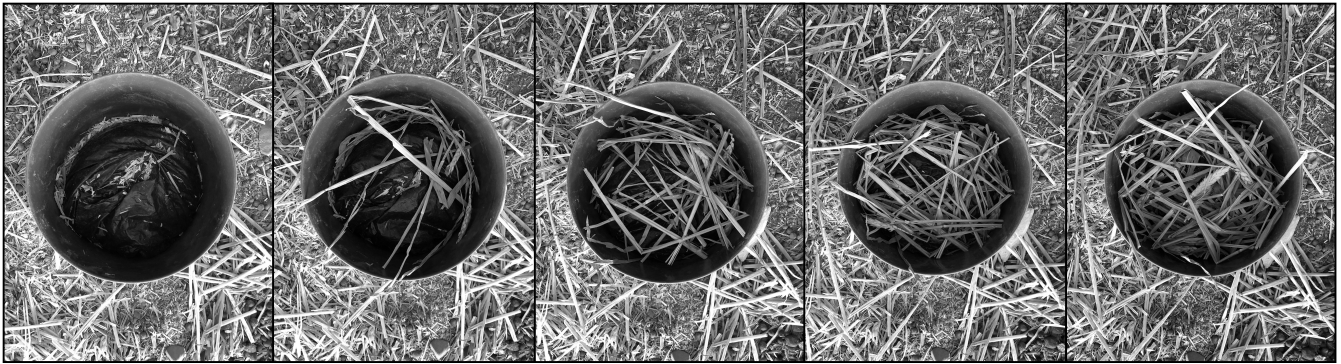
We tested exploration tendency indoors in pens of 28.10m<sup>2</sup> (figure 3) in the presence of other sheep that were not part of the experiment. We chose to control for potential confounding effects of the group on our focal individual by placing 8 ewes, unfamiliar to focal sheep, in an adjacent pen to mitigate the perceived stress of being held alone. These ewes were all the same age, but were post-reproductive. This allowed us to measure exploration tendency independent of group effects, such as leader-follower behaviour or social learning. Preliminary tests for exploration tendency (EXP), using animals not included in the study, were conducted in outdoor arenas with focal individuals kept separate from conspecifics. Individuals showed signs of stress in the outdoor arena, separate from and in the presence of conspecifics. This is presumably due to heightened fear in a large open space with no nearby conspecifics and no obvious foraging patches (as in the FID test). Animals also displayed common signs of stress (bleating, high activity levels and/or freezing (Cockram, 2004) during indoor tests when isolated from conspecifics.

Figure 3 illustrates the test design. Four buckets were placed 1.70 and 3.50 metres apart. Inside each was a handful amount of hay, which could only be seen if the sheep inspected the bucket. Prior to testing sheep were fasted for 24 hours to ensure all individuals had a similar level of food motivation for the task. Each individual entered the exploration assay from the opposite side to where the conspecifics were held. Individuals were released into the arena from the side opposite where the unfamiliar conspecifics were held. Each trial lasted five minutes and was filmed from one end of the arena at around 2m high (using GoPro Hero 5). No observer was present during this experiment so individuals were not affected by the presence of a human. After five minutes the individual was removed and kept separate from untested individuals. After testing an observer (MEG and KQ) scored the amount of remaining hay using a pre-determined set of categories (see fig 4). Eaten hay was replaced so each animal had the same amount of hay per test.





*Figure 3: layout of experimental arena for exploration tendency. Arena was indoors and focal sheep was separated from unfamiliar conspecifics by a metal gate.*



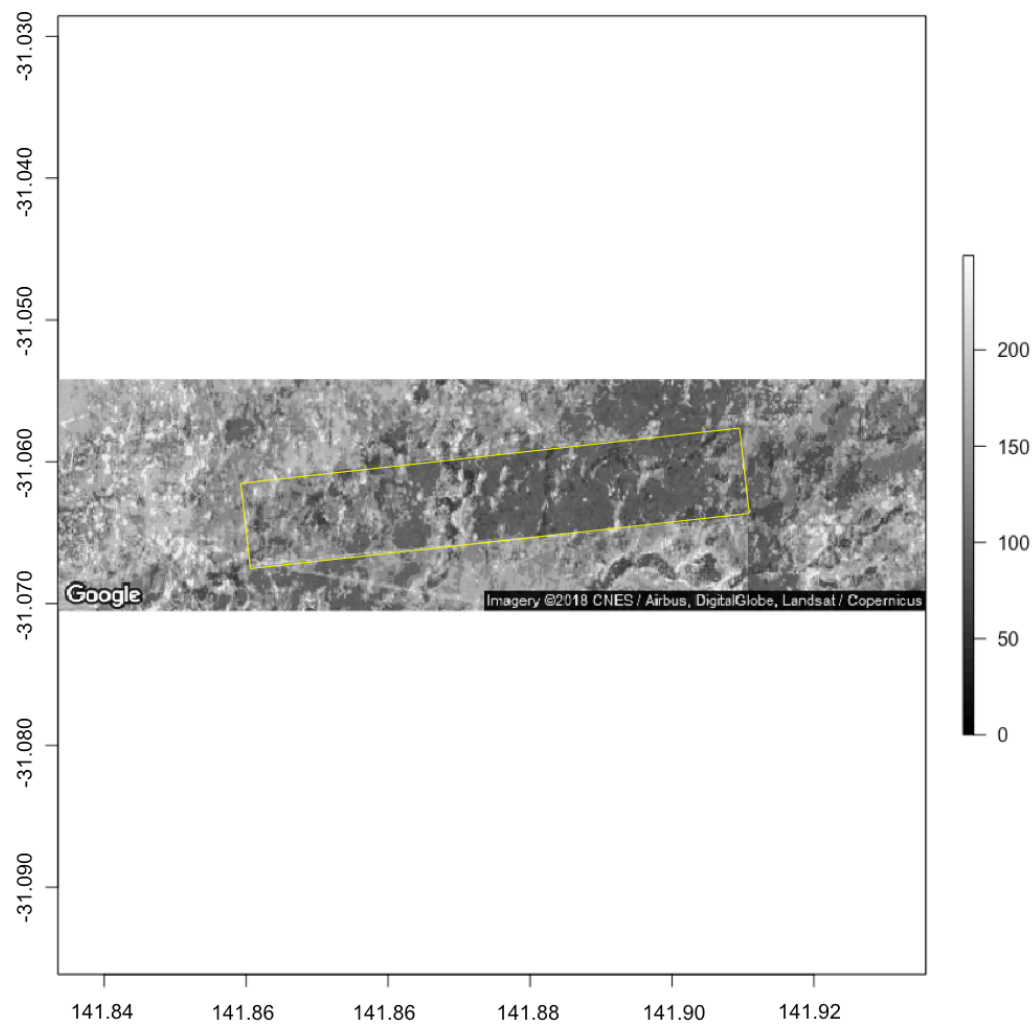
*Figure 4: Visual chart of hay content categories. From L - R: 'empty', 'mostly empty', 'half empty', 'mostly full', 'full'. This was used to score all bucket contents after exploration trials.*

Using video analysis, exploration tendency was quantified as the number of times an individual inspected buckets. This was done by one person (MEG) to avoid inter-individual observer differences. An animal was defined to be ‘inspecting’ a bucket when the tip of its nose was visibly touching the bucket in the video. This was considered a proxy for inspection as we assumed individuals that close to the bucket are highly likely to have seen the hay. Inspections were considered discrete events, delineated by the animal taking one full step in any direction away from the bucket. This allowed for individuals to look up during one bucket inspection, for instance performing vigilance behaviour during foraging). For this analysis the total number of bucket inspections,  $i$ , was recorded, allowing for repeat inspections. Comparable to FID, two tests were conducted five days apart in March, and another two tests five days apart in June 2018. March and June tests were 98 days apart.

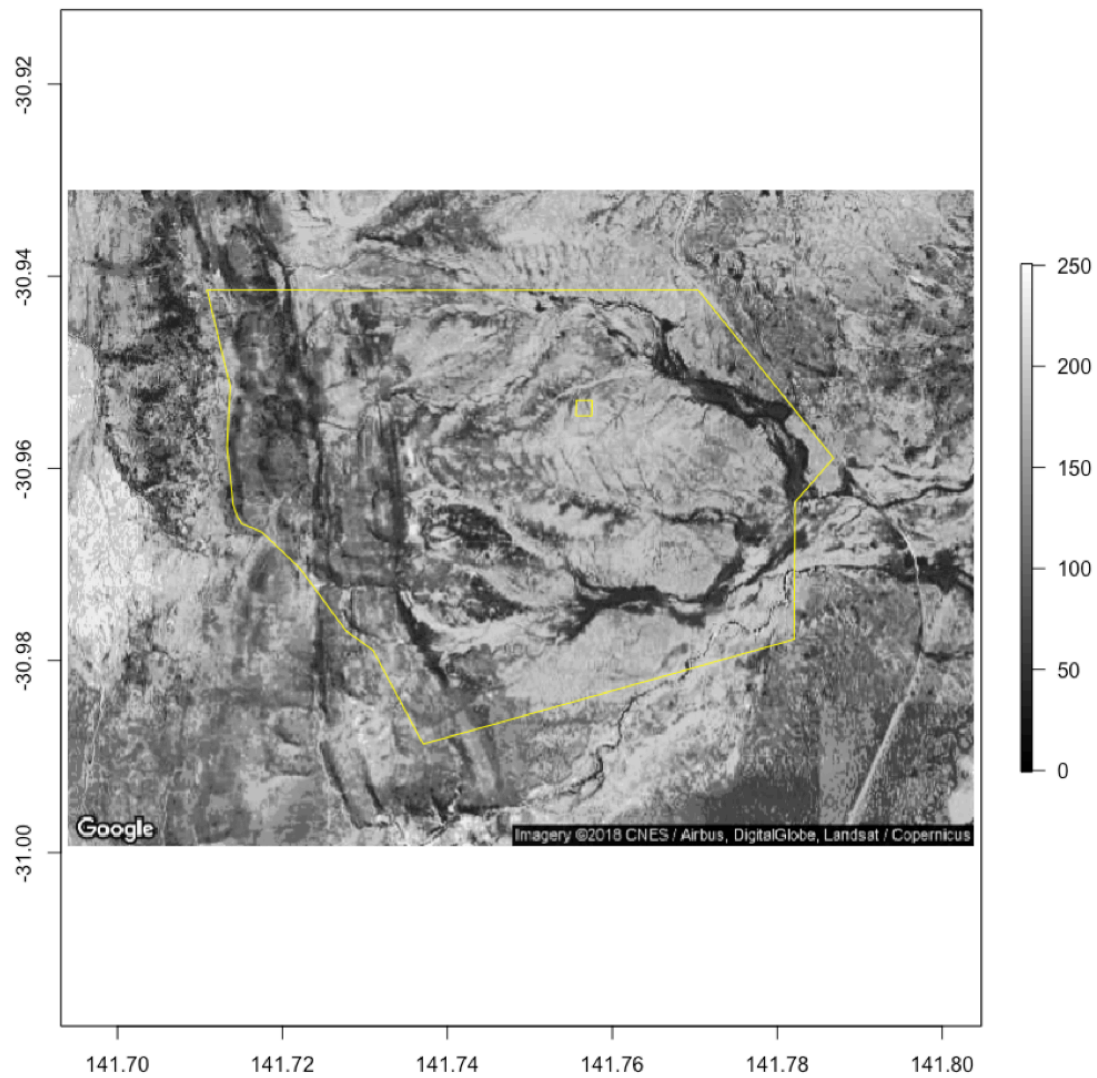
### *Field experimental design*

The same sheep used for personality tests were sent into field experiments. The experiment consisted of two treatments: complex and simple paddocks. Paddocks were qualitatively classified as ‘simple’ and ‘complex’ based on topography and hence perceived difficulty for resource acquisition by sheep. The ‘simple’ paddock was 6.39km<sup>2</sup> in size, had a single water source, and had flat terrain (figure 5). Conversely, the ‘complex’ paddock was 27.74km<sup>2</sup> and had more varied terrain including a large ridgeline at one end of the paddock (figure 6), one water source. Both groups experienced both treatments, but in opposite orders: group 1 went from the complex to simple paddock; group 2 went from simple to complex (figure 7). Sheep were in their

