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Shelter seeking behaviour of donkeys and horses in a temperate climate.

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Abstract

Domestic donkeys descended from wild asses, adapted to the semi-arid climates of Africa, whereas domestic horses originate from more temperate areas of Eurasia. Despite this difference in evolutionary history, modern domestic equids can be found throughout the world, in a wide range of conditions, many of which are very different from their natural environments. To explore the protection from the elements that different equid species may require in the temperate climate of the UK, the shelter seeking behaviour of 135 donkeys and 73 horses was assessed across a period of 16 months, providing a total of 13513 observations. The location of each animal (inside a constructed shelter, outside unprotected or using natural shelter) was recorded alongside measures of environmental conditions including temperature, wind speed, lux, precipitation and level of insect challenge. Statistical models revealed clear differences in the constructed-shelter-seeking behaviour of donkeys and horses. Donkeys sought shelter significantly more often at lower temperatures whereas horses tended to move inside when the temperature rose above 20°C. Donkeys were more affected by precipitation, with the majority of them moving indoors when it rained. Donkeys also showed a higher rate of shelter use when wind speed increased to moderate, while horses remained outside. Horses appeared to be more affected by insect challenge, moving inside as insect harassment outside increased. There were also significant differences in the use of natural shelter by the two species, with donkeys using natural shelter relatively more often to shelter from rain and wind and horses seeking natural shelter relatively more frequently when sunny. These results reflect donkeys' and horses' adaptation to different climates and suggest that the shelter requirements of these two equid species differ, with donkeys seeking additional protection from the elements in temperate climates.

Keywords: Equine welfare; animal welfare; environmental adaptation; domestication; protection from the elements; shelter use

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Introduction

Equids may seek shelter under various environmental and climatic conditions, such as hot or cold weather, heavy rain, or high levels of insect challenge. However, the extent to which each of these environmental factors affect shelter seeking behaviour in domestic donkeys and horses has yet to be directly compared and is likely to reveal differences based on their evolutionary history. Although the precise processes by which horses and donkeys were domesticated is still under debate, domestic donkeys are believed to have originated from the African wild ass (*Equus africanus*) in semi-arid regions of Northeast Africa and the Arabian peninsula, around 6,000 years ago (Rosenbom et al., 2015; Rossel et al., 2008). Modern horses are believed to have been domesticated at a similar time, but in the more temperate regions of Eurasia (Gaunitz et al., 2018; Outram et al., 2009). Although cave paintings in France depict a now extinct small equid with long ears, the earliest finds of domesticated donkey bones in Europe date from around 800 BCE (Geigl and Grange, 2012). It can therefore be assumed that modern domesticated donkeys, unlike native horse and pony breeds, have evolved for warmer and dryer climates and not for the conditions of Northern Europe.

Differences in the biology of donkeys and horses reflect their different evolutionary histories and suggest adaptation to different environments. Donkeys are able to extract moisture from low quality forage more efficiently than horses, have a lower sweat rate and can go without water for several days (Zakari et al., 2015). Their long ears are thought to aid temperature regulation, and their single coat layer is not thought to contain waterproof lanolin oil, although these attributes have not been systematically tested. The coat of standard donkeys does not significantly increase in weight during the winter in the temperate climate of the UK, whereas native pony coats can increase by over 200% in cold, winter climates (Autio et al., 2006; Osthaus et al., 2018). Horses have shorter ears, thicker tails, and a two-layered, waterproof coat, and they require water daily. Przewalski horses and Shetland ponies (a pony breed originating in a subarctic climate) are able to slow their metabolism down in winter, a process called hypometabolism (Brinkmann et al., 2012; Kuntz et al., 2006). Based on this, we may expect donkeys to have a reduced capacity to cope with cold, wet and windy conditions compared to horses. Differences in evolutionary home ranges, coupled with the associated differences in the biology of the species, are also likely to produce differences in the nature of, and response to, insect harassment.

Exposure to wet, cold and windy conditions require warm-blooded organisms to increase their metabolism to ensure a constant and sufficient body core temperature. The thermal neutral zone (TNZ) of an animal refers to the ambient temperature range in which core body

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temperature can be maintained without expending additional energy beyond that required for maintenance (Holcomb, 2017). TNZ may vary depending on other environmental factors beyond ambient temperature including wind speed, humidity, precipitation and solar radiation. The lower critical temperature (LCT) is the point below which the metabolism can no longer produce enough heat to avoid heat loss and is a valuable measure for recommendations of extra feeding and to determine minimal environmental temperatures required for health and welfare of a species. It is known for different horse breeds and their environments (see Autio et al., 2007 for review) and varies between -15˚ to 10˚C, depending on age, condition, breed and acclimatisation. The welfare of Equids may be compromised not just in cold conditions but also when adequate protection from the elements is not provided during hot weather. Above an ambient temperature of 20˚C horses show an increased evaporative heat flow (Morgan et al., 1997) and their upper critical limit (UCT) has been calculated to be 20-30˚C (Morgan, 1998). The TNZ has not been calculated for donkeys.

