Faculty of Science & Technology

An investigation of the variables affecting nest site suitability in the solitary ground nesting bees and wasps (*Hymenoptera*) on Dorset tertiary heathland

A Dissertation submitted as part of the requirement for BSc. Ecology and Wildlife Conservation

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i Abstract:

The life cycles of heathland ground nesting generalist and specialist pollinators must be aided through the management of soil exposures as nesting mediums. An analysis of data collected from 37 nest activity and 37 non-nest activity soil exposures was carried out across three Dorset National Nature Reserves. Variables recorded at each sample site were the exposure area of nesting surface, inclination and aspect, soil compaction, substrate type, percentage vegetation cover and surrounding vegetation structure. Also, species richness and morphological burrow richness were recorded per active nest site.

This research explored the questions;

- What is the distribution of active nests sites across study sites?

- Are there variations in the variables recorded across sites with and without nest activity?

- Do the variables affect nesting species richness? If so, which of these variables are most effecting nesting species richness?

- Does the social typing of the ground nesting hymenopteran bee and wasp species into gregarious nester and solitary nester categories uncover preferences for communal or isolated nesting?

- Can a measure of morphological burrow richness be used as a tool to indicate nesting species richness?

The findings demonstrate the most suitable nest sites for ground nesting bees and wasps to be large, south facing exposures with multiple substrate types and a locally pioneer stage vegetation structure. Strong negative associations between gregarious and solitary nesting species indicates preferences for isolated rather than communal nesting. This was also the case for gregarious bees and gregarious wasps. A moderate positive relationship between morphological burrow richness and nesting species richness supports the claim that morphological burrow richness is a reliable measure of nest site suitability.

ii Acknowledgments:

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1.0 Introduction:

1.1 Defining lowland heathland:

Lowland heathland is a semi-natural habitat which generally persists below 300m of altitude (English Nature, 2002). It is dominated by ericaceous vegetation which overlies shallow, acidic, and nutrient poor peat type soils (See Figure 1) (Biodiversity Reporting and Information Group, 2007). Ling (*Calluna vulgaris* L.) is a characteristic and abundant ericaceous species of heathlands, which forms vital pollinator networks for many generalist and specialist species (Vandvik et al, 2014; Descamps et al, 2015). As an early successional habitat, the intervention of man is needed to maintain habitat quality and prevent ecological succession to other states (Mitchell et al, 2015). Heathlands are also a priority habitat of high biodiversity value, protected under the UK biodiversity action plan and various agri-environment schemes which aim to halt habitat loss, maintain habitat quality and conserve biodiversity (Hewins et al, 2007; Biodiversity Reporting and Information Group, 2007).

Figure 1: Lowland heathland at Hartland moor National Nature Reserve, Dorset (Spiers, 2016a).

1.2 A history of heathlands:

Lowland heathland emerged 4000 years ago as a consequence of large scale deforestation for the creation of agricultural grazing pastures (Webb, 1998). The traditional uses of active grazing, and the burning and cutting of vegetation and turf for use as fuel and fodder, subsequently prevented ecological succession and woodland regeneration (Gimingham, 1972; Webb, 1986). It was the socio-economic climate produced after World War II which incentivised abandonment and mass conversion of heathland into more economically productive systems (Moore, 1962). Urban development as well as agricultural improvement developed with the use of artificial fertilisers for intensive crop and livestock production were main causes for heathland destruction, fragmentation and habitat degradation (Webb, 1989; Webb, 1998; Underhill-Day, 2005; Carboni and Dengler et al, 2015).

The heathlands of European countries once spanned several million hectares, but have since been reduced to an estimated 350,000 hectares (Diemont, Webb, and Degn, 1996; Carboni and Dengler et al, 2015). In reference to the study location of this research, Moore (1962) quantified that up to 66% of the total area of heathlands in Dorset had become lost and fragmented since 1811. Furthermore, loss of heathland in Dorset was still being experienced into the late 1990’s, regardless of preventative measures to control scrub encroachment and woodland regeneration (Michael, 1996; Webb and Rose et al 2000; Underhill-Day, 2005).

1.3 Implications of habitat loss and fragmentation:

Generally speaking, habitat loss and fragmentation causes biodiversity loss (Hanski, 2005). For instance, habitat fragmentation reduces genetic diversity as a result of restricted gene flow and genetic drift amongst isolated populations (Rivera-Ortíz et al 2014). This reduces effective population sizes and causes inbreeding depression and extinction vortices (Lopez-Uribe et al, 2015). If a critical threshold of fragmentation is exceeded, this may result in impaired ecosystem resilience to environmental change and irreversible regime shifts (Pardini et al, 2010). Many of the discussed processes above interact synergistically, creating amplified feedbacks which drive the cascading effects and abrupt species declines associated with biodiversity loss (Brook et al, 2008).