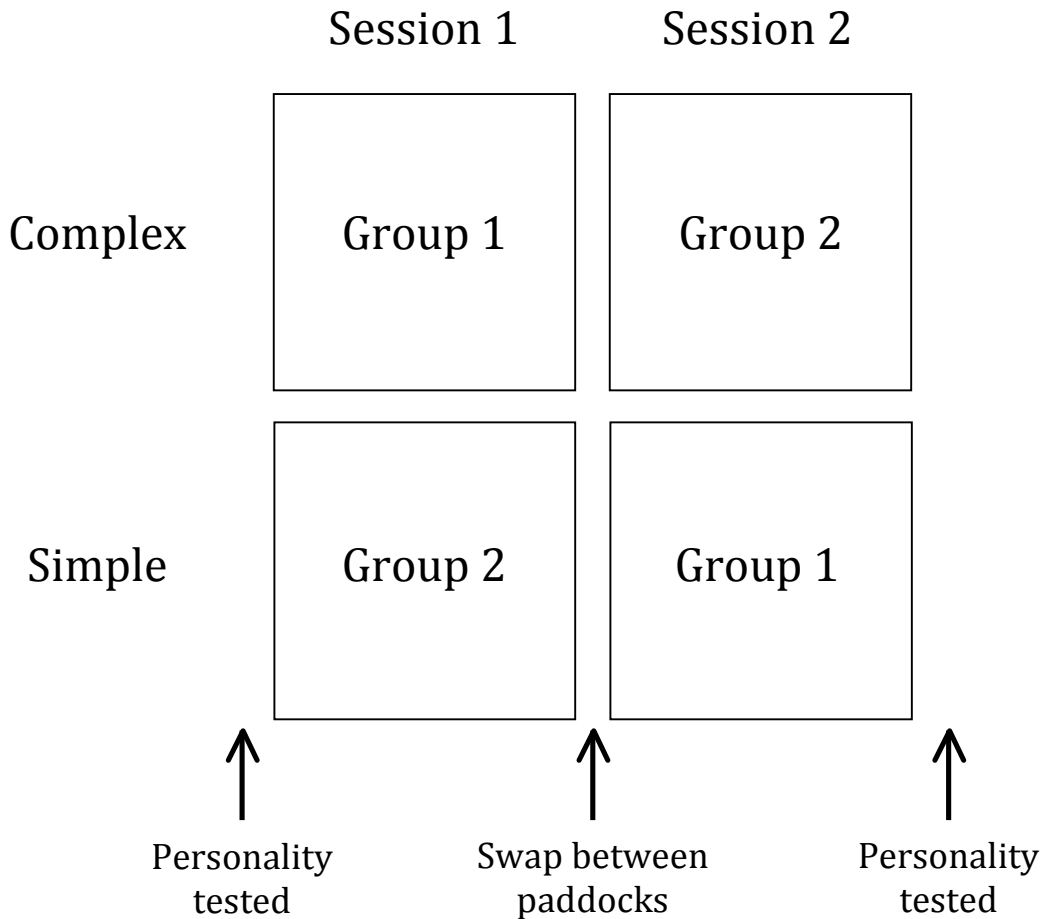
first paddock for 31 days and the second paddock for 38 days. Animals were weighed using a sheep weight crate and had hip and shoulder height measured, from the tallest point of the hip and shoulder bones, at the beginning of the experiment, during the transition between paddocks, and at the end (figure 7). All measurements were taken in holding pens away from the treatment paddocks. Groups were always kept separate with group composition unchanged. During the experiment sheep were left to range freely within the paddock; they were not managed by or interacted with any humans during their time in experimental paddocks.



*Figure 5: 'simple' experimental paddock at Fowlers Gap. The simple paddock is smaller in size, a regular shape, and has less topological variation than the 'complex'.*



*Figure 6: the 'complex' experimental paddock at Fowlers Gap. This paddock is larger in size, with more complicated topography than the 'simple' paddock.*



*Figure 7: Experimental design showing the order of groups in each treatment paddock. Sheep were mustered into holding pens before, during, and after time in treatment paddocks. Session 1 ran in April 2018 and session 2 in May 2018.*

#### *Behaviour in paddocks – spatial behaviour*

In March 2018 collars containing a GPS logger (i-Gotu GT-120, with increased battery capacity) were fitted to all study sheep. The collars have no noticeable effect on the behaviour of the animal or have any noticeable adverse effects. Collars weigh 700g around 0.025-0.020% of the animal's body weight, which is below the common threshold of 5% for fitting scientific devices. The collars were attached to individuals prior to their release into experimental paddocks. Batteries last three months, allowing us to continually record sheep locations throughout the experiment. GPS units recorded a location every 2 minutes. GPS files from each collar contain the latitude-longitude coordinates from each location, date and time of the recording in UTC, elevation, and a variable showing the number of satellite fixes used to find the location.

### *Data processing*

First, we filtered the raw GPS data to remove times when sheep were being handled and mustered, as well as errors in location recordings (detailed below). Location data were taken from the first full 24-hour period that sheep were in the paddocks onwards. We used three methods to filter the spatial data allowing us to extract the locational data with high spatial accuracy, improving the overall quality of the dataset. First, we filter by number of satellites because a minimum of three satellites is required to determine the location of the GPS units in a 2-D space. Second, we filtered based on visual observation. Latitude-longitude coordinates were plotted onto a map of the study area, with paddock boundaries outlined, and extreme outliers were selected and removed when they fell distinctly outside the boundary. Thirdly, data were filtered using two speed filters to remove sequential points that were biologically unlikely or impossible. We chose a maximum speed of 180m per two minutes based on recordings of a median sheep escape speed of 1.5m/s (Manning et al., 2014), wherein points that were further apart than 180m were removed. A second speed filter was also used, which also incorporated angle of movement (Bjørneraas et al., 2010). This filter uses max speed, just as the first filter does, but also considers that the relative angle between two successive points should fall within a given range. If the angle is greater than expected this indicates an outlier and the point is removed.

During the study eight sheep spent 10 days outside the paddock boundary, having passed through a partially damaged fence. As this was 33% of the study period these individuals were removed from analyses, as their movement behaviour was not comparable to other individuals as they spent a lot of time outside the treatment paddocks. After filtering, missing data points were interpolated to ensure that locations of all sheep were known at exactly the same time. Data were only interpolated up to 4 minutes (maximum 2 consecutive data points).

### *Home range analysis*

Animal home ranges, constituting the area an animal frequents (Boitani & Fuller, 2000), are often modelled by utilisation distributions (UD). Utilisation distributions estimate the areas of high use based on repeated measures of relocations of the same individual over time. Calculating an

animal's UD is often done using kernel density estimators (KDE) (Worton, 1989). Kernel estimates use location coordinates on a 2D surface to understand where an animal is in its space. Under the utilisation distribution definition, kernel density estimates assign a higher importance to areas with a greater density of points. Thereby this method assumes that more frequently used parts of an animal's space use are more important to its ecology. This method was originally developed for studies that used capture-mark-recapture methods or similar methods of repeatedly locating animals (Worton, 1989). Using kernel density estimates for utilisation distributions under this method are appropriate as they assume that location points are far enough apart in time to not be highly correlated with each other. However, sequential relocations of an animal are never fully independent of each other as the location of point 'b' is dependent on the location of point 'a', separated by time  $t$ . The spatio-temporal autocorrelation between two, or more, points has been widely discussed in the literature, both as a positive and negative aspect of animal movement studies (Dray et al., 2010). The issue with autocorrelation comes from the assumption of many methods of data analysis, ranging from home range calculations to statistical tests, assuming complete independence of data points. However, many argue that autocorrelation is an inherent part of animal movement studies and should be used to perform more accurate analyses instead of being controlled for or ignored. For home range analysis specifically, ignoring autocorrelation can lead to inaccurate home range sizes as the direction and pattern of movement can alter an animal's space use, thus it is important to consider patterns of movement when calculating animal home ranges (Benhamou & Corn  lis, 2010). When two locations are far enough apart in time the correlation between 'a' and 'b' is negligible. However as recording frequency increases so does the amount of autocorrelation, and it becomes more important to account for this when trying to accurately assess home range areas. To take movement into account when building home ranges/utilisation distributions, you build a movement track using date and time information alongside the relocation (e.g. latitude/longitude) data. The UD is then built based on the direction of travel rather than placing a cloud around all points.

Movement paths can be incorporated into home range modelling commonly using two methods. Because animal movement is continuous, but the process of recording locations at given time points is not, additional steps are interpolated to create a smoother movement path (Benhamou

& Corn  lis, 2010). These interpolated steps are built by a probability that an animal may move in any direction, but that this direction is limited by the location of points a and b. There are different methods of describing this probability distribution, including random movement, Brownian movement, and biased random walks. Therefore, the method of interpolation affects the outcome of movement model. For this analysis we built movement tracks using biased random bridging as it provides the most accurate model of animal movement compared to simple kernel estimates (Benhamou & Corn  lis, 2010). Biased random bridges (BRB) are built from biased random walks (Benhamou & Corn  lis, 2010). Biased random walks differ from Brownian movement in that they account for an increased likelihood of an animal moving in a direction towards a sequential point. This is in contrast to Brownian movement, which assumes that the potential spaces an animal will move are distributed randomly. Thus we built utilisation distributions using BRBs.

We built UD<sub>s</sub> using BRB methods implemented in R using the `kernelbb` and `BRB` functions from the `adehabitatHR` package (Calenge, 2006). The BRB function requires users to specify several parameters: the smoothing parameter  $D$ ; maximum time between known relocations, 'Tmax'; the smallest distance at which an animal is not considered moving or period of intense localised movement,  $L_{min}$ ; and an additional smoothing parameter taking into account the uncertainty of known relocations,  $H_{min}$  (Calenge, 2006). The user can also choose the size of the grid used and extent. Tmax,  $L_{min}$ , and  $H_{min}$  should reflect the species characteristics (Calenge, 2006). A Tmax of 120 seconds was chosen as it is the maximum time difference between subsequent locations in our interpolated data. Following D  rr and Ward 2014, we used double the value of measurement uncertainty to select an  $L_{min}$  value of 8m. This was based on maximum GPS error of 2m in one direction, i.e. a circle of error around a single location point with a radius of 2m and diameter of error at 4m. An  $H_{min}$  value of 12m was chosen. As with  $L_{min}$  this is selected on ecological grounds. Benhamou and Cornelis (2010) and Jay et al. (2012) suggest adding half the distance an animal can travel over a "long time period" at maximum velocity to the value for measurement uncertainty. However, many other studies often use a value double  $L_{min}$  for  $H_{min}$ . Using the method suggested by Benhamou and Cornelis (2010) produced UD<sub>s</sub> that were biologically unrealistic, so we selected an  $H_{min}$  value 1.5 times greater than  $L_{min}$ . This was chosen during initial investigations of the biological sensibility and computational intensity of input variables. A



range of Hmin values were tried and 12m provided the most accurate and fast estimate of UD relevant for this study. However the value of Hmin (and Lmin) is essentially arbitrary and only useful for interstudy comparisons, so are not particularly important as long as they are kept consistent within a study. The grid and extent parameters were set at 1000 cells and 0.3, respectively, as they produced a grid large enough to estimate all home range UD and were not too computationally intensive. All other parameters specified in the BRB function were left at default.

Home range sizes were calculated for increasingly longer time periods, days beginning with 1 day, and increasing by one day to the number of days spent in each paddock. We calculated how many days it took each individual to explore an area of 3km<sup>2</sup> within each paddock. Using an actual size, instead of a percentage of the paddock explored, allowed us to compare measurements between paddocks, which differed in size (the complex paddock was 4.3x larger than the simple paddock).

We also calculated the mean total distance each individual travelled each day during the period within a paddock, by summing the distance between consecutive relocations on a given day. Longitude-latitude coordinates were converted to distances using the moveHMM package (Michelot et al., 2016). Distance travelled per day and time taken to explore 3km<sup>2</sup> were used to estimate space use in our study.

### *Statistical analysis*

All statistical analyses were conducted in R using RStudio (R Core Team, 2017; RStudio Team, 2015). Behavioural traits were assessed for repeatability using intra-class correlation coefficients implemented using the rptR package in R (Stoffel et al., 2017). Two linear mixed models, with daily dist and time<sub>3km</sub> as dependent variables, were modelled using lmerTest function (Calenge, 2006), models 1-2 below. Each model included individual ID as a random effect and the two personality traits, FID and EXP, as independent variables. Group identity and paddock treatment were included as covariates. Interactions between these terms - group identity x paddock treatment and personality traits x paddock treatment - were also included. Covariates were

selected biologically, rather than statistically. Interactions between personality traits and paddock accounted for possible different movement strategies between paddock treatments. A group x paddock interaction allowed us to control for any possible effect of the groups experiencing the paddocks in different orders. Three-way interactions terms were not included as they are difficult to interpret and do not always represent biologically meaningful results. We included session as a weighting factor in our models to satisfy the assumption of homoscedasticity.