To date, the shelter seeking behaviour of wild and domestic horses has been documented across a range of climates – showing that they seek shelter in wet (Michanek and Bentorp, 1996), windy (Heleski and Murtazashvili, 2010), hot and cold conditions (Holcomb et al., 2014; Mejdell and Bøe, 2005; Tyler, 1972) and in times of increased fly activity (Keiper and Berger, 1982). Feral horses have been observed moving as a group to shade areas at the hotter times of day and shade use in domestic horses can rise to over 70% when temperatures increase above the UCT (Holcomb, 2017; Keiper and Berger, 1982). Breezy areas may also be sought out when temperatures or insect challenge are high (Crowell-Davis, 1994; Tyler, 1972), with insect challenge suggested as a strong motivator to seek protection during hot, sunny days (Rubenstein and Hohmann, 1989). Several studies have reported an increase in shelter use during rain, but primarily when this occurs in conjunction with breezy or cold conditions (Heleski and Murtazashvili, 2010; Snoeks et al., 2015). A recent study of shelter seeking behaviour in horses in a temperate climate showed a significant increase in shelter use at temperatures below 7˚C and above 25˚C, corresponding to horses' TNZ, with significant shelter use (41%) even within the TNZ, potentially due to factors such as insect harassment (Snoeks et al., 2015). In contrast, a study of Icelandic horses during the cold, Nordic winter (with temperatures reaching -31˚C) reported low levels of shelter use (average 30%) across weather conditions (Mejdell and Bøe, 2005).

To our knowledge, there have been no physiological or behavioural studies of donkeys in colder climates, but hypothermia is a problem for donkeys during cold weather (Stephen et al., 2000). A few studies have assessed the responses of donkeys to climatic conditions in

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tropical environments and animals have been observed shivering when temperatures drop below 20˚C, a temperature far higher than the LCT reported for horses (Ayo et al., 2014). Baseline physiological measures of donkeys in the tropics, including heart rate, rectal temperature and respiration rate, have been recorded and can be used to assess heat stress (Ayo et al., 2014). The Nigerian rainy season, with its high ambient temperature and humidity, is thought to be thermally stressful to donkeys (Ayo et al., 2008). Research conducted in the hot-dry season showed that pack donkeys provided with shade after working experienced significantly lower levels of heat stress than those without shade (Minka and Ayo, 2007). However, the few studies of the effects of the climate on donkeys in tropical environments tend to be conducted on working equids, whose welfare and body condition is often poor. There are also no studies of shelter seeking behaviour in donkeys in any climate. It is therefore important to conduct research with healthy, unrestrained animals to assess the natural shelter seeking behaviours and baseline heat tolerance of donkeys in both hot and cold climates.

Here we provide an assessment and direct comparison of the shelter seeking behaviour of healthy, semi-free ranging donkeys and horses in a temperate climate. A sample of 208 donkeys and horses were observed over a 16 month period and the location and shelter use of the animals were recorded. Climatic conditions and levels of insect challenge were measured to assess the factors that influence shelter seeking behaviour and the extent to which the two species differ in their responses to environmental conditions.

Methods

Study Animals And Housing Details

A total of 135 donkeys (mean age = 17.56 ± 8.4 S.D., 53 females, 81 males) and 73 horses/ponies (mean age = 13.95 ± 7.72 S.D.; 29 females, 43 males) were observed during this study. Twenty-two of the donkeys in the sample were Poitou donkeys and the rest were standard donkeys. The horses were from a variety of breeds with 43 being classified as native/coldblooded types and 30 being classified as warm-blooded types. Some subjects were removed from the study due to relocation, illness, death, wearing a rug or being clipped. A total of 74 donkeys and 57 horses and ponies (subsequently referred to as horses throughout the paper) were monitored for the full observation period. When subjects were removed, additional subjects were added to replace lost subjects.

All donkeys and 30 horses were owned by The Donkey Sanctuary, the remaining horse subjects were either owned by LM, a private owner, the Dartmoor Pony Heritage Trust or were privately owned by staff at The Donkey Sanctuary. Animals at The Donkey Sanctuary

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were under the care of the veterinary team and all subjects were considered to be in good health with no history of disease in the preceding two years. All animals were unclipped and unrugged in the winter. Subjects were identified by their individual markings and, for the subjects kept at The Donkey Sanctuary, by neck collars showing their names. Subjects were from 18 social groups, kept at seven separate locations across Devon and Somerset, UK. All groups had an outside space throughout the study and free access to constructed shelters. All constructed shelters included a roof to protect the animals from rain and were of sufficient size for all group members to seek shelter if required (based on DEFRA guidelines (Department for Environment Food and Rural Affairs UK Government, 2018)). Natural shelter included the presence of bushes and trees in, or growing along the perimeter, of the enclosures (see Supplementary Material for details of the shelter available at each location).