The biodiversity loss experienced by heathlands as a result of habitat destruction and fragmentation has altered species community composition, reduced ecosystem functioning and therefore hampered critical ecosystem services such as pollination (Exeler et al, 2010; Fagúndez, 2013; Oliver et al, 2015). The ability of an ecosystem to combat the effects of habitat loss and fragmentation depends on its stability and resilience, which in turn is dependent on the continuation of key trophic interactions (Loreau et al, 2013; Truchy et al, 2015). Ensuring ecosystems continue to function in a natural and healthy manor has been universally demonstrated as being achieved through conservation of biodiversity (Loreau et al, 2013; Truchy et al, 2015). For example; habitat loss and fragmentation threatens the ecosystem service relating to the pollination of crops and wild flowers, therefore, by protecting pollinators and their associated habitats this ecosystem service can continue and ecosystem resilience can be maintained (Bommarco et al 2012; Potts et al, 2016).

1.4 Opportunities and Complications of Heathland management:

Conservation management of heathlands aims to prevent habitat loss and fragmentation, but also to maintain habitat quality. As heathlands are early successional semi-natural habitats, they require human intervention to exist (Mitchell et al, 2015). This intervention takes place in the form of controlled burns, brush cutting, sod cutting, grazing regimes, and herbicidal treatments. These measures are employed for the purpose of creating mosaics of vegetation structure and bare ground, preventing scrub encroachment, and arresting ecological succession (Webb, 1986; Bokdam & Gleichman 2000; Newton et al, 2009).

The structural habitats developed by heathland management are essential for the life cycles of niche species (Webb, 1986). For instance, heathland management practices ensure the creation of exposed soil as an essential nesting and basking resource for the sand lizard (*Lacerta agilis* L.), smooth snake (*Coronella austriaca* L.), invertebrate Coleoptera and ground nesting Hymenoptera (Yeo and Corbet 1995; Falk and Lewington, 2015; English Nature, 2005; Pickess and Burgess et al, 1989; Chadwick, 1982). Furthermore, species such as the stone curlew (*Burhinus oedicnemus* L.) and the *Myrmica* ant hosts of the endangered butterfly *Maculinea arion* require management that maintains short and open heathland vegetation as a structural habitat for foraging and nesting (Green and Griffiths, 1994; Thomas et al, 1998). Conversely, the Dartford warbler (*Sylvia* *undata* B.) requires management that maintains both mature stands of European gorse (*Ulex europeaus*) for nesting, and bare ground for insectivorous foraging (Berg et al, 2001).

The responses of the heathland ecosystem to different types and intensities of management must be investigated to understand if management is being carried out effectively (Lindenmayer and Hobbs et al, 2008; Bargmann et al, 2015). If management is inappropriate, this might negatively affect the biotic and abiotic drivers for ecosystem interactions and thus ecosystem functional stability (Mitchell et al, 2000). This is often investigated in the scientific literature, and can inform heathland management practices by improving the understanding of ecosystem responses to management types (Fischer & Lindenmayer 2007; Mitchell et al 2000). For example; the study composed by Henning et al (2017) investigated the effects of mowing, grazing and creation of bare ground at different intensities on seedling recruitment for the restoration of an abandoned heathland. Henning et al (2017) was able to recommend strategies for the creation of bare ground as a crucial step to seedling recruitment and heathland restoration, thus informing management and improving the prospects for reconnecting heathland fragments.

1.5 Effects of Heathland loss and fragmentation on pollinators:

The combined interplay of habitat loss, fragmentation and agricultural intensification on semi-natural systems such as lowland heathland has caused significant losses to pollinator diversity, disrupted plant-pollinator communities and hindered the pollination ecosystem service which they provide (Ollerton et al, 2014; Kovacs-Hostyanski et al, 2017. Pollinators are able to disperse over long distances and consequently interact with a large diversity of species and resources, which influences trophic interactions at large spatial scales (Tscharntke et al, 2005). Therefore, a recent historic decline in pollinators puts plant-pollinator networks at risk of homogenization, driving further instability of the pollination ecosystem service, loss of biodiversity, reduced crop production and food insecurity issues (Lever et al, 2014; Winfree et al, 2009; Potts et al, 2010).