*distance travelled per day ~ FID + EXP + group ID + treatment paddock + FID \* paddock + EXP \* paddock + (1|individual ID), weights = session*

Model 1: model structure investigating distance travelled per day

*time to explore 3km ~ FID + EXP + group ID + treatment paddock + FID \* paddock + EXP \* paddock + (1|individual ID), weights = session*

Model 2: model structure investigating time taken to explore 3km<sup>2</sup>

## RESULTS

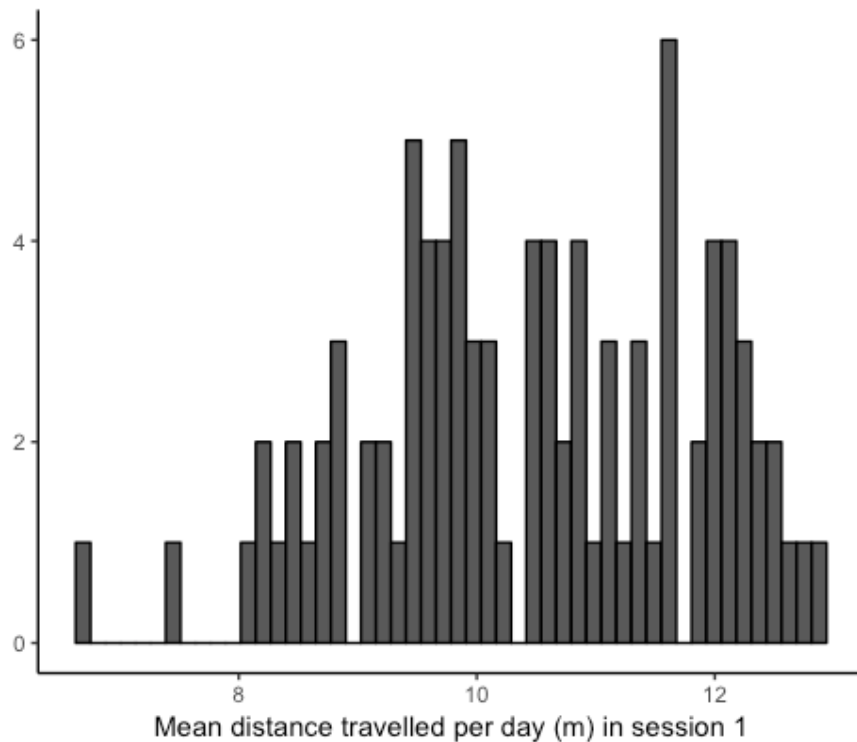
### *Behaviour in yards – personality traits*

We found evidence for moderate within-individual repeatability of both flight initiation distance (ICC:  $r = 0.661$ ,  $CI = 0.563 - 0.734$ ,  $p < 0.0001$ ) and exploration tendency (ICC:  $r = 0.457$ ,  $CI = 0.306 - 0.585$ ,  $p < 0.0001$ ) in our sheep. Both model residuals met assumptions normality and data were homoscedastic.

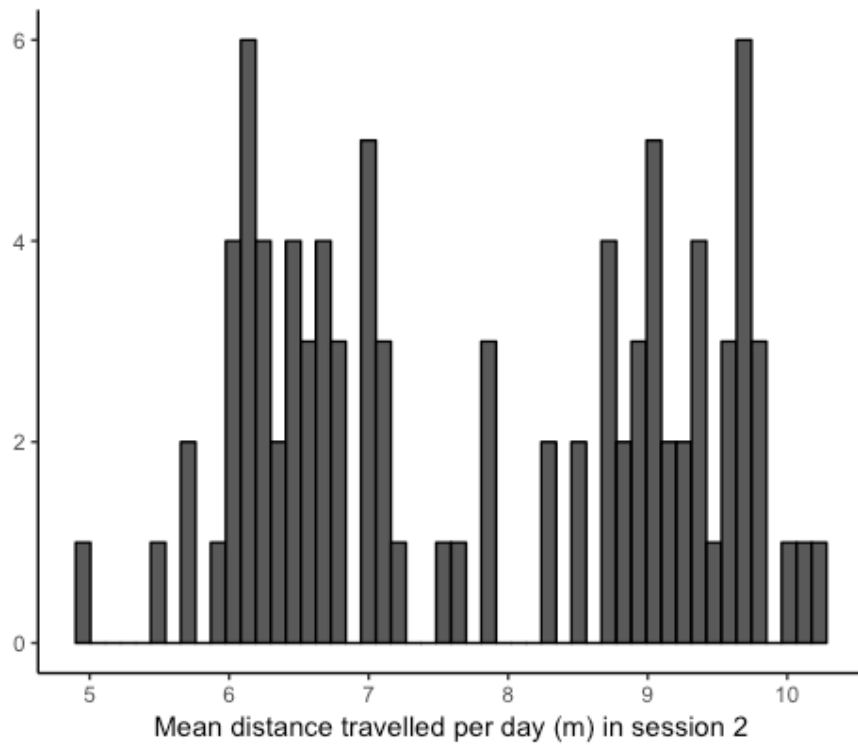
### *Behaviour in the field – space-use behaviour*

Data from GPS records yielded 4,572,044 location points across 89 individuals used in our final analysis. Individual distance travelled varied greatly among days, ranging from 0.23km to 21.58km (mean =  $9.00\text{km} \pm 0.05$ ). Time taken to explore 3km<sup>2</sup> also had a wide range, from 11 days to 36 days (mean =  $20.94 \pm 0.62$ ). Both distance travelled per day and days to explore 3km<sup>2</sup>

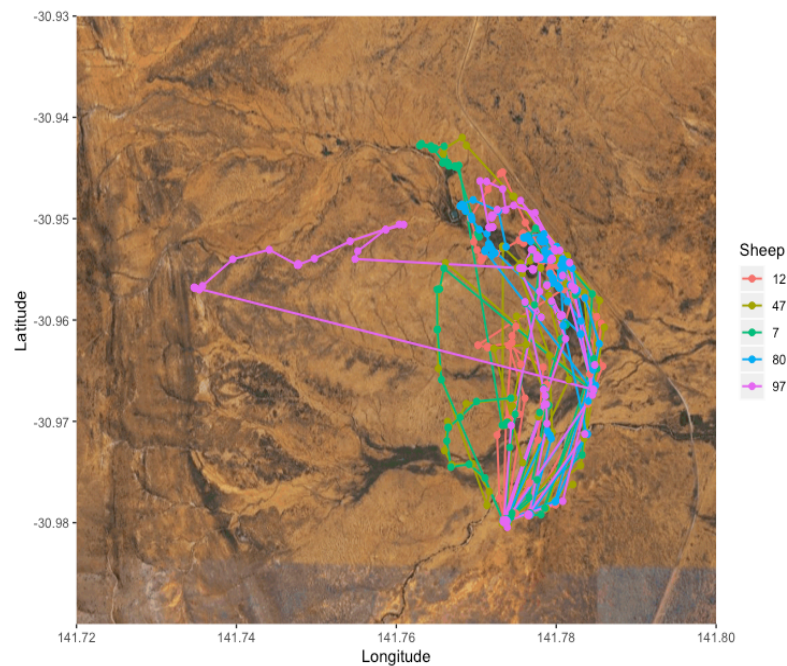
differed significantly between experimental sessions 1 and 2 ( $t_{5056.3} = 27.93$ ,  $CI = 2.43 - 2.80$ ,  $p < 0.0001$ , and  $t_{72.267} = 4.73$ ,  $CI = 3.34 - 8.21$ ,  $p < 0.0001$ , respectively), suggesting a temporal component affecting sheep movement across our study. Although sheep are likely moving in groups quite often, they do appear to show individual level movement (figure 8-9). Figure 10 shows a subset of movement tracks for five individuals over five days, showing that sheep are not always moving in a single group.



*Figure 8: frequency distribution of the mean distances travelled per day per individual in session 1. There is a high amount of variation between individuals, suggesting that individuals do not always move as part of a group.*



*Figure 9: frequency distribution of the mean distances travelled per day per individual in session 2. The variation between individuals seen in session 1 is similar in session 2.*



*Figure 10: The movement patterns of five sheep across a five-day period. Although animals do move together, there are some departures from group movement in the formation of subgroups. In this*

*graph the green and yellow individuals move slightly away from the majority of the group. The individual represented by the purple line goes much further than the rest of the group, towards the other side of the paddock. Note: as this is a subset of sheep this graph does not give an accurate indication of group size.*

We found no evidence for within-individual repeatability for movement behaviour in our sheep while in the paddock. Total distance travelled per day had a repeatability of  $r = 0.11$  (ICC: CI = 0.08 - 0.14,  $p < 0.0001$ ), while time taken to explore 3km<sup>2</sup> was not significantly repeatable (ICC:  $r = 0.00$ , CI = 0.00 - 0.30,  $p = 0.50$ ). Additionally, data were ranked from 1<sup>st</sup> to n<sup>th</sup> position and tested again for repeatability. We ranked our two spatial behaviours to see if individuals were consistently differing from one another in their patterns. However, rank of both distance travelled per day and time taken to explore 3km<sup>2</sup> also showed low repeatability (ICC:  $r = 0.19$ , CI = 0.14 - 0.23,  $p < 0.0001$  and  $r = 0$ , CI = 0,  $p = 1$ , respectively). The model residuals also satisfied the assumptions of normality.

#### *Personality and spatial behaviours*

As total distance travelled per day was not repeatable within individuals, our two measures of personality could not significantly predict differences between individuals, i.e. boldness (figure 11) or exploration tendency (figure 12) ( $\beta = -0.009132$ ,  $t = -0.027$ ,  $p = 0.979$ , and  $\beta = -0.074302$ ,  $t = -0.233$ ,  $p = 0.816$ , respectively, see Table 1). However, we did find significant effects of group and treatment paddock (Table 1, figure 15).

*Table 1: Movement behaviour: effect of two personality traits on total distance travelled per individual per day, using a linear mixed model. Individual identity was included as a random effect and explained 5.27% of the variance.*

Parameter	Estimate	SE	t value	p-value
FID	-0.009132	0.339001	-0.027	0.98
EXP	-0.074302	0.318746	-0.233	0.82
<b>Group ID</b>	<b>-7.901173</b>	<b>0.748297</b>	<b>-10.559</b>	<b>&lt; 0.0001</b>
<b>Treatment paddock</b>	<b>12.693600</b>	<b>1.114140</b>	<b>11.393</b>	<b>&lt; 0.0001</b>
Group : treatment paddock	-1.897331	1.386804	-1.368	0.18
FID : treatment paddock	0.001816	0.636856	0.003	0.99
EXP : treatment paddock	0.745465	0.571643	1.304	0.20

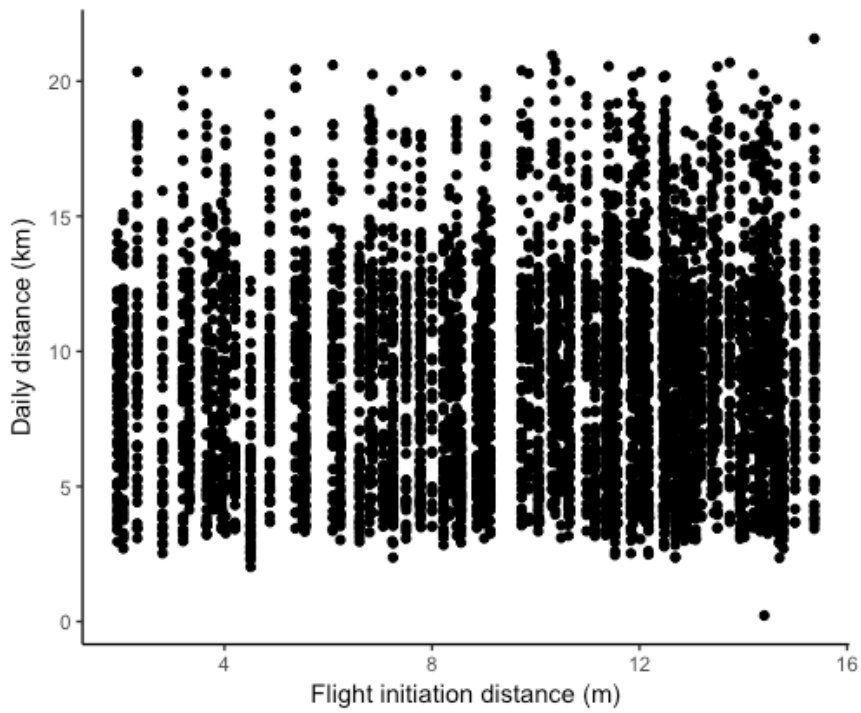
Neither personality trait explained the time taken to explore 3km<sup>2</sup> in a paddock (Table 2, figure 13-14). Similar to our previous model we saw a significant effect of both group ID and treatment, but also a significant interaction between the two here (figure 16).

*Table 2: Spatial behaviour: effect of two personality traits on the number of days taken to explore 3km<sup>2</sup> using a linear mixed model. Individual ID was included as a random effect and explained 1.00% of the variance.*

Parameter	Estimate	SE	t value	p-value
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FID	0.06218	0.07398	0.840	0.40
EXP	0.06518	0.06957	0.937	0.35
<b>Group ID</b>	<b>-0.34170</b>	<b>0.15007</b>	<b>-2.277</b>	<b>0.02</b>
<b>Treatment paddock</b>	<b>-3.02932</b>	<b>0.12387</b>	<b>-24.456</b>	<b>&lt; 0.0001</b>
<b>Group : treatment paddock</b>	<b>5.32204</b>	<b>0.17938</b>	<b>29.669</b>	<b>&lt; 0.0001</b>
FID : treatment paddock	-0.12371	0.08671	-1.427	0.15
EXP : treatment paddock	-0.05416	0.08464	-0.640	0.52

Total distance travelled per day decreased in session 2 compared to session 1 (mean of 10.43km per day across all individuals compared to 7.82km), while time to explore 3km<sup>2</sup> decreased (23.50 days vs. 17.72). The groups also differed in their space use compared to each other, with group two travelling further per day than group one (mean of 7.86 km per day compared to 10.21km,  $t_{5854} = -25.54$ ,  $p < 0.0001$ ), and accordingly exploring 3km<sup>2</sup> faster (mean of 24.83km vs. 18.85km,  $t_{72.267} = 4.73$ ,  $p < 0.0001$ ). Both groups also had different spatial behaviours in the same paddocks, with group two travelling longer distances per day on average in the simple paddock, but less than group one in the complex paddock (mean = 6.49, 11.455 for group 1 and 2, respectively,  $t_{1930.5} = -36.22$ ,  $p\text{-value} < 0.0001$ ; mean = 9.48, 9.20, group 1 and 2 respectively,  $t_{2936.7} = 2.44$ ,  $p\text{-value} = 0.015$ ). In both treatment paddocks, however, group 2 took less time to explore 3km<sup>2</sup> than group 1. This may be due to an order-effect in our experimental design. The groups experienced the paddocks in different orders: group 1 was initially in the complex paddock and then in the simple, while group 2 went into the simple paddock first and then complex. Thus group-level movement differences may be the result of each group being exposed to conditions in a different order, which may have influenced their overall movement behaviour.