Procedure

Data were collected from September 2015 to December 2016. Watson W-8681-Solar Weather stations were kept at each farm in a central position throughout the duration of the study to record precipitation levels. Researchers carried with them handheld weather stations (Skywatch Meteos - Anemo-thermometer with Ø 54 mm propeller) that recorded temperature and wind speed, and a lux meter (Sinometer MS6612). At the start of each observation session the precipitation rate from the previous hour was recorded from the fixed weather stations. In addition to this measure, researchers coded the current precipitation condition as either dry, drizzle/intermittent rain, or rain when collecting subject data. From outside the enclosure, so the animals were not disturbed, the location of each subject was recorded as either outside or inside a constructed shelter. If more than one constructed shelter was present in the field, the specific shelter was recorded. If an animal was outside, researchers recorded whether they were using any natural shelter as protection from the sun, rain or wind, whether they were not using natural shelter or whether no protection was required. To do this, researchers assessed whether it was sunny or overcast (determined by whether there were any clearly defined shadows visible) and, if it was sunny, whether the animal was standing in the sun or shade. When raining, researchers recorded whether the animal was using any natural protection such as trees. When the weather was calm, natural shelter from the wind was deemed not applicable but at higher wind speeds researchers recorded if subjects were standing exposed to the wind or using natural protection. If it was unclear from a distance whether animals were protected from the wind or rain, the location was recorded on a map and once all subject information was collected, the researcher stood in the location and assessed whether protection was afforded by that location. Observation of whether the mane hair was moving less on the subject than those animals in an exposed location was also a useful indicator of protection from the wind.

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Once the subject data were recorded for a group, the researcher entered the field and determined the location of any subjects that were previously out of sight in a shelter. To gain measures of the effects of insects on shelter use, three animals from each group in each of the possible locations (inside, outside, using natural shelter) were selected. Where possible subjects included an individual with a light, a medium and a dark coat. To prevent any bias in subject selection, the animal nearest the researcher in the correct position (i.e. side-on to the researcher) and with the correct coat colour was chosen. To obtain a measure of relative insect density across observations, researchers recorded the number of insects visible on one side of subjects' bodies. To assess insect harassment, researchers timed one minute, and with the help of a handheld tally counter, recorded the number of behaviours performed that were indicative of insect harassment. The behaviours recorded were tail swishing, foot stamping, head shaking, biting the body and skin twitching (panniculus reflex). The average number of insects and behaviours observed across the three animals in each location were recorded as the measures of insect density and harassment respectively for the observation session. When fewer than three animals were present in a given location, data were recorded for as many animals as possible. When no group members were found in a location (inside, outside or in shade), no insect challenge data could be collected for that location.

The temperature, wind speed, and lux outside, away from any natural shelter, were recorded. To assess the conditions within each shelter, and to account for variations in these condition across locations, temperature, wind speed (to measure any draughts), and lux level in each of the available constructed shelters were recorded. Finally, the measure of hourly precipitation rate at the central wind station in the farm was recorded again. If observations took longer than one hour to complete, this central measure of precipitation rate was taken at one hour intervals. Care was taken to make observations at a range of times and in a range of weather conditions across groups. Observations were made between 07:00 and 19:10. Where possible, each subject was observed at least once per week. When more than one observation of a subject occurred in a day, a minimum of 30 minutes elapsed between observations and no more than two observations of a subject occurred in a single day.

Statistical Analysis

The range of climate conditions and levels of insect challenge experienced by subjects during the study are presented in the results section. A series of pairwise comparisons (repeated measures ANOVAs) were used to compare harassment behaviour and density measures of insect challenge across the three locations (outside vs. shade, shade vs inside,

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inside vs. outside) at the level of the observation session. To analyse the extent to which the environmental factors influenced the shelter seeking behaviour of donkeys and horses, and to determine if there were significant differences between the two equid species in their shelter seeking behaviour, a series of generalised linear mixed models (GLMM) with a binomial logit function were performed using the statistical package lme4 in R (R Core Development Team, 2018). A series of a-priori candidate models were generated for the response variable Location (inside a constructed shelter versus outside). The fixed factors of Species, Temperature Outside, Temperature in the Shelter, Rain, Wind, Lux, Insect Challenge, Time and Month were included in a global model. To assess the extent to which the shelter seeking behaviour of donkeys and horses differed, all environmental conditions were included as an interaction with Species as well as a main effect. We further explored the potential interaction of climatic variables, for example Wind*Rain, Wind*Insects, Temperature*Wind, in a series of interactions, with Species and without Species. Subject nested in Social Group then Farm was included as a random factor.

Where multiple measures of an environmental factor were taken, e.g. precipitation rate prior, during and after observation sessions, models were constructed to determine the best predictor of the environmental condition to be included in the final set of models. From the three measures of precipitation (precipitation measured at the start of the observation session, precipitation measured after the session was conducted and precipitation rate at the time of observation), precipitation level at the time of observation was the best predictor and was included in the main analysis. From the measures of insect challenge – insect density outside, insect harassment behaviours outside, density inside, harassment behaviours inside and relative measures of density and harassment – both insect density outside and insect harassment behaviours were good predictors of shelter seeking, however, insect harassment behaviours were deemed slightly more predictive and included in the final analysis. Due to the complexity of the global model, candidate models were assessed using the Bayesian information criterion (BIC) because it penalizes model complexity more heavily than Akaike information criterion (AIC). A GLMM was run with the null model, followed by the global model. Factors with little or no predictive value were systematically removed from the global model to produce the final, best fit model.