Cane (1997) refers to the ground nesting hymenoptera as a neglected group of effective specialist and generalist pollinators. The Purbeck mason wasp (*Pseudepipona herichii* S.) is a good example of this as it is a rare and gregarious ground nesting aculeate wasp (figure 2). In the United Kingdom It is exclusive to the lowland heathlands of the Poole basin, in Dorset, but can also be found in central Asia, North Africa, Western Europe and North America (Roberts, 2001). Its habitat requirements include exposed clay as a nesting medium, mid-succession regenerating heathland with a main component being that of bell heather (*Erica cinerea*), open water to aid nest construction, and the presence of the Tortricid moth *Acleris hyemana* as its only known prey item (Roberts, 2008). The rarity and highly specialised requirements of this species mean that it is at higher risk to local extinction by allee effects and demographic stochasticity than other generalist species (Amarasekare, 1998; Underhill-Day, 2005; Roberts, 2001). Much alike the declines of other pollinator species, reasons for its decline are not well understood, however, land use intensification, lack of food sources, pesticide use, disease, natural population dynamics, suitable habitat loss, and climate change are likely responsible (Vanbergen et al, 2013; RSPB, 2004).

Figure 2: A Purbeck mason wasp (*Pseudepipona herichii* S.) (Spiers, 2016b).

1.6 Options for Heathland pollinator conservation:

There is a lack of modern scientific research targeting the conservation of specialist heathland invertebrates such as the ground nesting pollinators (Steffan-Dewenter and Leschke, 2003). Many of the ground nesting Hymenoptera have specialised nesting and habitat requirements, which are very different and in some cases unknown (Potts and Vulliamy et al, 2005). This consequently limits management options to target their conservation. Here, it is inferred that the conservation of ground nesting pollinators such as the Purbeck mason wasp (Pseudepipona herichii S.) could be improved if their habitat requirements and nesting biology were better understood.

The creation of exposed soil as a basic and universal requirement for nesting is carried out by current management, however, there is little known about the detailed factors effecting the suitability of nest sites for nest excavation and habitation. Hypothetically, the creation of soil exposures which cover a range of Hymenopteran habitat requirements should maximise the suitability of nest sites, thus encouraging nesting and improving their conservation. Therefore, an investigation into the factors affecting nest site suitability for ground nesting hymenoptera presents a valuable research opportunity (Brockmann, 1979).

1.7 Variables affecting nest site suitability:

The presence or absence of nest activity between locations is determined by factors effecting nest site suitability. Variables determining nest site suitability in the ground nesting hymenoptera are broad ranging in the literature. Many are edaphic factors relating to substrate type, substrate hardness, softness, temperature and moisture (Rosenheim, 1990; Potts and Willmer, 1997; Cane, 1991; Brockmann's (1979). Other factors said to affect nest site suitability are biotic ones. These include vegetation structure, parasite presence and nest density (Steffan-Dewenter and Leschke, 2003; Rosenheim, 1987; Brockmann, 1979).
Brünnert and Kelber et al, (1994) assesses the use of landmarks on the ability of ground nesting bees to locate nest entrances, whereas Brockmann, (1979)'s study in assessing the nest-site selection of the great golden digger wasp (*Sphex ichneumoneus* L.) recorded variables such as inclination, soil compaction, and substrate type at nest sites. Sardiñas and Kremen's (2014) evaluation of micro-habitat nesting for ground-nesting bees also uses these variables as factors effecting nest site suitability.

1.7.1 Abiotic Variables:

The size of available nesting surfaces might affect the suitability of nest sites. Very large surfaces might be preferred by gregarious nesting species as there exists a larger nesting resource through which conspecific attraction can act (Polidori et al, 2008). Some species of ground nesting bee prefer inclined, southern facing soil exposures as these exposures are subject to solar warming for longer periods of the day than are those that are not of a south facing aspect and with little inclination (O'Toole et al, 2013; Potts and Willmer, 1997). For some species such as the solitary bee *Anthophora plumipes*, basking for the purpose of solar warming offers a reproductive edge to the intraspecific competition experienced by males for female mates (Stone et al, 1995). Nesting in a warm environment is a reproductive strategy as this has been demonstrated to increase the speed of brood development in underground nest cells by maintaining consistent soil-temperature gradients (Weissel et al, 2006). Various species of solitary wasp have interspecific preferences for nesting in slopes and flat surfaces (Yeo and Corbet, 1995). Thus, aspect and inclination of nest sites are limiting factors to nest site suitability.