*Figure 11: Flight initiation distance of all individuals compared to distance travelled per day per individual (km).*



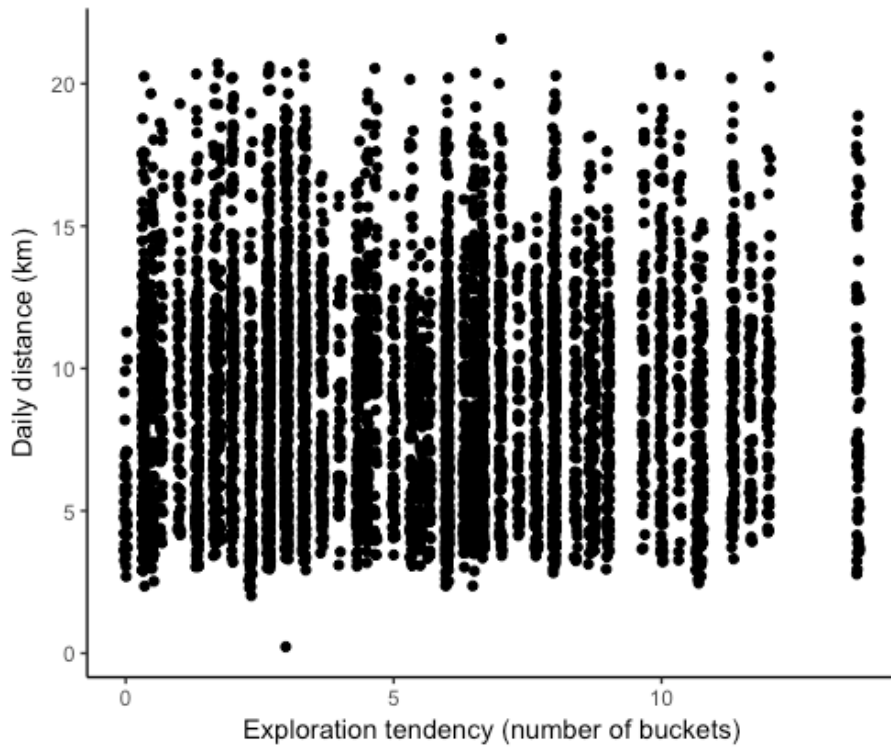


Figure 12: Exploration tendency of each individual compared to distance travelled per day per individual (km).

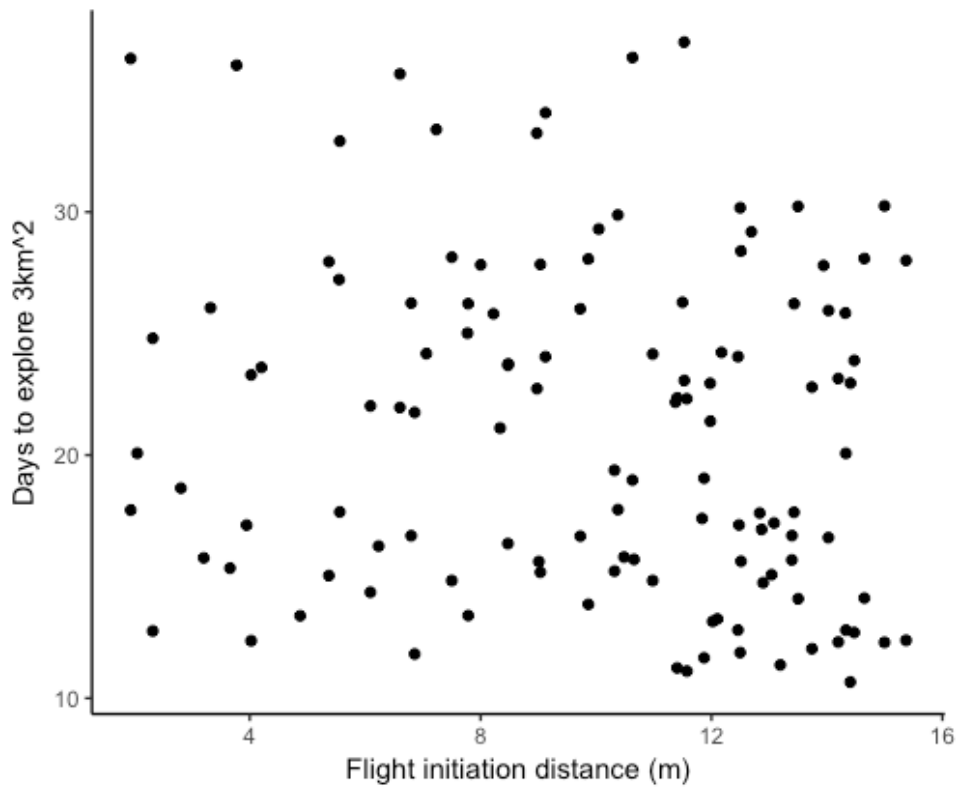
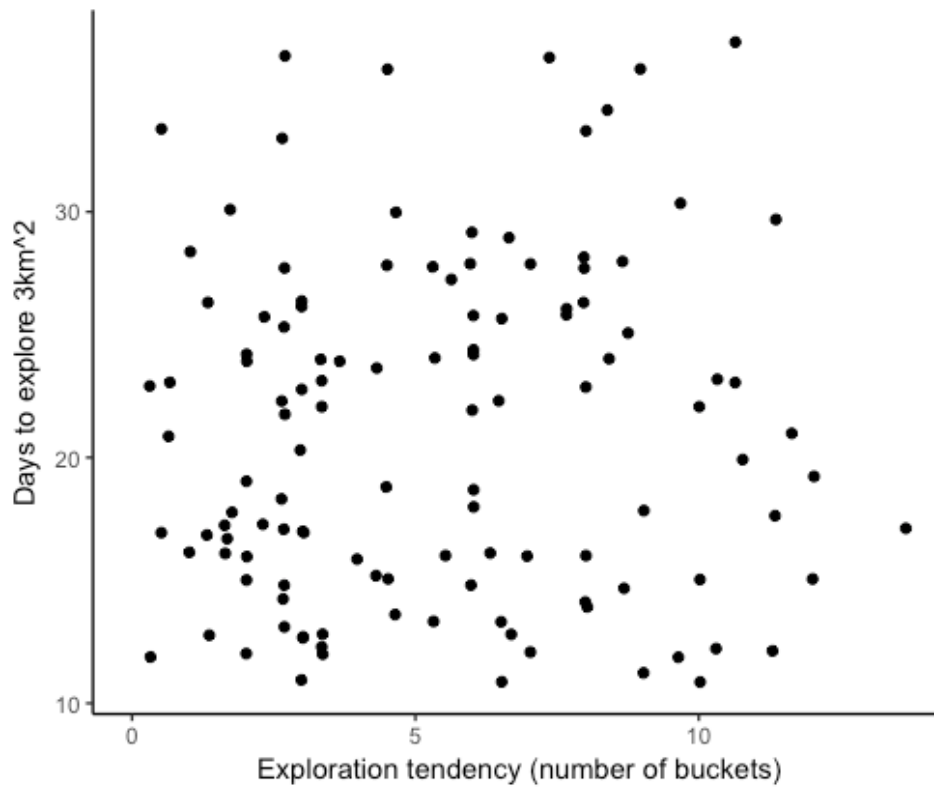


Figure 13: Flight initiation distance of each individual compared to the days taken to explore 3km<sup>2</sup>.



*Figure 14: Exploration tendency of each individual compared to the days taken to explore 3km<sup>2</sup>.*

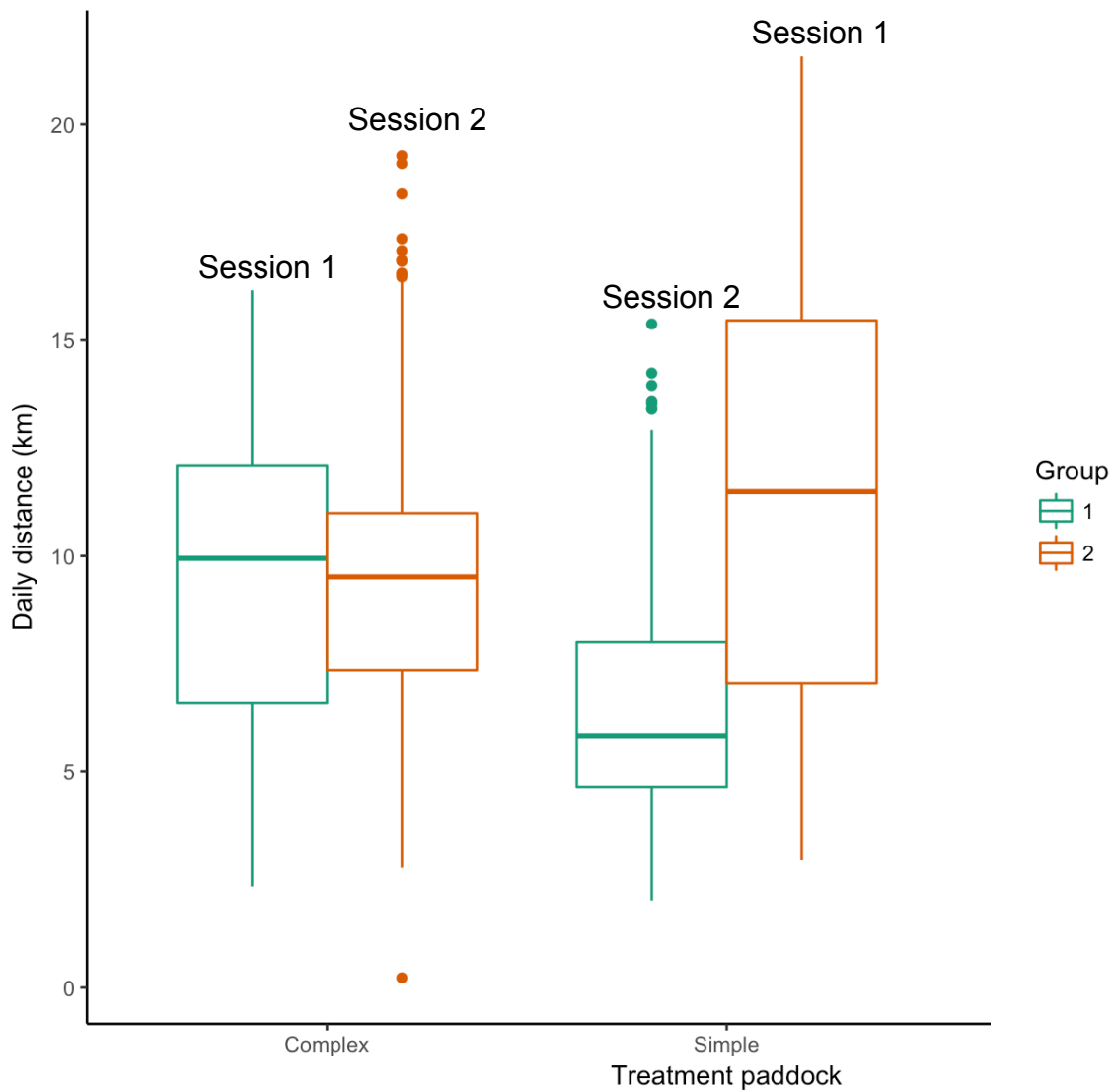


Figure 15: Distance individuals moved per day in 'simple' and 'complex' paddocks. Each group moved less in session 1 than in session 2. However, groups had opposing patterns of movement when swapped between the 'simple' and 'complex' paddocks. Group 1 moved more in the 'complex' than in the 'simple', whereas group 2 moved less in the 'complex' compared to the 'simple'.