To assess if natural shelter was sought more in windy, rainy or sunny conditions and whether the two species were affected differently by these factors, a complete series of binomial GLMMs were run on the response variable Outside Location (using natural protection versus unprotected). The fixed factors of Type of Protection Afforded (from sun, wind or rain), Species and Protection Type*Species were included in the global model with Subject nested in Social Group then Farm included as a random factor. The best fit model

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was determined using AIC. Only instances where natural protection would have been of benefit were included in the analysis, i.e. only instances where subjects were outside, and it was sunny, rainy or windy were included.

Results

<u>Session Conditions</u>

A total of 13513 data points were collected from 1728 separate observations of the different social groups. The average number of observations per subject for subjects present throughout the study was 86.39 ± 23.2 (M ± SD = Mean ± Standard Deviation) and 64.97 ± 37.1 (M ± SD) across all subjects. The following descriptions of environmental conditions are at the level of the group observation session.

Weather Conditions

Precipitation: The mean hourly rainfall during the observation sessions was 0.12mm ± 0.56 with a maximum of 6.5mm and a minimum of 0mm. 1423 (82.3%) observation sessions were conducted during dry weather, 177 (10.2%) during intermittent/light rain and 128 (7.4%) during rain/heavy rain. The average monthly rainfall for South West England and South Wales during the study period was 105.1mm, range 41.8-215.4mm (MET Office, 2018).

Wind speed: The mean wind speed during the observation sessions was 1.22m/s ± 1.47 with a maximum of 8.3m/s and a minimum of 0m/s. Based on the Beaufort Scale, 728 (42.1%) observation sessions were conducted in calm conditions (<0.3m/s), 460 (26.6%) sessions during a light air (0.3-1.5m/s), 391 (22.6%) sessions during a light breeze (1.6-3.3m/s), 105 (6.1%) during a gentle breeze (3.4-5.4m/s) and 43 (2.5%) during a moderate to fresh breeze (5.5-8.3m/s). For most observations, the wind was minimal in the constructed shelter: 1515 (91.2%) of observations reported calm conditions and 1615 (97.2%) observation sessions reported calm or light air (<1.6m/s) in the shelters.

Temperature: The mean average outside temperature recorded during the observation sessions was 14.16°C ± 5.18 (M ± SD) with a maximum of 33.3°C and minimum of 1°C. Similar conditions were found in the constructed shelters (M ± SD = 14.31°C ± 5.35, Max. 32.8°C, Min. 1°C in shelter 1 and where there was an additional shelter: M ± SD = 14.29°C ± 5.06, Max. 29.2°C, Min. 0°C in shelter 2). The average difference between the temperature outside and in the constructed shelter (shelter 1) was small (M ± SD = -0.25°C ± 1.20), although there were some instances of large variations across locations, with differences in

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temperature ranging from -4.7°C to 13.5°C. The average monthly temperature per month for South West England and South Wales during the study period was 9.65°C, range 3.9-15.4°C (MET Office, 2018).

Lux: Lux is a measurement of luminance and can be used to quantify the brightness of outside and inside light. The average lux level outside during the observation sessions was 27764.52 ± 25721.97 with a maximum of 125,300 and a minimum of 0. The average number of hours of sunshine per month for South West England and South Wales during the study period was 107.2, range 24-227 (MET Office, 2018).

Insect Challenge

Insect Density: The average number of insects observed on the exemplar animals outside was 0.95 ± 1.97 (max. = 22, min. = 0), the average for outside shade was 1.29 ± 3.24 (max. = 38, min. = 0) and for inside shelters was 0.43 ± 1.04 (max. = 11, min. = 0). However, these figures are not directly comparable because there were many sessions where animals were not found in all three locations at the same time (no animals were observed outside, in the shade and inside in 61%, 50% and 73% of sessions respectively), thus these overall averages are affected by systematic sampling bias e.g. animals are more likely to be found in the shade in hot weather when insect numbers are higher across all locations. Pairwise comparisons of observation sessions where the insect challenge in two or more locations was recorded at the same time reveal that insect density was significantly higher outside exposed compared to in the shade ($t_{1,147} = 3.24$, $p = 0.001$) and inside shelters ($t_{1,491} = 5.93$, $p < 0.0001$), and higher in the shade compared to inside ($t_{1,46} = 2.40$, $p = 0.02$). The number of insects observed on horses outside was higher than on donkeys (donkeys: 0.60 ± 1.34, horses: 1.10 ± 2.17; $t_{1,1349} = 5.43$, $p < 0.0001$).

Insect Harassment Behaviours: The average number of insect harassment behaviours on the exemplar animals outside was 3.19 ± 5.85 (max. = 44, min. = 0), the average for outside shade was 4.04 ± 7.35 (max. = 50, min. = 0) and for inside constructed shelter was 1.60 ± 3.50 (max. = 27, min. = 0). Pairwise comparisons of the observation sessions where the insect challenge in two or more locations was recorded reveal that animals showed more harassment behaviours outside than inside ($t_{1,491} = 5.61$, $p < 0.0001$), more outside exposed than in the shade ($t_{1,147} = 3.46$, $p = 0.001$) but there was no significant difference between the number of behaviours observed in the shade and inside ($t_{1,46} = 1.58$, $p = 0.12$). There was no significant difference in number of insect harassment behaviours produced by horses and donkeys outside (donkeys: 3.59 ± 7.02, horses: 3.01 ± 5.27; $t_{1,696} = 1.61$, $p = 0.11$).