Soil compaction is mentioned as a factor affecting nest site preference in the gregarious nesting bee, *Dieunomia triangulifera* (Wueller, 1999). Wueller Explains that ground nesting bees might prefer compacted soils for nesting as these are a better conductor of heat. This conduction of heat maintains soil temperature regimes which are important for hymenopteran larval development as stated before (wueller, 1999). Therefore, soil compaction is considered a variable that affects nest site suitability. Westrich (1996) talks of the nesting preferences for some bee species in sandy substrates and of others to nest in clay type substrates, therefore the type of substrate is considered an important variable affecting nest site suitability.

1.7.2 Biotic Variables:

The amount of vegetation covering a nest site is seen as an important factor influencing nest site suitability for the reason that a higher proportion of vegetation cover to exposed soil reduces the spatial availability of the nesting medium. Srba and Heneberg (2012) found the digger wasp *Ammophilla pubescens* has a strict requirement for low vegetation cover in its nesting environment. It is inferred that mature vegetation structure might cast shade over nest sites at certain points throughout the day and so interrupt soil temperature regimes, thus affecting larval development (Wueller, 1999).

A factor not discussed in the literature as affecting nest site suitability is the social typing of ground nesting hymenoptera. Species are generally gregarious nesters or solitary nesters. For example, the sand tailed digger wasp (Cerceris arenaria) is a semi-social wasp which nests in dense aggregations with conspecifics (Else and Field, 2012). However, species such as *Astata boops* prefer solitary nesting (Yeo and Corbet et al 1995; Allen, 1998). A research opportunity is presented here to investigate the communal or isolated nesting preferences of social types of ground nesting bee and wasp.

1.8 Indicators of suitable nest sites:

Potts and Willmer's (1997) study on nest-site selection by the ground nesting bee, *Halictus rubicundus* assumes that high nest density infers nest site suitability. A criticism of this assumption is that high nest density could be caused by a lack of available nest sites and so causes high rates of nest aggregation (Rosenheim, 1990). In some cases, high nest density might better reflect poor nest site suitability, as species nesting in high densities become susceptible to amplified interspecific and intraspecific competition for resources as is suggested in Cushman et al's (1988) study of *Formica altipetens* colonies.

Relying on nest density as an indication of nest site suitability is limited in that it does not relay information of the number of species using that site, only the density of nests. If a diverse group of specialist and generalist hymenoptera are found nesting together, this suggests that their varying habitat requirements are being met, and so nest sites with a high nesting species richness should be considered as highly suitable nest sites. The identification of such sites is of interest to conservation managers as this allows priority action to be taken to protect and maintain species rich nest sites for the protection of biodiversity. Conventional methods to identify such sites are resource and time intensive, in many cases requiring surveys for the visual observation of species entering and leaving nests for accurate identification.

As morphological differences exist between the nests of various ground nesting hymenopteran species, it stands to reason that a richness of morphological burrow types should infer richness of nesting species. For instance; Roberts (2001) states that nests of the Purbeck mason wasp (*Pseudepipona herichii* S.) have characteristic granular spoil. In the case that high morphological burrow richness strongly correlates to high nesting species richness, this would accurately and efficiently help managers to identify highly suitable nest sites.

1.9 Aims and Objectives:

The first aim of this research is to assess the distribution of nest activity and non-nest activity sites. This will be accomplished by recording GPS coordinates of each site and digitizing the ten figure grid references into ArcMap GIS software so that maps can be produced. A qualitative analysis of site distribution can then be undertaken.

The second aim of this research is to determine if biotic and abiotic differences in nesting environments of ground nesting hymenopteran bee and wasp can explain the presence of nest activity in some locations and not in others. Data will be collected for the various biotic and abiotic variables across sites with nest activity and paired sites of non-nest activity (see table 1). Data for biotic and abiotic variables will be assessed for variation between sites with and without nest activity to determine if nest activity occurs in some locations and not in others as a result of differences in the nesting environment.

The third aim of this research is to determine if variations in the biotic and abiotic nesting environment of ground nesting hymenopteran bee and wasp have an effect upon their nesting species richness. This will be accomplished by carrying out timed surveys to identify the nesting species and provide a species richness count across study sites. Data for the various biotic and abiotic variables will be collected and statistically tested for the significance of their affect upon nesting species richness (see table 1).