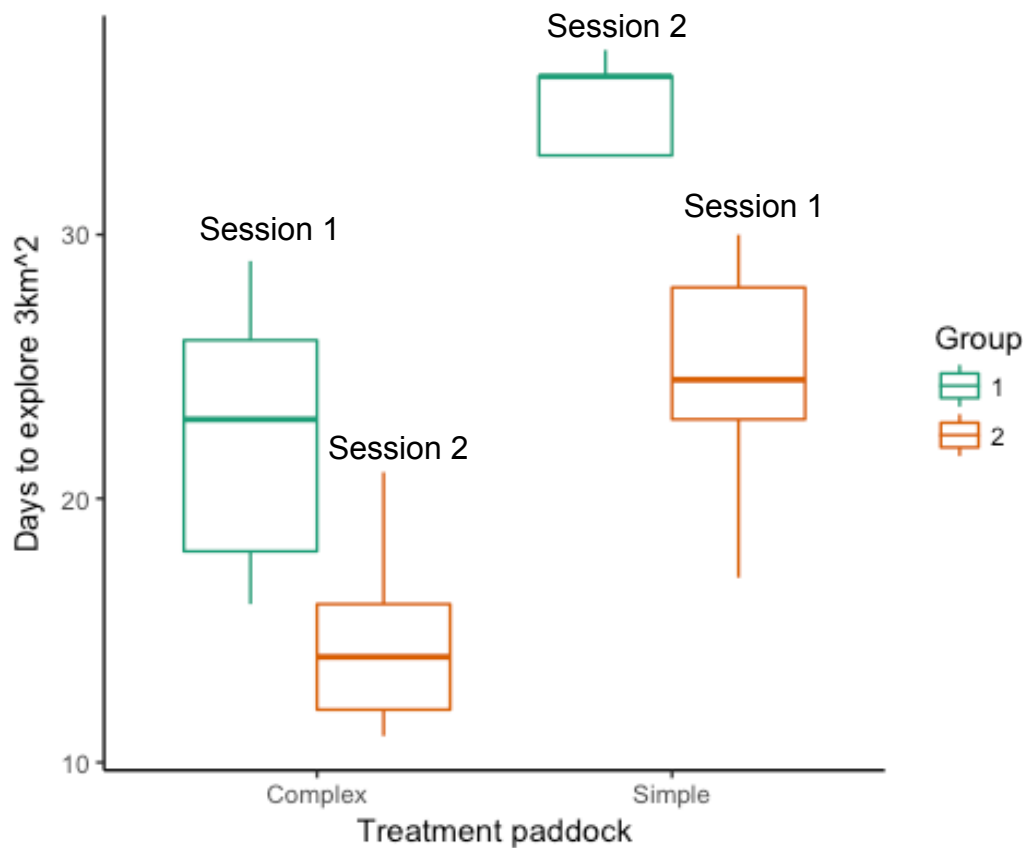


Figure 16: The days taken for individuals to explore 3km<sup>2</sup> in 'simple' and 'complex' paddocks. Both groups were faster to explore in the complex paddock compared to the simple. However, while group 1 took longer to explore the area in session 2, group 1 was faster.

## DISCUSSION

Our research combines measures of animal personality with field-based movement data to get a clearer understanding of the relationship between personality traits and space use in sheep. We found evidence for two consistent personality traits, boldness and exploration tendency, measured repeatedly over 3 months in captive assays. However, we did not find a similar inter-individual repeatability of movement behaviours measured from field data measured over an extended period in the wild. Variation in space use and movement behaviour was neither significantly explained by boldness nor exploration tendency, measured in the yards. Instead experimental group and paddock treatment significantly affected movement and space use behaviour. Thus, our results do not support personality-dependent movement in sheep. We provide evidence not often found in the literature for a null relationship between personality

traits and movement behaviours. This study is one of few that use high-density location data to assess space use behaviour in relationship to personality traits.

We found evidence for the existence of two personality traits in Merino ewes. This backs up previous research conducted in sheep, where individuals showed repeatability over 3 months in boldness as well (Michelana, 2008). It also adds to the large body of literature supporting the existence of personality traits in many different species, from amphibians to birds, mammals, and reptiles (Stamps & Groothuis, 2010). In particular, boldness and exploration have been quantified in many animals. Boldness and exploration have been linked to many other behavioural traits across species, including social position, group composition, learning tendency, foraging decisions, dispersal tendency, and home range patterns (Toscano et al., 2016). In sheep specifically, boldness influenced the tendency for sheep to split into smaller foraging groups and how individuals positioned themselves in space (Michelena et al., 2009). However, this research quantified boldness using different tests to our own. This is not uncommon in personality research. Many different tests exist to examine the “same” trait in many species (for a summary see: Carter et al., 2013), making it difficult to compare between studies. For example, boldness can be measured by how willing an individual is to interact with a novel object, how willing it is to leave its ‘home’, how it behaves in a novel environment, or how it responds to perceived predation threat. Exploration tendency is often measured in a species-specific manner, such as counting the number of branches explored in caged birds, number of rooms entered for mammals, time to complete a maze task in rats, or latency to enter a room also in birds. This limits our ability to compare measures of personality between studies. However, even when tests are conducted using the same methods results are often not comparable between studies due to variation in external factors. Therefore it is important to validate the personality trait being measured through multiple tests measuring what appears to represent the same personality trait, while still performing a biologically relevant measure of personality for that species. However it is also important to ensure the behaviour that you are trying to explain with personality traits is also relevant for your species.

In this study, we successfully recorded and analyzed spatio-temporal data on a fine and precise scale in a long-term experiment in the field. There was no within-individual repeatability for either of our measures of spatial behaviour. This indicates that sheep are not moving consistently differently from one another in our study. This may be the result of group-level influences on movement patterns or suggests that movement behaviour is not an individual-level behavioural trait in this species. Our measures of space use represent daily movement patterns that are reflective of factors affecting short-term movement decisions. These patterns may include areas of the paddocks utilized on a given day for water and food resources, short-term area preference or avoidance, or short-term exploratory behavior, which are not explicitly examined by this research but covered by our measures of movement. The absence of inter-individual repeatability for either of our measures of space use suggests that these parameters are not indicative of a personality trait in this species. This indicates a dynamic response from the individuals to the environment. Variation in space use is often influenced by environment in many species. In caribou, for example, greater resource heterogeneity in winter months resulted in higher variation in movement behaviour of individuals (Johnson et al., 2002). Similarly, migration tendency in Galapagos tortoises (*Chelonoidis sp.*) was influenced by resource reliability, i.e. tortoises that migrated did so towards areas of predictable resource availability (Bastille-Rousseau et al., 2017). Abiotic factors can also influence animal movement, such as in red deer, where individuals moved more at intermediate temperatures (Signer & Ovaskainen, 2017). While for some species individual differences in this movement behaviour remain consistent over time (e.g. Cote et al., 2010), for others this represents behavioural flexibility within individuals (e.g. density-dependent switching between migratory strategies in elk (Eggeman et al., 2016). Thus the measures of space use in our study likely reflect behaviours that are influenced more strongly by external environmental factors rather than internal constraints in sheep.

The GPS data revealed that movement behaviour patterns were only marginally repeatable in merino sheep, which explains the absence of evidence for evidence for personality-dependent spatial behaviour in this study. This is contrary to many studies that investigated personality-dependent space use in other species. Personality traits have been linked to space use in reptiles, mammals, fish, and birds (Chapman et al., 2011; Harrison et al., 2015; Spiegel et al., 2017; van Overveld & Matthysen, 2010). However, a few examples of personality-independent movement

can be found in the literature. Previous research in wild starlings found no influence of an exploration personality trait on home range size, frequently used habitat areas, or sensitivity to environmental change (Minderman et al., 2009, 2010). The authors of those studies suggested that the measure of exploration used in their research, although comparable to other bird research at the time, might not be ecologically relevant for their species (Minderman et al., 2009, 2010). This seems unlikely for our own study, though, as boldness has been previously shown to influence foraging behaviour in merino sheep (Michelena et al., 2009). Instead personality-dependent space use may be affected by other factors more strongly than internal constraints. The 'landscape of fear' can affect behaviour, via the perceived threat of predation. Research in mosquitofish found evidence for personality-dependent dispersal under conditions with no predation threat (Cote et al., 2013). However when predation risk was added, this personality-dependent movement disappeared (Cote et al., 2013). Although our study did not explicitly include a predation component, sheep have been bred to flock into highly cohesive groups, which is an anti-predatory strategy for many species (e.g. Beauchamp, 2004; Cresswell, 1994; Magurran, 1990.; Siegfried & Underhill, 1975). It is possible that through artificial selective breeding for increased flocking and group cohesion, sheep have been bred to have an increased anti-predator response. In fact, the fear responses of domestic sheep are greater than those of wild sheep (Dwyer, 2004), suggesting they may engage in anti-predatory behaviours, such as cohesive movement, more often than wild sheep. Merino sheep in particular have been noted to be more gregarious and form larger daily subgroups than other domestic sheep breeds, with their increased gregariousness making them easy livestock to keep and manipulate (Keeling, 2001). Thus it is possible that by breeding for increased anti-predatory responses, the relationship between personality traits and space use has become uncoupled in domestic sheep.

Personality-dependent movement may also not exist in low-resource environments for some species. Mathematical models proposed show that personality traits (specifically boldness) are not adaptive in low-resource environments unless an individual is close to starvation (Luttbegg & Sih, 2010). This is because being bold would not allow individuals to gain enough condition to be 'safe' later on as resources are too limited to acquire (Luttbegg & Sih, 2010). Some studies have noted that personality traits may also display a degree of plasticity (Dingemanse et al., 2010). The degree of plasticity depends on the environment under which the trait was selected (DeWitt et

al., 1998; Dingemanse et al., 2010). Our study population has strong selective pressure not only from the environment but is also artificially selected for breeding. Merino sheep have historically been bred to survive in highly resource variable environments, especially areas like Australia's semi-arid zone where resources are often quite depleted and very patchy. It is likely that by selecting for traits that promote growth and survival in these areas, merino sheep were also bred to have high levels of behavioural plasticity in movement and space use behaviours. Thus personality-dependent space use may only occur when resources allow behavioural specialization, which would reduce intra-individual competition. But in low-resource environments a high degree of behavioural plasticity may be required both within and between individuals in order maximize resource utilization.

It is also possible that personality-dependent movement does exist in this species but we cannot detect it in this study. As a highly gregarious species, it is possible that sheep social group composition affects individual spatial behaviours and that individual's are making trade-offs between their own needs and remaining part of a group. Previous research in merinos found that they stayed closer to the present conspecific compared to when they were alone (Michelena, 2005). When in the presence of two conspecifics at opposite ends of the experimental arena, sheep appeared to remain at mid-distance between both individuals, perhaps to maintain group cohesion (Michelena, 2005). Michelena (2005) further suggested that sheep appear to show low, or no, revulsion to other sheep as seen with other species, and that movement away from conspecifics was a trade-off between individual gregariousness and foraging opportunities. This is supported by other research on sheep foraging behaviour, showing that individuals will not move away from a group to a far foraging patch unless followed by conspecifics (Dumont & Boissy, 2000). The willingness to move away from a group and pursue other foraging opportunities is affected by boldness and gregariousness in sheep, with bolder individuals more likely to split from a large group and graze in smaller groups (Michelena et al., 2009). They found that when a group began to crowd at a resource, the group would eventually split into two subgroups to maximize foraging efficiency (Michelena et al., 2009). Bold individuals were more likely to initiate a split into a smaller group, and subgroups were often equal-sized (Michelena et al., 2009). However the authors made no comment on the personality composition of the subgroups, so it's unclear how personality may have affected 'follower' individuals. In other



species, shy individuals follow bold individuals into new food sources (Dyer et al., 2009), so it is likely that a similar thing happens in sheep as well. However, since familiarity of conspecifics also affects an individual's likelihood of moving to a different foraging patch (Hauschildt & Gerken, 2015), we would need to disentangle any effects of personality on social network structure in sheep first. Given this, it is possible that our measures of spatial behaviour, although variable among individuals, were strongly affected by social attraction in sheep. By accounting for sociability before assessing space use in sheep, we would be able to get a better understanding of whether or not space use is personality-dependent in this species.

Another confounding factor for personality studies in highly gregarious species is personality-assortative grouping. Personality-assortative group occurs when individuals of the same (positive) or opposing (negative) personality type, e.g. boldness, aggressiveness, are found more frequently in the same group or have non-random social network associations. Examples of positive and negative assortment between personality types are found in many species. Positive and negative assortment can both have benefits for individuals depending on the phenotype by which they are grouped, or how they form subgroups. For instance, positive assortment can decrease uncertainty in interactions and promote cooperation (Massen & Koski, 2014). However in a resource-rich environment positive assortment may increase competition for resources, as individuals are utilizing the same foods; negative assortment would allow individuals to specialize their diets and avoid dietary overlap (van Valen, 1965). We see evidence of phenotypic assortment across species. Shy sticklebacks and guppies were more likely to associate with one another than with bolder individuals (Croft et al., 2009; Pike et al., 2008). Similar positive assortment by behavioural traits has also been shown in chimpanzees, horses, and great tits (Briard et al., 2015; Johnson et al., 2017; Massen & Koski, 2014). However burrow sharing in rodents was negatively assorted; exploratory individuals shared burrows with less-exploratory individuals more often than expected (Chock et al., 2017). Although social bonds in sticklebacks are predicted by positive assortment, shy fish prefer to follow a bold leader rather than a shy one (Nakayama et al., 2016). Thus if sheep in our study are negatively assorting, i.e. shy and bold individuals are grouping together, then bold and shy individuals will be moving in the same way. This means any effect of personality-dependent movement will be masked without accounting for phenotypic assortment, if present.

## *Conclusion*

Our results show that movement based space use is not personality-dependent in merino sheep. We found low repeatability of field-based measurements of spatial behaviour, indicating that movement is more influenced by environment rather than internal constraints. Alternatively, identifying different behavioral states, such as grazing, resting, and directional movement is another area of more subtle, potentially personality-based behaviours that may be present in domestic animals like sheep. Also looking at how areas of the paddocks and foraging patches are utilized by individuals may provide further insight into spatial behaviour in these species. Investigating the relationship between these field-based measures and yard-based personality traits may provide further insight into the effect of personality traits. However, these complex and time-consuming analysis were beyond the scope of the study and not feasible in the available time. As sheep are highly gregarious it is possible that the social environment has a strong effect on individual spatial behaviours. However, as some social behaviour is linked to personality traits, and can affect space use on a finer scale, more research should be conducted in order to untangle the effects of social environment of space use in merino sheep. This research provides a rare example of personality-independent space use, which can help us to understand how and when personality traits may be valuable for a species.