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<u>*Effects of Environment on Shelter Use*</u>

Effects of environmental conditions on constructed shelter use of donkeys and horses

The predictors contained in the best fit model for whether an animal was observed inside a constructed shelter or outside, can be seen in Table 1. Overall, donkeys spent significantly less time outside (Species: $z = 2.45$, $p = 0.014$). The factor Species and its interactions with a range environmental conditions were present in the final model showing that across the different measures of climatic conditions, the horses and donkeys responded differently in their shelter use (see Figure 1).

Table 1. Factors included in the best fit model of constructed shelter use by horses and donkeys.

Factor	Z score	P value
Species	2.45	0.014
Rain	9.94	<0.0001
Wind Speed	4.31	<0.0001
Temperature (Outside)	1.63	0.10
Lux	11.75	<0.0001
Insect Harassment Outside	3.26	0.001
Temperature (Shelter)	0.39	0.70
Month	5.06	<0.0001
Time	5.06	<0.0001
Species*Rain	2.48	0.013
Species*Wind Speed	3.80	0.0001
Species*Lux	4.93	<0.0001
Species*Insect Harassment Outside	7.04	<0.0001
Species*Temperature (Shelter)	8.65	<0.0001
Rain*Wind Speed	5.06	<0.0001
Rain*Temperature (Outside)	5.40	<0.0001
Species*Rain*Wind Speed	5.49	<0.0001

Rain: When it was raining, both species spent significantly less time outside (Rain: $z = 9.94$, $p < 0.0001$) however, the donkeys were significantly more affected by the rain than the horses (Species*Rain: $z = 2.48$, $p = 0.013$). There was a 54% increase in the number of donkeys inside a constructed shelter when it was raining heavily compared to when it was dry (from 35% to 89%). In contrast, there was only a 16% increase in the number of horses inside when it was raining compared to when it was dry (from 10% to 26%) (see Figure 1a).

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Wind: Despite the relatively small range of wind speeds observed (see environmental conditions detailed above), there was still a significant main effect of wind (Wind: $z = 4.31$, $p < 0.0001$). There was also a significant interaction of wind speed and species, showing that the two species responded differently to the wind (Species*Wind: $z = 3.80$, $p = 0.001$). The lowest number of donkeys were found inside when the wind speeds were light (39% at 0.3-3.3m/s), with donkeys tending to move inside as the winds rose, until 61% were inside during a fresh to moderate breeze (5.5-8.3m/s). In contrast the number of horses inside reduced slightly as the wind speed rose, from 16% in calm weather (0-0.2) to 5% during a fresh to moderate breeze (5.5-8.3m/s) (see Figure 1b). There was also a significant interaction of wind and rain, as well as a significant three-way interaction with species, suggesting that the donkeys and horses were affected differently by combinations of wind and rain levels (Species*Rain*Wind: 5.49, $p < 0.0001$). Donkeys were relatively unaffected by changes in wind speed when the weather was dry but when it was raining they tended to seek shelter more as wind speeds increase. Perhaps surprisingly, although overall shelter use by horses increased when it rained, shelter use was lower at higher wind speeds.

Temperature and Lux: There was a significant main effect of lux, with more animals being found outside at higher lux levels (Lux: $z = 11.75$, $p < 0.0001$), however the two species showed different patterns of shelter use (Species*Lux: $z = 4.93$, $p < 0.0001$), with the number of donkeys outside steadily increasing as lux levels rose while the number of horses remained relatively stable, with a possible increase in shelter use at the lowest and highest lux levels (see Figure 1d). As may be expected, the relationship between temperature and shelter use showed a similar pattern to the relationship with lux (Figure 1e). Horses seemed relatively unaffected by the temperatures experienced during the study, with the number of horses inside remaining at around 10% in temperatures from 0-20°C but increasing to 22% as temperatures rose above 20°C. In contrast donkey shelter use was much more varied across the temperature range with 69% staying indoors in the coldest weather (0-9°C) and donkeys tending to move outside as the temperature became warmer until, at the highest temperatures (>20°C) the same percentage of horses and donkeys were found outside (22%) (see Figure 1e). Although outside temperature was included in the global model, the main effect was not significant, and the interaction of species and temperature in the shelter was found to be a better predictor of shelter use than the temperature outside (Species*Temperature (Shelter): $z = 8.65$, $p < 0.0001$), reflecting the relatively stable, low level of shelter use in horses across temperatures and the reduction in shelter use as shelter (and outside) temperatures rise (Figure 1f). There was also a significant interaction effect of temperature and rain (Rain*Temperature (Outside): $z = 5.40$, $p < 0.0001$); shelter use was

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not strongly affected by temperature when the weather was dry, however, when it was raining, shelter use was much higher at cold temperatures.

Insect Challenge: There was significant main effect of insect challenge (Insect Harassment Outside: $z = 3.26$, $p = 0.001$) as well as a significant interaction with species, showing that as the level of insect harassment increased, horses tended to move inside whereas the donkeys tended to move outside (Species*Insect Harassment: $z = 7.04$, $p < 0.0001$) (see Figure 1c).