The fourth aim of this research is to determine if the social typing of ground nesting hymenoptera into gregarious nesting and solitary nesting types will uncover preferences for separate or communal nesting. This will be done by processing the data for the richness of species across nest sites into the four following categories; gregarious nesting bee, gregarious nesting wasp, solitary nesting bee, and solitary nesting wasp. Data for these categories will then be tested for strength of association to determine preferences for separate or communal nesting.

The fifth aim of this research is to determine if the richness of morphological burrow types across active nest sites can be used as a measure for nesting species richness and therefore indicate nest site suitability. The morphological burrow types and nesting species richness will be recorded per active nest site. These data will then be correlation tested to assess significance of a relationship between morphological burrow richness and nesting species richness.

Table 1: Biotic and abiotic variables referred to in the aims and objectives

Abiotic variables	Biotic variables
Exposure area of nesting surface	Species richness of nesting hymenopteran bees and wasps
Soil compaction	Vegetation cover of nesting surface
Inclination of nesting surface	Local vegetation structure
Aspect of nest site Eg: (North,East,South,West)	
Substrate type	

2.0 Methodology:

2.1 Introduction to study sites:

Data collection took place across Godlingston Heath national nature reserve (NNR), Hartland Moor NNR and Slepe Heath NNR, which are located to the south of Poole Harbour in the Isle of Purbeck, Dorset (see Figure 3). The study sites are reserves managed by the Purbeck National Trust, whom had given permission to access these sites for the purpose of this research.

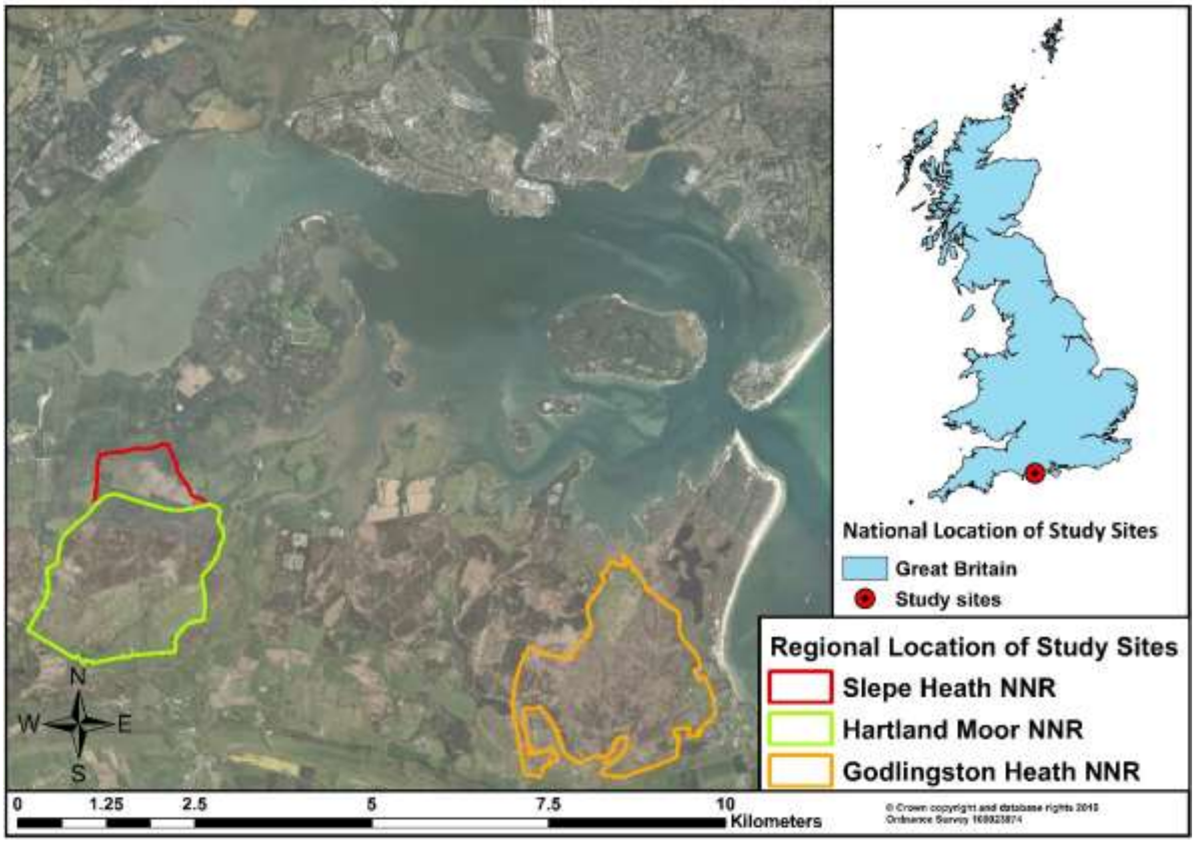


Figure 3: National and regional locations of study sites with regional reference to Poole Harbour (Spiers, 2017a).