## REFERENCES

- Acworth, R. I., Rau, G. C., Cuthbert, M. O., Jensen, E., & Leggett, K. (2016). Long-term spatio-temporal precipitation variability in arid-zone Australia and implications for groundwater recharge. *Hydrogeology Journal*, 24(4), 905–921. <https://doi.org/10.1007/s10040-015-1358-7>
- Andreassen, H. P., & Ims, R. A. (1998). The effects of experimental habitat destruction and patch isolation on space use and fitness parameters in female root vole *Microtus oeconomus*. *Journal of Animal Ecology*, 67(6), 941–952. <https://doi.org/10.1046/j.1365-2656.1998.6760941.x>
- Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cole, E.F., Cockburn, A., & Sheldon, B.C. (2013). Individual personality predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters*, 16(11), 1365–1372. <https://doi.org/10.1111/ele.12181>
- Aplin, L.M., Farine, D.R., Mann, R.P., & Shledon, B.C. (2014). Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B: Biological Sciences*, 281(1789). <https://doi.org/10.1098/rspb.2014.1016>
- Aragón, P., Clobert, J., & Massot, M. (2006). Individual dispersal status influences space use of conspecific residents in the common lizard, *Lacerta vivipara*. *Behavioral Ecology and Sociobiology*, 60(3), 430–438. <https://doi.org/10.1007/s00265-006-0183-3>
- Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, 14(9), 948–958. <https://doi.org/10.1111/j.1461-0248.2011.01662.x>
- Aronsson, M., Low, M., López-Bao, J. V., Persson, J., Odden, J., Linnell, J. D. C., & Andrén, H. (2016). Intensity of space use reveals conditional sex-specific effects of prey and conspecific density on home range size. *Ecology and Evolution*, 6(9), 2957–2967. <https://doi.org/10.1002/ece3.2032>
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, 88(2), 310–326. <https://doi.org/10.1111/brv.12000>
- Barbraud, C., Johnson, A. R., & Bertault, G. (2003). Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. *Journal of Animal Ecology*, 72(2), 246–257. <https://doi.org/10.1046/j.1365-2656.2003.00695.x>
- Bastille-Rousseau, G., Gibbs, J. P., Yackulic, C. B., Frair, J. L., Cabrera, F., Rousseau, L.-P., ... Blake, S. (2017). Animal movement in the absence of predation: environmental drivers of movement strategies in a partial migration system. *Oikos*, 126(7), 1004–1019. <https://doi.org/10.1111/oik.03928>
- Beauchamp, G. (2004). Reduced flocking by birds on islands with relaxed predation. *Proceedings. Biological Sciences*, 271(1543), 1039–1042. <https://doi.org/10.1098/rspb.2004.2703>
- Beauchamp, J., Hart, K., Cherkiss, M., & Mazzotti, F. (2018). Variation in home range size and patterns in adult female American crocodiles *Crocodylus acutus*. *Endangered Species*

*Research*, 36, 161–171. <https://doi.org/10.3354/esr00900>

- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77(4), 771–783. <https://doi.org/10.1016/J.ANBEHAV.2008.12.022>
- Benhajali, H., Boivin, X., Sapa, J., Pellegrini, P., Boulesteix, P., Lajudie, P., & Phocas, F. (2010). Assessment of different on-farm measures of beef cattle temperament for use in genetic evaluation1. *Journal of Animal Science*, 88(11), 3529–3537. <https://doi.org/10.2527/jas.2010-3132>
- Benhamou, S., & Cornélis, D. (2010). Incorporating Movement Behavior and Barriers to Improve Kernel Home Range Space Use Estimates. *The Journal of Wildlife Management*, 74(6), 1353–1360. <https://doi.org/10.1111/j.1937-2817.2010.tb01257.x>
- Berger, J. (2009). Social ontogeny and behavioural diversity: consequences for Bighorn sheep *Ovis canadensis* inhabiting desert and mountain environments. *Journal of Zoology*, 188(2), 251–266. <https://doi.org/10.1111/j.1469-7998.1979.tb03403.x>
- Bergvall, U. A., Schäpers, A., Kjellander, P., & Weiss, A. (2011). Personality and foraging decisions in fallow deer, *Dama dama*. *Animal Behaviour*, 81(1), 101–112. <https://doi.org/10.1016/J.ANBEHAV.2010.09.018>
- Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23(7), 361–368. <https://doi.org/10.1016/J.TREE.2008.04.003>
- Bjørneraas, K., Van Moorter, B., Rolandsen, C. M., & Herfindal, I. (2010). Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics. *Journal of Wildlife Management*, 74(6), 1361–1366. <https://doi.org/10.2193/2009-405>
- Blumstein, D. T. (2003). Flight-Initiation Distance in Birds Is Dependent on Intruder Starting Distance. *The Journal of Wildlife Management*, 67(4), 852. <https://doi.org/10.2307/3802692>
- Blumstein, D. T., & Daniel, J. C. (2003). Foraging behavior of three Tasmanian macropodid marsupials in response to present and historical predation threat. *Ecography*, 26(5), 585–594. <https://doi.org/10.1034/j.1600-0587.2003.03516.x>
- Boitani, L., & Fuller, T. K. (2000). *Research techniques in animal ecology : controversies and consequences*. Columbia University Press. Retrieved from [https://books.google.com.au/books?hl=en&lr=&id=4YuPf9eHbpIC&oi=fnd&pg=PA65&dq=animal+home+range&ots=z-ylkzZsj4&sig=Py3\\_ZX8LvuzQDc4lmvVEyAKuL8c#v=onepage&q=animal+home+range&f=false](https://books.google.com.au/books?hl=en&lr=&id=4YuPf9eHbpIC&oi=fnd&pg=PA65&dq=animal+home+range&ots=z-ylkzZsj4&sig=Py3_ZX8LvuzQDc4lmvVEyAKuL8c#v=onepage&q=animal+home+range&f=false)
- Bolnick, D. I., & Doebeli, M. (2003). Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. *Evolution*, 57(11), 2433–2449. <https://doi.org/10.1111/j.0014-3820.2003.tb01489.x>
- Boon, A. K., Réale, D., & Boutin, S. (2008). Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos*, 117(9), 1321–1328. <https://doi.org/10.1111/j.0030-1299.2008.16567.x>

- Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, 80(2), 205–225. <https://doi.org/10.1017/S1464793104006645>
- Boyer, N., Réale, D., Marmet, J., Pisanu, B., & Chapuis, J.-L. (2010). Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology*, 79(3), 538–547. <https://doi.org/10.1111/j.1365-2656.2010.01659.x>
- Briard, L., Dorn, C., & Petit, O. (2015). Personality and Affinities Play a Key Role in the Organisation of Collective Movements in a Group of Domestic Horses. *Ethology*, 121(9), 888–902. <https://doi.org/10.1111/eth.12402>
- Brown, C., Jones, F., & Braithwaite, V. (2005). In situ examination of boldness–shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour*, 70(5), 1003–1009. <https://doi.org/10.1016/J.ANBEHAV.2004.12.022>
- Brown, D. J., Fogarty, N. M., Iker, C. L., Ferguson, D. M., Blache, D., & Gaunt, G. M. (2016). Genetic evaluation of maternal behaviour and temperament in Australian sheep. *Animal Production Science*, 56(4), 767. <https://doi.org/10.1071/AN14945>
- Bureau of Meteorology. (n.d.). Daily Rainfall - 046128. Retrieved October 25, 2018, from [http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p\\_nccObsCode=136&p\\_display\\_type=dailyDataFile&p\\_startYear=&p\\_c=&p\\_stn\\_num=046128](http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=136&p_display_type=dailyDataFile&p_startYear=&p_c=&p_stn_num=046128)
- Cafe, L. M., Robinson, D. L., Ferguson, D. M., McIntyre, B. L., Geesink, G. H., & Greenwood, P. L. (2011). Cattle temperament: Persistence of assessments and associations with productivity, efficiency, carcass and meat quality traits1. *Journal of Animal Science*, 89(5), 1452–1465. <https://doi.org/10.2527/jas.2010-3304>
- Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197(3–4), 516–519. <https://doi.org/10.1016/J.ECOLMODEL.2006.03.017>
- Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlshaw, G., & Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biological Reviews*, 88(2), 465–475. <https://doi.org/10.1111/brv.12007>
- Carter, A. J., Heinsohn, R., Goldizen, A. W., & Biro, P. A. (2012). Boldness, trappability and sampling bias in wild lizards. *Animal Behaviour*, 83(4), 1051–1058. <https://doi.org/10.1016/J.ANBEHAV.2012.01.033>
- Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlshaw, G. (2012). How not to measure boldness: novel object and antipredator responses are not the same in wild baboons. *Animal Behaviour*, 84(3), 603–609. <https://doi.org/10.1016/J.ANBEHAV.2012.06.015>
- Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlshaw, G. (2013). Personality predicts decision making only when information is unreliable. *Animal Behaviour*, 86(3), 633–639. <https://doi.org/10.1016/J.ANBEHAV.2013.07.009>
- Chapman, B. B., Hulthén, K., Blomqvist, D. R., Hansson, L.-A., Nilsson, J.-Å., Brodersen, J., ... Brönmark, C. (2011). To boldly go: individual differences in boldness influence migratory

tendency. *Ecology Letters*, 14(9), 871–876. <https://doi.org/10.1111/j.1461-0248.2011.01648.x>

Chock, R. Y., Wey, T. W., Ebensperger, L. A., & Hayes, L. D. (2017). Evidence for a behavioural syndrome and negative social assortment by exploratory personality in the communally nesting rodent, *Octodon degus*. *Behaviour*, 154(5), 541–562. <https://doi.org/10.1163/1568539X-00003433>

Cockram, M. (2004). A review of behavioural and physiological responses of sheep to stressors to identify potential behavioural signs of distress. *Animal Welfare*, 13(3), 283–291. Retrieved from <https://www.ingentaconnect.com/content/ufaw/aw/2004/00000013/00000003/art00003>

Colléter, M., & Brown, C. (2011). Personality traits predict hierarchy rank in male rainbowfish social groups. *Animal Behaviour*, 81(6), 1231–1237. <https://doi.org/10.1016/j.ANBEHAV.2011.03.011>

Conradt, L., Zollner, P. A., Roper, T. J., Frank, K., & Thomas, C. D. (2003). Foray search: an effective systematic dispersal strategy in fragmented landscapes. *The American Naturalist*, 161(6), 905–915. <https://doi.org/10.1086/375298>

Cooper, W. E. (2006). Dynamic Risk Assessment: Prey Rapidly Adjust Flight Initiation Distance to Changes in Predator Approach Speed. *Ethology*, 112(9), 858–864. <https://doi.org/10.1111/j.1439-0310.2006.01240.x>

Cooper, W. E. (2009). Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). *Behavioral Ecology and Sociobiology*, 63(12), 1765–1771. <https://doi.org/10.1007/s00265-009-0799-1>

Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings. Biological Sciences*, 274(1608), 383–390. <https://doi.org/10.1098/rspb.2006.3734>

Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1560), 4065–4076. <https://doi.org/10.1098/rstb.2010.0176>

Cote, J., Fogarty, S., Tymen, B., Sih, A., & Brodin, T. (2013). Personality-dependent dispersal cancelled under predation risk. *Proceedings. Biological Sciences*, 280(1773), 20132349. <https://doi.org/10.1098/rspb.2013.2349>

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T., & Sih, A. (2010). Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings. Biological Sciences*, 277(1687), 1571–1579. <https://doi.org/10.1098/rspb.2009.2128>

Couzin, I. D., Krause, J., James, R., Ruxton, G. D., & Franks, N. R. (2002). Collective Memory and Spatial Sorting in Animal Groups. *Journal of Theoretical Biology*, 218(1), 1–11. <https://doi.org/10.1006/JTBI.2002.3065>

Cresswell, W. (1994). Flocking is an effective anti-predation strategy in redshanks, *Tringa*