Time and Month: As would be expected, shelter use differed across months of the year and time of day (Month: $z = 5.06$, $p < 0.0001$; Time: $z = 5.06$, $p < 0.0001$), with shelter use highest over the winter months (November-February) and early in the morning (before 10am). However, there was no difference in the shelter use of the two species as a function of time or month.

Insert Figure 1 here.

Figure 1. Shelter use of donkeys and horses in relation to environmental conditions, measured by percentage of animals observed inside a constructed shelter. A. during three levels of precipitation B. as a factor of wind speed. C. as a factor of outside insect harassment D. as a factor of lux levels. E. as a factor of outside temperature F. as a factor of temperature inside the shelter.

Effects of environmental conditions on natural shelter use of donkeys and horses

Rate of natural shelter use was very low; there were only 78/1728 observation sessions and 1646/13513 specific instances in which animals were seen using natural shelter, probably due to the availability of constructed shelters. The global model containing the factors Species, Protection Type and Species* Protection Type was the best fit model to explain natural shelter use (see Figure 2). Overall, donkeys sought natural shelter when outside more often than horses ($z = 15.14$, $p < 0.0001$). The rate of natural shelter use also varied depending on the environmental conditions ($z = 20.08$, $p < 0.0001$), with protection being sought most often in windy conditions, followed by rainy conditions, and least often for sunny conditions. Finally, there was a significant difference in the environmental factors that led to natural shelter use across the two species ($z = 15.28$, $p < 0.0001$), with donkeys seeking shelter relatively more than horses in windy and rainy conditions and horses seeking natural shelter relatively more readily in sunny conditions.

Insert Figure 2 here.

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Figure 2. Natural shelter use by donkeys and horses as protection from sun, wind and rain. Shelter was more likely to be sought in windy conditions, and least often in sunny conditions. Overall, donkeys used natural shelter more than horses but there was a significant difference in the use of natural shelter by the two species, with donkeys seeking shelter from rain and wind and horses seeking shelter relatively more often when sunny.

Discussion

Even in the relatively mild climate of the UK, changes in environmental conditions significantly affected shelter seeking behavior in domestic equids, with significant differences in the patterns of shelter use in horses versus donkeys. Overall donkeys spent more time in constructed shelters and were more affected by changes in the weather conditions than horses. The use of constructed shelters by donkeys increased significantly in temperatures below 10˚C, when it was raining, and when winds increased from light to moderate speeds. In contrast, shelter use by horses remained relatively low across the observed temperatures, with a slight increase as temperatures rose above 20˚C. Across wind speeds, constructed shelter use by horses was low and reduced further in moderate winds. Horses did seek shelter more when it rained but the effect was smaller than that seen in the donkey population. The pattern of natural shelter use was similar: donkeys used natural shelter more than horses and sought natural shelter as protection from the rain and wind more than horses, whereas horses sought natural protection from the sun more than donkeys. Unlike the other environmental conditions, horses appeared more affected by insect challenge than donkeys, moving inside as insect numbers rose.

Donkeys sought constructed and natural shelter more readily than horses when it was raining and when wind speed increased, as would be expected by an animal adapted to a semi-arid environment. The number of horses outside increased slightly at higher wind speeds, this may be because they sought relief from insect challenge. Shelter use is unlikely to be affected by different environmental features in isolation but reflects a response to a complex interaction of environmental conditions. For cattle, an increase in wind speed from 0.3 to 3.9 m/s (i.e. from calm to a gentle breeze) was found to increase the LCT from -2˚ to 7˚C if the animal was dry, and from 6˚ to 16˚C if the animal had a wet coat. Exposure to wind and rain therefore leads to a significant rising of the LCT of cattle to above the average temperature in the UK (Gregory, 1995). Similarly, studies of horses have reported that precipitation levels affect shelter seeking behaviour considerably more when wind speeds are higher and temperatures are lower (Heleski and Murtazashvili, 2010; Snoeks et al., 2015). We found the same interaction of weather conditions in this study, however, again,

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the species showed different behavioural patterns in response to the combinations of environmental conditions. When raining, donkeys sought shelter more readily as the wind speeds increased but surprisingly, horses did not seek shelter more in higher winds. This is contrary to previous research but may be due to the climatic conditions remaining relatively mild for the horses.

Donkeys' shelter use also varied significantly across the observed temperature range (0-33˚C), with around 70% staying indoors when the temperature was below 5˚C and around 70% observed outside as the temperature rose above 15˚C. In contrast, horses' shelter use remained relatively low (≈10%) from 0-20˚C and slightly increased as temperatures rose. The pattern of shelter use by the horses is in line with previous research showing significant increases in shelter use above 25˚C (Holcomb et al., 2014; Snoeks et al., 2015). Previous research indicates that horses' TNZ is approximately 0-25˚C, and the slight increase in shelter use at temperatures above 20 ˚C supports this, indicating they may be approaching their UCT and are attempting to find shelter from the sun (Autio et al., 2007; Morgan, 1998). There are no estimations of donkeys' TNZ but these results suggest that their TNZ may be higher than that of horses. Future work assessing the rates of heat loss in donkeys across climatic conditions, taking in to account demographic factors such as age and breed, would be of benefit. In this study, ambient temperature often did not vary significantly between outside and constructed shelters which may explain why lux levels were also a significant predictor of shelter use across species. This finding highlights the importance of including measures that assess animal comfort levels, such as measures of solar radiation, or, more accurately, globe temperature (Holcomb et al., 2014).