Prior to data collection, Godlingston heath NNR, Hartland moor NNR and Slepe heath NNR were visited multiple times to locate access points and familiarize navigation of the sites. Data collection and analysis were trialled to ensure data collection methods and analysis were feasible and reliable. Official data collection commenced on the 25th June 2016 and ended on the 25th August 2016. As most ground nesting hymenoptera are univoltine to the summer months, this study coincided with the peak height of nesting activity

2.2 Site Selection:

The site selection process entailed surveys for nest activity along foot paths, vehicle tracks and accessible isolated soil exposures (Figure 4 and Figure 5). Sites were selected when nest activity could be observed. The extent of sites was defined by the area populated with nests and bordered by vegetation. Site selection was biased towards foot paths and vehicle tracks for two reasons; the first dictates preference of these environments as nesting habitats as stated by entomologists and literature, the second reasons that site selection along foot tracks and paths made travel times between sites shorter, and nest sites easily accessible.

Figure 4: A typical vehicle track surveyed for nest activity at Hartland moor NNR (Spiers, 2016c).

Figure 5: An active nest site along a foot path at Hartland moor NNR (Spiers, 2016d).

Sites with nest activity were selected if occupation and/or excavation of nests by ground nesting hymenopteran bees and wasps could be observed. Active nest sites were paired with non-nest activity sites for comparison and were defined as those sites without active excavation and devoid of hymenopteran derived nests. Non-nest activity sites were located within a 15 meter radius of their paired nest activity site. This was done to increase the likelihood that non-nest activity sites were being deliberately ignored by the hymenoptera as potential nest sites for reasons relating to some environmental limiting factor other than that of dispersal distance.

Sketch maps were drawn for each study site and target notes added indicating the locations of data collection for variables such as soil compaction, Inclination, vegetation cover, vegetation structure and substrate type (See Appendix 20; 21; 22; 23; 24). For nest activity sites sketch maps included target notes for location and frequency of burrow types (See Appendix 20; 21; 22; 23).

2.3 Dependent variables:

The dependent variable recorded for this study is nesting species richness. Species were recorded if they were observed entering, leaving or actively excavating nests (See Figure 6, Figure 7, and Figure 8). Identification of species was achieved with the use of pentax papilio 8.5 x 21 close focus binoculars, certified field guides and training with help from expert entomologists. The requirement of bodily measurements for the identification of some species challenged identification in the field, and thus meant that some species such as *Ammophila* could only be identified to the family and genus level.

Figure 6: A Purbeck mason wasp (*Pseudepipona herichii*) excavating a nest at Hartland moor NNR (Spiers, 2016e).

Figure 7: A sand tailed digger wasp (*Cerceris arenaria*) returning to its nest to provision its nest with prey (Spiers, 2016f).

Figure 8: A sand tailed digger wasp (*Cerceris arenaria*) inhabiting a nest at Hartland moor NNR (Spiers, 2016g).

Timed surveys for nesting species richness were designed to be relative to the exposure area of the nest site. Timed surveys were repeated three times per site over the study period. Species richness surveys for nest sites less than one square meter were 5 minutes, whereas larger nest sites were surveyed for 5 minutes per square meter of exposure area. A 10 minute disturbance period was given before surveys commenced to allow for the effects of human presence to be normalised and for natural nest activity to resume.

Surveys for nesting species richness did not occur on days with an ambient temperature lower than 20°C, or that were overcast, had strong winds, or precipitation, as these factors would most likely reduce hymenopteran nest activity. As a precautionary measure to standardise observation of nest activity, timed surveys were carried out on clear, warm and bright days with little wind and less than a 25% chance of precipitation.

2.4 Independent variables:

Data was collected for abiotic variables considered to effect the suitability of soil exposures as nesting environments. These include exposure area of nest sites, substrate type, soil compaction, inclination, and aspect. Likewise, data was collected for biotic variables considered to have the same effect. These include the local vegetation structure and percentage vegetation cover of study sites. Soil compaction, inclination, and substrate type were recorded at each nest across nest activity sites so as to collect data most closely resembling that of the point where nest excavation occurred (Figure 9). The number of samples collected at nest activity sites for these variables were replicated at evenly distributed intervals across their paired non-nest activity sites. These data were then averaged to generate a mean value for variables across each study site.