- totanus. *Animal Behaviour*, 47(2), 433–442. <https://doi.org/10.1006/ANBE.1994.1057>
- Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R. (2009). Behavioural trait assortment in a social network: patterns and implications. *Behavioral Ecology and Sociobiology*, 63(10), 1495–1503. <https://doi.org/10.1007/s00265-009-0802-x>
- Curley, K. O., Paschal, J. C., Welsh, T. H., & Randel, R. D. (2006). Technical note: Exit velocity as a measure of cattle temperament is repeatable and associated with serum concentration of cortisol in Brahman bulls1. *Journal of Animal Science*, 84(11), 3100–3103. <https://doi.org/10.2527/jas.2006-055>
- Dall, S. R. X., & Griffith, S. C. (2014). An empiricist guide to animal personality variation in ecology and evolution. *Frontiers in Ecology and Evolution*, 2, 3. <https://doi.org/10.3389/fevo.2014.00003>
- David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour*, 81(1), 219–224. <https://doi.org/10.1016/j.ANBEHAV.2010.10.008>
- Davies, N. B. (1977). Prey selection and the search strategy of the spotted flycatcher (*Muscicapa striata*): A field study on optimal foraging. *Animal Behaviour*, 25, 1016–1033. [https://doi.org/10.1016/0003-3472\(77\)90053-7](https://doi.org/10.1016/0003-3472(77)90053-7)
- DeWitt, T. J., Sih, A., & Wilson, D. S. (1998). Costs and limits of phenotypic plasticity. *Trends in Ecology & Evolution*, 13(2), 77–81. [https://doi.org/10.1016/S0169-5347\(97\)01274-3](https://doi.org/10.1016/S0169-5347(97)01274-3)
- Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings. Biological Sciences*, 271(1541), 847–852. <https://doi.org/10.1098/rspb.2004.2680>
- Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). *Proceedings. Biological Sciences*, 270(1516), 741–747. <https://doi.org/10.1098/rspb.2002.2300>
- Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25(2), 81–89. <https://doi.org/10.1016/j.TREE.2009.07.013>
- Dingemanse, N., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*, 142(9), 1159–1184. <https://doi.org/10.1163/156853905774539445>
- Dray, S., Royer-Carenzi, M., & Calenge, C. (2010). The exploratory analysis of autocorrelation in animal-movement studies. *Ecological Research*, 25(3), 673–681. <https://doi.org/10.1007/s11284-010-0701-7>
- Duckworth, R. A. (2006). Aggressive behaviour affects selection on morphology by influencing settlement patterns in a passerine bird. *Proceedings. Biological Sciences*, 273(1595), 1789–1795. <https://doi.org/10.1098/rspb.2006.3517>
- Duckworth, R. A. (2008). Adaptive dispersal strategies and the dynamics of a range expansion. *The American Naturalist*, 172 Suppl 1(S1), S4–17. <https://doi.org/10.1086/588289>

- Duckworth, R. A., & Badyaev, A. V. (2007). Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America*, 104(38), 15017–15022. <https://doi.org/10.1073/pnas.0706174104>
- Dumont, B., & Boissy, A. (2000). Grazing behaviour of sheep in a situation of conflict between feeding and social motivations. *Behavioural Processes*, 49(3), 131–138. [https://doi.org/10.1016/S0376-6357\(00\)00082-6](https://doi.org/10.1016/S0376-6357(00)00082-6)
- Dwyer, C. (2004). How has the risk of predation shaped the behavioural responses of sheep to fear and distress? *Animal Welfare*, 13(3), 269–281. Retrieved from <https://www.ingentaconnect.com/content/ufaw/aw/2004/00000013/00000003/art00002>
- Dwyer, C., & Lawrence, A. (2000). MATERNAL BEHAVIOUR IN DOMESTIC SHEEP (OVIS ARIES): CONSTANCY AND CHANGE WITH MATERNAL EXPERIENCE. *Behaviour*, 137(10), 1391–1413. <https://doi.org/10.1163/156853900501999>
- Dyer, J. R. G., Croft, D. P., Morrell, L. J., & Krause, J. (2009). Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, 20(1), 165–171. <https://doi.org/10.1093/beheco/arn129>
- Eggeman, S. L., Hebblewhite, M., Bohm, H., Whittington, J., & Merrill, E. H. (2016). Behavioural flexibility in migratory behaviour in a long-lived large herbivore. *Journal of Animal Ecology*, 85(3), 785–797. <https://doi.org/10.1111/1365-2656.12495>
- Fox, R. A., Ladage, L. D., Roth, T. C., & Pravosudov, V. V. (2009). Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. *Animal Behaviour*, 77(6), 1441–1448. <https://doi.org/10.1016/J.ANBEHAV.2009.02.022>
- Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. (2001). Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *The American Naturalist*, 158(2), 124–135. <https://doi.org/10.1086/321307>
- Garthe, S., Montevecchi, W. A., Chapdelaine, G., Rail, J.-F., & Hedd, A. (2007). Contrasting foraging tactics by northern gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields. *Marine Biology*, 151(2), 687–694. <https://doi.org/10.1007/s00227-006-0523-x>
- Godin, J. G., & Dugatkin, L. A. (1996). Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proceedings of the National Academy of Sciences of the United States of America*, 93(19), 10262–10267. <https://doi.org/10.1073/PNAS.93.19.10262>
- Griesser, M., Nystrand, M., Eggers, S., & Ekman, J. (2008). Social constraints limit dispersal and settlement decisions in a group-living bird species. *Behavioral Ecology*, 19(2), 317–324. <https://doi.org/10.1093/beheco/arm131>
- Hall, M. L., van Asten, T., Katsis, A. C., Dingemanse, N. J., Magrath, M. J. L., & Mulder, R. A. (2015). Animal personality and pace-of-life syndromes: do fast-exploring fairy-wrens die young? *Frontiers in Ecology and Evolution*, 3, 28. <https://doi.org/10.3389/fevo.2015.00028>



- Harcourt, J. L., Ang, T. Z., Sweetman, G., Johnstone, R. A., & Manica, A. (2009). Social Feedback and the Emergence of Leaders and Followers. *Current Biology*, 19(3), 248–252. <https://doi.org/10.1016/J.CUB.2008.12.051>
- Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Patterson, D. A., Cooke, S. J., & Power, M. (2015). Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*). *Behavioral Ecology*, 26(2), 483–492. <https://doi.org/10.1093/beheco/aru216>
- Hauschildt, V., & Gerken, M. (2015). Individual gregariousness predicts behavioural synchronization in a foraging herbivore, the sheep (*Ovis aries*). *Behavioural Processes*, 113, 110–112. <https://doi.org/10.1016/J.BEPROC.2015.01.013>
- Hensley, N. M., Cook, T. C., Lang, M., Petelle, M. B., & Blumstein, D. T. (2012). Personality and habitat segregation in giant sea anemones (*Condylactis gigantea*). *Journal of Experimental Marine Biology and Ecology*, 426–427, 1–4. <https://doi.org/10.1016/J.JEMBE.2012.05.011>
- Hiendleder, S., Janke, A., & Wassmuth, R. (2001). *Molecular data on wild sheep genetic resources and domestic sheep evolution*. Arch. Tierz., Dummerstorf (Vol. 44). Retrieved from <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.627.5199&rep=rep1&type=pdf>
- Huey, R. B., & Pianka, E. R. (1981). Ecological Consequences of Foraging Mode. *Ecology*, 62(4), 991–999. <https://doi.org/10.2307/1936998>
- Ioannou, C. C., & Dall, S. R. X. (2016). Individuals that are consistent in risk-taking benefit during collective foraging. *Scientific Reports*, 6(1), 33991. <https://doi.org/10.1038/srep33991>
- Johnson, C. J., Parker, K. L., Heard, D. C., & Gillingham, M. P. (2002). Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology*, 71(2), 225–235. <https://doi.org/10.1046/j.1365-2656.2002.00595.x>
- Johnson, K. V.-A., Aplin, L. M., Cole, E. F., Farine, D. R., Firth, J. A., Patrick, S. C., & Sheldon, B. C. (2017). Male great tits assort by personality during the breeding season. *Animal Behaviour*, 128, 21–32. <https://doi.org/10.1016/J.ANBEHAV.2017.04.001>
- Jolles, J. W., Aaron Taylor, B., & Manica, A. (2016). Recent social conditions affect boldness repeatability in individual sticklebacks. *Animal Behaviour*, 112, 139–145. <https://doi.org/10.1016/J.ANBEHAV.2015.12.010>
- Jolles, J. W., Boogert, N. J., Sridhar, V. H., Couzin, I. D., & Manica, A. (2017). Consistent Individual Differences Drive Collective Behavior and Group Functioning of Schooling Fish. *Current Biology*, 27(18), 2862–2868.e7. <https://doi.org/10.1016/J.CUB.2017.08.004>
- Keeling, J.L. & Gonyu, H.W. (2001). *Social Behavior in Farm Animals*. Oxon: Wellington Publishing, (Chapter 8).
- Krackow, S. (2003). Motivational and Heritable Determinants of Dispersal Latency in Wild Male House Mice (*Mus musculus musculus*). *Ethology*, 109(8), 671–689. <https://doi.org/10.1046/j.1439-0310.2003.00913.x>
- Kurvers, R. H. J. M., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C., & Prins, H. H. T. (2009). Personality differences explain leadership in barnacle geese. *Animal*

*Behaviour*, 78(2), 447–453. <https://doi.org/10.1016/J.ANBEHAV.2009.06.002>

Kurvers, R. H. J. M., Prins, H. H. T., van Wieren, S. E., van Oers, K., Nolet, B. A., & Ydenberg, R. C. (2010). The effect of personality on social foraging: shy barnacle geese scrounge more. *Proceedings. Biological Sciences*, 277(1681), 601–608. <https://doi.org/10.1098/rspb.2009.1474>

Kurvers, R. H. J. M., Van Oers, K., Nolet, B. A., Jonker, R. M., Van Wieren, S. E., Prins, H. H. T., & Ydenberg, R. C. (2010). Personality predicts the use of social information. *Ecology Letters*, 13(7), 829–837. <https://doi.org/10.1111/j.1461-0248.2010.01473.x>

Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J. E., Kindberg, J., & Pelletier, F. (2016). Quantifying consistent individual differences in habitat selection. *Oecologia*, 180(3), 697–705. <https://doi.org/10.1007/s00442-015-3500-6>

Luttbeg, B., & Sih, A. (2010). Risk, resources and state-dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1560), 3977–3990. <https://doi.org/10.1098/rstb.2010.0207>

Machado, R. F., Cerezer, F. O., Hendges, C. D., & Cáceres, N. C. (2017). Factors affecting the home range size of felids (Mammalia, Carnivora) with emphasis on three American species. *Ecología Austral*, 27(2), 232–241. Retrieved from [http://www.scielo.org.ar/scielo.php?pid=S1667-782X2017000300004&script=sci\\_arttext&tlng=en](http://www.scielo.org.ar/scielo.php?pid=S1667-782X2017000300004&script=sci_arttext&tlng=en)

Maddox, J. F., Davies, K. P., Crawford, A. M., Hulme, D. J., Vaiman, D., Cribiu, E. P., ... van Hest, B. (2001). An enhanced linkage map of the sheep genome comprising more than 1000 loci. *Genome Research*, 11(7), 1275–1289. <https://doi.org/10.1101/gr.135001>

Magurran, A. E. (1990). The adaptive significance of schooling as an anti-predator defence in fish. *Annales Zoologici Fennici*. Finnish Zoological and Botanical Publishing Board. <https://doi.org/10.2307/23736019>

Maniatis, N., & Pollott, G. E. (2003). The impact of data structure on genetic (co)variance components of early growth in sheep, estimated using an animal model with maternal effects. *Journal of Animal Science*, 81(1), 101–108. <https://doi.org/10.2527/2003.811101x>

Manning, J. K., Fogarty, E. S., Trotter, M. G., Schneider, D. A., Thomson, P. C., Bush, R. D., & Cronin, G. M. (2014). A pilot study into the use of global navigation satellite system technology to quantify the behavioural responses of sheep during simulated dog predation events. *Animal Production Science*, 54(10), 1676. <https://doi.org/10.1071/AN14221>

Massen, J. J. M., & Koski, S. E. (2014). Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*, 35(1), 1–8. <https://doi.org/10.1016/J.EVOLHUMBEHAV.2013.08.008>

McLaughlin, R. L., & Montgomerie, R. D. (1989). Brood dispersal and multiple central place foraging by Lapland longspur parents. *Behavioral Ecology and Sociobiology*, 25(3), 207–215. <https://doi.org/10.1007/BF00302920>

Meat and Livestock Australia. (n.d.). *Australian sheep*. Retrieved from

[https://www.mla.com.au/globalassets/mla-corporate/prices--markets/documents/trends-analysis/sheep-projections/mla\\_australian-sheep-industry-projections-2017.pdf](https://www.mla.com.au/globalassets/mla-corporate/prices--markets/documents/trends-analysis/sheep-projections/mla_australian-sheep-industry-projections-2017.pdf)