There is contradicting evidence as to whether insect challenge is generally higher outside, in shade, or inside constructed shelters (Holcomb, 2017), with these differences probably reflecting variations in environment and climatic conditions (Powell et al., 2006). In our study, levels of insect challenge were lower inside shelters compared to outside. As the level of insect harassment increased, horses tended to move inside, in contrast, donkeys tended to move outside, thus it is possible that insect challenge is not as significant a driver of location choice for donkeys than horses in this climate. Although donkeys and horses showed similar levels of harassment behaviours, suggesting that they experienced similar levels of discomfort, overall insect numbers tended to be higher on horses than donkeys. It is therefore possible that horses experienced higher levels of insect challenge. Measures of insect density and insect harassment behaviours are standard ways to assess insect challenge (Holcomb, 2017), however, there is currently no definitive measure of insect challenge. Insect harassment behaviours give an indication of the extent to which insects are causing actual discomfort and, in our study, this was a slightly more accurate indicator of

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shelter use than insect density. Future research could explore in more depth the relationship between measures of density and harassment.

Taken together these results appear to reflect the differences in evolutionary history of donkeys and horses. It is important to assess the behavioural and physiological effects of the environment on domestic species to ensure that the disparity between the climates to which they are adapted, and those they find themselves in, does not cause welfare problems. Horses were less affected by changing climate conditions and showed less shelter use overall than donkeys, although there was an increase in shelter use as temperatures rose. Even in the relatively mild climate of the UK, donkeys readily sought adequate, i.e. constructed, shelter during cold, windy or wet weather. These findings suggest that management and particularly, shelter provision, of each species should be considered separately, and that donkeys may require more protection from the elements than horses in temperate climates.

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Ethical Statement

This study was approved by Canterbury Christ Church Animal Welfare Ethics Research Board and adhered to the EU Directive 2019/63/EU for animal experiments and the Association of Animal Behaviour guidelines for the treatment of animals. The study did not affect the management practices and decisions made by the equid owners. Any subjects that ceased to meet the inclusion criteria of the study (free access to an outside area and a constructed shelter, no rug or clipping and in good health) were excluded from further observations.

Conflict of Interest Statement: The authors declare no conflict of interest.