Figure 9: The use of a Silva clino-master Clinometer to measure the inclination of a burrow (Spiers, 2016h).

2.5.1 Abiotic variables:

Exposure area was recorded as the area of exposed soil containing nests and which was limited in extent by bordering vegetation. This was recorded by taking two measurements; the length of the exposed soil surface with visible nesting activity, and the width of the exposed soil surface with visible nesting activity. Nest site length and width were then multiplied to give nest site area. Exposures of a similar size to paired nest activity sites were used for non-nest activity sites. This was done to replicate the area across which samples were taken from active nest sites to standardise data comparison.

Substrate types were recorded by defining whether the substrate was predominantly clay, sand, gravel, or a mix of these three types. This was achieved by feeling and visually identifying the coarseness of substrates. Soil compaction of study sites was recorded using a hand-held Humboldt H-4200 soil penetrometer. Inclination of study sites was recorded using a hand-held silva clino-master clinometer, and aspect of study sites was recorded by determining the direction of dominant facing slopes using a compass. Sites with species nesting on multiple surfaces with conflicting aspects were recorded as multiple aspect.

2.5.2 Biotic variables:

Vegetation cover was recorded using a one meter square quadrat for sites that were larger than one square meter in size. Percentage cover of vegetation against bare ground were then recorded per quadrat per square meter of exposure area. For sites less than one square meter in size, vegetation cover was recorded by using a segmented fifty centimetre square quadrat (See Figure 10). Vegetation structure was recorded by assessing the height and openness of vegetation to the north, east, south, and west of study sites. Only vegetation within a 2 meter radius of the study site boundary was assessed. Categories assigned to vegetation structure were pioneer, building and mature stage stands, which develop in height and density respectively.

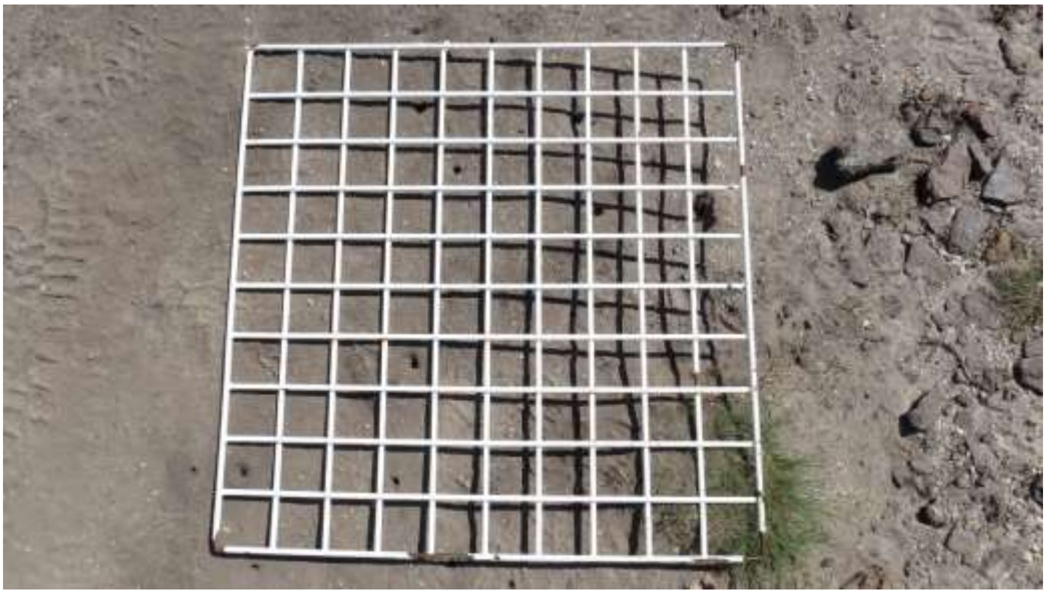
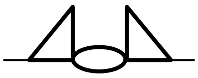
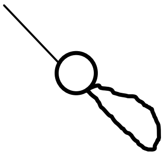
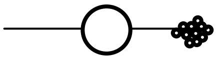
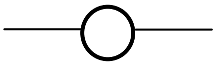
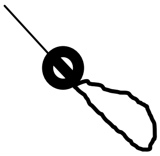


Figure 10: A segmented 50cm squared quadrat overlying an active nest site for the purpose of recording percentage vegetation cover (Spiers, 2016i).