- Michelena, P. (2005). An experimental study of social attraction and spacing between the sexes in sheep. *Journal of Experimental Biology*. <https://doi.org/10.1242/jeb.01909>
- Michelena, P., Jeanson, R., Deneubourg, J.-L., & Sibbald, A. M. (2010). Personality and collective decision-making in foraging herbivores. *Proceedings. Biological Sciences*, 277(1684), 1093–1099. <https://doi.org/10.1098/rspb.2009.1926>
- Michelena, P., Sibbald, A. M., Erhard, H. W., & McLeod, J. E. (2009). Effects of group size and personality on social foraging: the distribution of sheep across patches. *Behavioral Ecology*, 20(1), 145–152. <https://doi.org/10.1093/beheco/arn126>
- Michelot, T., Langrock, R., & Patterson, T. A. (2016). moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution*, 7(11), 1308–1315. <https://doi.org/10.1111/2041-210X.12578>
- Minderman, J., Reid, J. M., Evans, P. G. H., & Whittingham, M. J. (2009). Personality traits in wild starlings: exploration behavior and environmental sensitivity. *Behavioral Ecology*, 20(4), 830–837. <https://doi.org/10.1093/beheco/arp067>
- Minderman, J., Reid, J. M., Hughes, M., Denny, M. J. H., Hogg, S., Evans, P. G. H., & Whittingham, M. J. (2010). Novel environment exploration and home range size in starlings *Sturnus vulgaris*. *Behavioral Ecology*, 21(6), 1321–1329. <https://doi.org/10.1093/beheco/arq151>
- Müller, R., & von Keyserlingk, M. A. G. (2006). Consistency of flight speed and its correlation to productivity and to personality in *Bos taurus* beef cattle. *Applied Animal Behaviour Science*, 99(3–4), 193–204. <https://doi.org/10.1016/j.APPLANIM.2005.05.012>
- Munday, P. L. (2001). Fitness consequences of habitat use and competition among coral-dwelling fishes. *Oecologia*, 128(4), 585–593. <https://doi.org/10.1007/s004420100690>
- Nakayama, S., Harcourt, J. L., Johnstone, R. A., & Manica, A. (2016). Who directs group movement? Leader effort versus follower preference in stickleback fish of different personality. *Biology Letters*, 12(5), 20160207. <https://doi.org/10.1098/rsbl.2016.0207>
- Namba, T. (1980). Density-dependent dispersal and spatial distribution of a population. *Journal of Theoretical Biology*, 86(2), 351–363. [https://doi.org/10.1016/0022-5193\(80\)90011-9](https://doi.org/10.1016/0022-5193(80)90011-9)
- Pays, O., Benhamou, S., Helder, R., & Gerard, J.-F. (2007). The dynamics of group formation in large mammalian herbivores: an analysis in the European roe deer. *Animal Behaviour*, 74(5), 1429–1441. <https://doi.org/10.1016/J.ANBEHAV.2007.02.012>
- Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. A., & Blumstein, D. T. (2013). Development of boldness and docility in yellow-bellied marmots. *Animal Behaviour*, 86(6), 1147–1154. <https://doi.org/10.1016/J.ANBEHAV.2013.09.016>
- Petherick, J. C., Doogan, V. J., Holroyd, R. G., Olsson, P., & Venus, B. K. (2009). Quality of handling and holding yard environment, and beef cattle temperament: 1. Relationships with flight speed and fear of humans. *Applied Animal Behaviour Science*, 120(1–2), 18–27.

<https://doi.org/10.1016/J.APPLANIM.2009.05.008>

- Pike, T. W., Samanta, M., Lindström, J., & Royle, N. J. (2008). Behavioural phenotype affects social interactions in an animal network. *Proceedings. Biological Sciences*, 275(1650), 2515–2520. <https://doi.org/10.1098/rspb.2008.0744>
- Purchas, R. W., Davies, A. S., & Abdullah, A. Y. (1991). An objective measure of muscularity: Changes with animal growth and differences between Genetic lines of southdown sheep. *Meat Science*, 30(1), 81–94. [https://doi.org/10.1016/0309-1740\(91\)90037-Q](https://doi.org/10.1016/0309-1740(91)90037-Q)
- Quinn, J. L., Cole, E. F., Patrick, S. C., & Sheldon, B. C. (2011). Scale and state dependence of the relationship between personality and dispersal in a great tit population. *Journal of Animal Ecology*, 80(5), 918–928. <https://doi.org/10.1111/j.1365-2656.2011.01835.x>
- R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/>
- Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1560), 4051–4063. <https://doi.org/10.1098/rstb.2010.0208>
- Reed, B. M. (2018). Interspecific and Intraspecific Variation in the Movement Ecology of Ectotherms across Different Spatial and Temporal Scales. *ETD Collection for University of Nebraska - Lincoln*. Retrieved from <http://digitalcommons.unl.edu/dissertations/AAI10845582>
- Reynolds, M. H., Hatfield, J. S., Laniawe, L. P., Vekasy, M. S., Klavitter, J. L., Berkowitz, P., ... Walters, J. R. (2012). Influence of space use on fitness and the reintroduction success of the Laysan teal. *Animal Conservation*, 15(3), 305–317. <https://doi.org/10.1111/j.1469-1795.2012.00520.x>
- RStudio Team. (2015). RStudio: Integrated Development for R. Retrieved October 25, 2018, from <http://rstudio.com>
- Saïd, S., Gaillard, J.-M., Widmer, O., Débias, F., Bourgoïn, G., Delorme, D., & Roux, C. (2009). What shapes intra-specific variation in home range size? A case study of female roe deer. *Oikos*, 118(9), 1299–1306. <https://doi.org/10.1111/j.1600-0706.2009.17346.x>
- Selmann, M. W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K., & Hollmén, T. (2012). Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Animal Behaviour*, 84(4), 889–896. <https://doi.org/10.1016/J.ANBEHAV.2012.07.012>
- Serrano-Davies, E., Araya-Ajoy, Y. G., Dingemanse, N. J., & Sanz, J. J. (2017). Personality-related differences in response to habitat in Mediterranean blue tits. *Ethology*, 123(11), 861–869. <https://doi.org/10.1111/eth.12656>
- Seyfarth, R. M., Silk, J. B., & Cheney, D. L. (2014). Social bonds in female baboons: the interaction between personality, kinship and rank. *Animal Behaviour*, 87, 23–29. <https://doi.org/10.1016/J.ANBEHAV.2013.10.008>

- Sheep Producers Australia. (2017). Our Industry. Retrieved October 25, 2018, from <http://sheepproducers.com.au/about-us/our-industry/>
- Sibbald, A. M., Erhard, H. W., McLeod, J. E., & Hooper, R. J. (2009). Individual personality and the spatial distribution of groups of grazing animals: An example with sheep. *Behavioural Processes*, 82(3), 319–326. <https://doi.org/10.1016/J.BEPROC.2009.07.011>
- Siegfried, W. R., & Underhill, L. G. (1975). Flocking as an anti-predator strategy in doves. *Animal Behaviour*, 23, 504–508. [https://doi.org/10.1016/0003-3472\(75\)90126-8](https://doi.org/10.1016/0003-3472(75)90126-8)
- Signer, J., & Ovaskainen, O. (2017). Detecting the influence of environmental covariates on animal movement: a semivariance approach. *Methods in Ecology and Evolution*, 8(5), 561–570. <https://doi.org/10.1111/2041-210X.12692>
- Sih, A., Mathot, K. J., Moirón, M., Montiglio, P.-O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state–behaviour feedbacks: a review and guide for empiricists. *Trends in Ecology & Evolution*, 30(1), 50–60. <https://doi.org/10.1016/J.TREE.2014.11.004>
- Singleton, J. M., & Garland, T. (2018). Among-Individual Variation in Desert Iguanas (Squamata: *Dipsosaurus dorsalis*): Endurance Capacity Is Positively Related to Home Range Size. *Physiological and Biochemical Zoology : PBZ*, 91(1), 725–730. <https://doi.org/10.1086/695692>
- Sloan Wilson, D., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, 9(11), 442–446. [https://doi.org/10.1016/0169-5347\(94\)90134-1](https://doi.org/10.1016/0169-5347(94)90134-1)
- Spiegel, O., Leu, S. T., Bull, C. M., & Sih, A. (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters*, 20(1), 3–18. <https://doi.org/10.1111/ele.12708>
- Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biological Reviews*, 85(2), 301–325. <https://doi.org/10.1111/j.1469-185X.2009.00103.x>
- Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation*, 141(9), 2159–2173. <https://doi.org/10.1016/J.BIOCON.2008.06.026>
- Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8(11), 1639–1644. <https://doi.org/10.1111/2041-210X.12797>
- Street, G. M., Fieberg, J., Rodgers, A. R., Carstensen, M., Moen, R., Moore, S. A., ... Forester, J. D. (2016). Habitat functional response mitigates reduced foraging opportunity: implications for animal fitness and space use. *Landscape Ecology*, 31(9), 1939–1953. <https://doi.org/10.1007/s10980-016-0372-z>
- Toscano, B. J., Gownaris, N. J., Heerhartz, S. M., & Monaco, C. J. (2016). Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia*, 182(1), 55–69. <https://doi.org/10.1007/s00442-016-3648-8>

- van Overveld, T., & Matthysen, E. (2010). Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). *Biology Letters*, 6(2), 187–190. <https://doi.org/10.1098/rsbl.2009.0764>
- Van Valen, L. (1965). Morphological Variation and Width of Ecological Niche. *The American Naturalist*, 99(908), 377–390. <https://doi.org/10.1086/282379>
- Viana, D. S., Granados, J. E., Fandos, P., Pérez, J. M., Cano-Manuel, F. J., Burón, D., ... Soriguer, R. C. (2018). Linking seasonal home range size with habitat selection and movement in a mountain ungulate. *Movement Ecology*, 6(1), 1. <https://doi.org/10.1186/s40462-017-0119-8>
- Walton, Z., Samelius, G., Odden, M., & Willebrand, T. (2017). Variation in home range size of red foxes *Vulpes vulpes* along a gradient of productivity and human landscape alteration. *PLOS ONE*, 12(4), e0175291. <https://doi.org/10.1371/journal.pone.0175291>
- Ward, A. J. W., Thomas, P., Hart, P. J. B., & Krause, J. (2004). Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, 55(6), 561–568. <https://doi.org/10.1007/s00265-003-0751-8>
- Wilson, A. D. M., & McLaughlin, R. L. (2007). Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour*, 74(4), 689–698. <https://doi.org/10.1016/j.ANBEHAV.2007.01.009>
- Worton, B. J. (1989). Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology*, 70(1), 164–168. <https://doi.org/10.2307/1938423>
- Zera, A. J., & Denno, R. F. (1997). PHYSIOLOGY AND ECOLOGY OF DISPERSAL POLYMORPHISM IN INSECTS. *Annual Review of Entomology*, 42(1), 207–230. <https://doi.org/10.1146/annurev.ento.42.1.207>
- Zollner, P. A., & Lima, S. L. (1999). SEARCH STRATEGIES FOR LANDSCAPE-LEVEL INTERPATCH MOVEMENTS. *Ecology*, 80(3), 1019–1030. [https://doi.org/10.1890/0012-9658\(1999\)080\[1019:SSFLI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1019:SSFLI]2.0.CO;2)

## Appendix I: Ethics Approval

### Animal Ethics Application AEC Meeting Outcome - 5201832493657



donotreply@infonetica.net

Thu 6/09, 10:44 AM

Stephan Leu; Animal Ethics; Stephan Leu; Simon Griffith; Molly Gilmour (HDR) ✕



Reply all | ▾

Inbox

Dear: Dr Leu,

Your notification of collaboration for the following project was considered and noted by the Animal Ethics Committee at the meeting of 23 August 2018.

3249 - 5201832493657 - Leu - Social networks and movement ecology in domestic sheep

#### Decision:

The Committee noted the collaborative report.

This email serves as official notification of the AEC decision. Please keep a copy for your records. Should you have any queries or require clarification, please contact the AEC Secretariat.

Regards,

#### Animal Ethics

Research Services | CSC-17 Wallys Walk L3,

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# Animal Care & Ethics Committee

Authority to Conduct Animal Research Project

Never Stand Still

Division of Research

Research Ethics and Compliance Support Unit

Modification Approval Date:	30/04/2018
Modification Type:	Personnel

**ACEC Number:** 18/19B

**Title:** Social networks and movement ecology in domestic sheep

**Start/Expiry Dates:** 22 February 2018 to 21 February 2021

*Please note that under Section 27 of the NSW Animal Research Act, 1985, the Animal Research Authority is current for a period of 12 months from the date of issue unless cancelled sooner. Renewal of the authority is conditional upon submission of a satisfactory annual report to the ACEC.*

**Chief Investigator:** Dr Keith Eric Andrew Leggett

**Address:** Fowler's Gap Arid Zone Res Sta

**Contact Phone Number:** 08-80912511

**Email Address:** z3317332@unsw.edu.au

**Authorised Personnel** Dr Simon Charles Griffith, Dr Stephan Leu, Ms Molly Gilmour, Mr Garry Phillip Dowling

## Conditions of Approval Particular to this Project

Please also download the Adverse or Unexpected Report Form from the following site:

<http://research.unsw.edu.au/animal-research-ethics-unsw>

## Conditions of Approval Applicable to All projects

1. All cages holding animals for this project should be labelled with its ACEC Number, Expiry Date, Chief Investigator, and Contact Phone Number, as listed above.
2. Modifications to this project and the addition of new personnel must have prior written approval of the ACEC. Requests should be made on the online system.
3. All projects are subject to annual review by the ACEC.
4. Please have this letter of authority available during site inspection by ACEC members
5. Please distribute copies of this letter of authority to the other authorised personnel listed above.
6. In the event of an unforeseen adverse incident (e.g. unexpected deaths), the NHMRC Code (2.4.18ix) requires that investigators promptly notify the ACEC ([animalethics@unsw.edu.au](mailto:animalethics@unsw.edu.au) and [animalcare@unsw.edu.au](mailto:animalcare@unsw.edu.au)).
7. If a project involves surgery, the researchers are required to monitor animals daily for at least the first 7 days post operatively.

The ACEC considered the above project and is pleased to advise that this project meets the requirements as set out in the Australian Code for the care and use of animals for scientific purposes\* The committee recommends approval.

\* (<http://www.nhmrc.gov.au/guidelines/publications/ea28>)

Having taken into account the advice of the Committee, the Deputy Vice-Chancellor (Research) has approved this project to proceed.



Authorised on behalf of the Deputy Vice-Chancellor (Research) on 30 April 2018



Professor Richard Bryan Lock

Presiding Member, Committee 'A'