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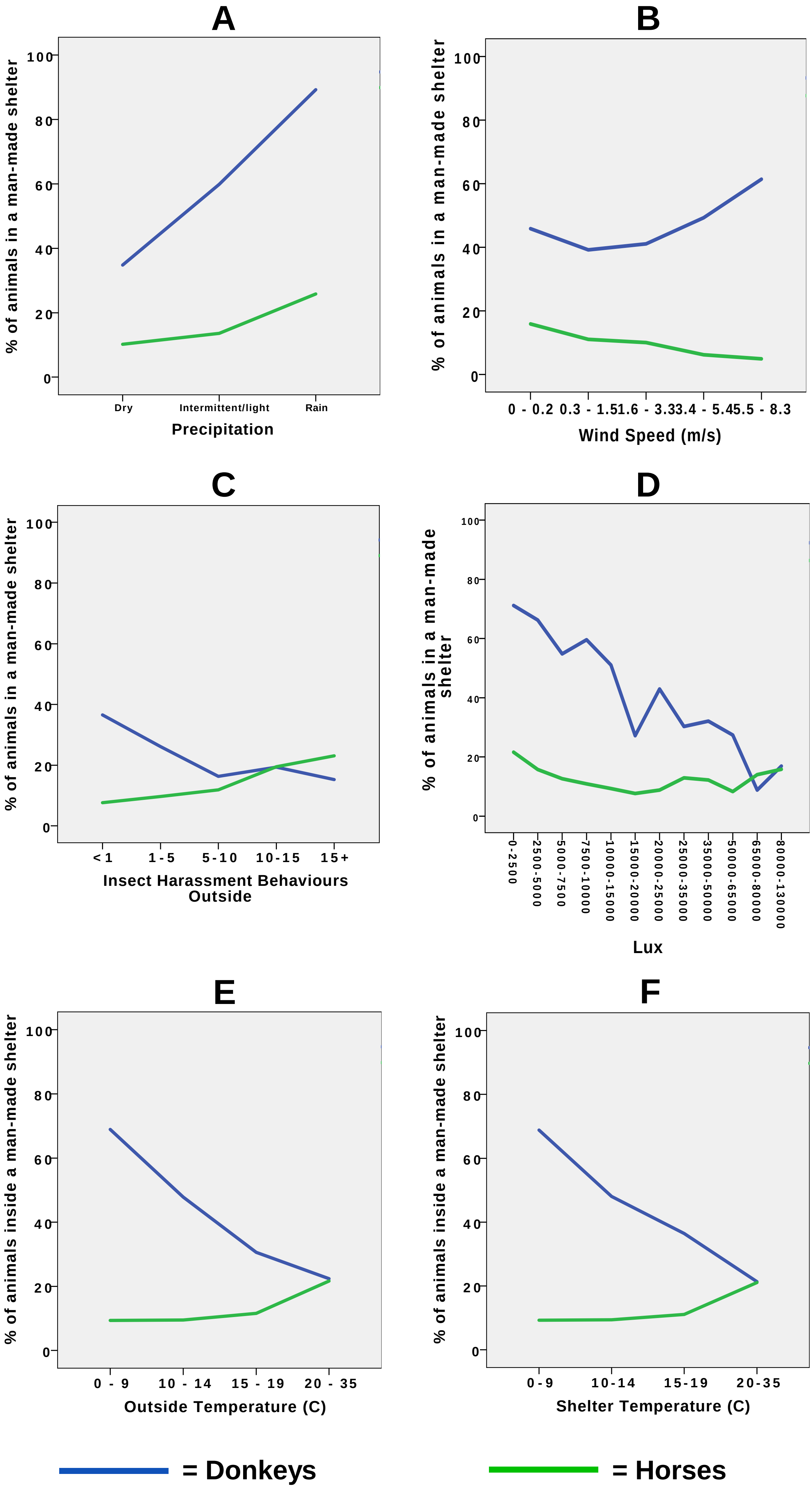
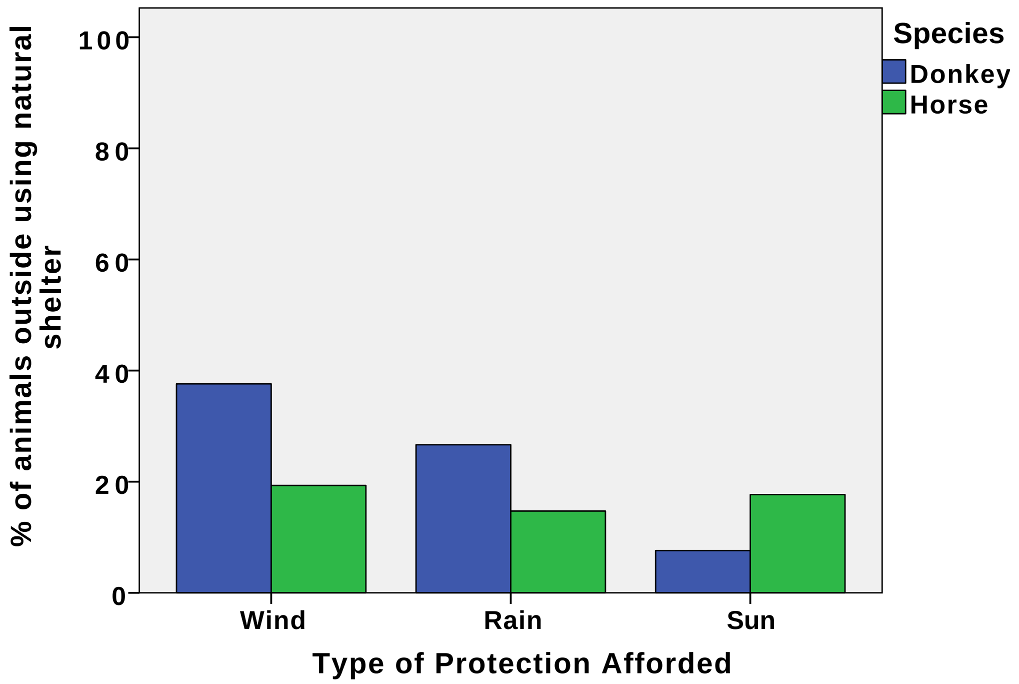

A
% of animals in a man-made shelter
100
80
60
40
20
0
Dry
Intermittent/light
Rain
Precipitation
B
% of animals in a man-made shelter
100
80
60
40
20
0
0 - 0.2 0.3 - 1.51.6 - 3.33.4 - 5.45.5 - 8.3
Wind Speed (m/s)
C
% of animals in a man-made shelter
100
80
60
40
20
0
< 1
1 - 5
5 - 10
10 - 15
15 +
Insect Harassment Behaviours Outside
D
% of animals in a man-made shelter
100
80
60
40
20
0
0-2500
2500-5000
5000-7500
7500-10000
10000-15000
15000-20000
20000-25000
25000-35000
35000-50000
50000-65000
65000-80000
80000-130000
Lux
E
% of animals inside a man-made shelter
100
80
60
40
20
0
0 - 9
10 - 14
15 - 19
20 - 35
Outside Temperature (C)
F
% of animals inside a man-made shelter
100
80
60
40
20
0
0 - 9
10 - 14
15 - 19
20 - 35
Shelter Temperature (C)
= Donkeys
= Horses



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Highlights

- We observed the shelter seeking behaviour (SSB) of donkeys and horses in a temperate climate.
- Overall donkeys sought shelter more frequently than horses, particularly when cold (<10˚C), rainy and windy.
- Constructed shelter use by horses was low but they started to move inside as temperatures rose (>20 ˚C).
- Horses sought natural shelter more than donkeys when sunny and appeared more affected by insects.
- Differences in SSB appear to reflect donkeys' and horses' adaptation to different climates.

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