Social typing of the observed hymenoptera was inferred by researching species nesting biology and systematically assigning species into gregarious nesting or solitary nesting categories. Categorising burrows into burrow types was achieved by identifying simple morphological differences. Six burrow types were clearly identified and are illustrated as diagrams to highlight key morphological differences in table 2.

Table 2: Morphological burrow types with morphological differences explained.

Burrow Type Name	Burrow Type Illustration	Morphology Explained
Spoil heap burrow		This burrow is associated with gregarious nesting wasps, usually present on flat surfaces, and is characterised by spoil heaps of sediment residing either side of the nest entrance. (See Appendix 7)
Sloped spoil heap burrow		This burrow is associated with gregarious nesting bees, usually present on sloped surfaces, and is characterised by a collapsed spoil heap of sediment flowing down the sloped surface from the nest entrance (See Appendix 8).
Purbeck burrow		This burrow is strictly associated to the Purbeck mason wasp (*Pseudepipona herichii* S.). It is constructed on flat or sloped surfaces of clay type soils. The immediate nest entrance is clear of debris, but aggregations of clay spoil can be located nearby (See Appendix 9).
Clean burrow		On the basis of observation, this burrow is associated to solitary nesting species. The nest entrance is clear of debris and can be excavated on flat or sloped surfaces (See Appendix 10).
Cryptic burrow		This burrow is associated to solitary nesting species, usually present on sloped surfaces, and is characterised by a collapsed spoil heap from the nest entrance. The nest entrance is usually blocked with debris as an anti-parasite measure and can normally be identified when species are entering or leaving the nest, making it difficult to identify (See Appendix 11; 12; 13; 14; 15).
Pin hole burrow		On the basis of observation, this burrow is associated to miniscule solitary nesting species, present on flat or sloped surfaces, with a nest entrance that is usually less than 2mm in diameter and clear of debris (See Appendix 16).

2.6 Statistical analysis:

2.6.1 Variation of data between sites with and without nest activity:

Data between nest activity and the control non-nest activity sites were statistically tested for variance. Continuous data for the independent variables soil compaction, inclination and vegetation cover were statistically tested using T-tests. Categorical data for the variable vegetation structure was statistically tested using an ANOVA test, and substrate type was statistically tested using a kruskal wallis test. These statistical tests tested the null hypothesis stating there to be no difference in variation of abiotic and biotic variables between nest activity sites and non-nest activity sites.

2.6.2 Correlation testing grouped data for sites with and without nest activity:

Continuous data amongst nest activity and non-nest activity sites for the variables soil compaction, inclination and vegetation cover were correlation tested to species richness using spearman's rank tests. This tested the null hypothesis stating there to be no relationship between the independent variables across nest activity and non-nest activity sites to the dependent variable of nesting species richness.

2.6.3 Correlation testing data exclusively for sites with nest activity:

Continuous data exclusively from nest activity sites for the variables exposure area, soil compaction, inclination and vegetation cover were also correlation tested to species richness using spearman's rank tests. This tested the null hypothesis stating no relationship between independent variables and nesting species richness. Categorical data for the variables vegetation structure, and substrate type were statistically tested for variation amongst nest activity sites using an ANOVA test, and a kruskal wallis test respectively. These tests tested the null hypothesis stating there to be no variation amongst the groups for independent variables and species richness.

2.6.4 Association testing of social nesting types:

Social types of gregarious nesting and solitary nesting species were tested using a chi-squared test to assess the strength of association between the social types across nest sites. This was repeated for the gregarious nesting bees and gregarious nesting wasps.

2.6.5 Correlation of species richness to morphological burrow types:

Morphological burrow richness was correlation tested to species richness using a spearmans rank. This tested the null hypothesis stating there to be no relationship between morphological burrow richness and nesting species richness.

2.7 Limitations:

Data recorded from slepe heath NNR and Hartland Moor NNR were grouped together for comparison to data recorded from Godlingston heath NNR. Grouping of Slepe heath NNR data and Hartland Moor NNR data was justified as these sites border one another (See Figure 11). It was discovered that there were significant variances in the data for the variables soil compaction, inclination and substrate type between the Godlingston heath data sets and Hartland moor data sets (See Appendix 2; 3; 6). Those variables of significant difference between sites should have been correlation tested to species richness on a site specific basis, however, the sample sizes for these data were ineffectively small to produce correlations to species richness at the site specific level. Therefore data from all sites were grouped together to increase the statistical power of discovering correlations amongst the data.

Data for aspect could not be statistically tested as there was not enough variation amongst the data. For this reason, diagrams showing species richness and aspect for nest activity and non-nest activity sites were produced and a qualitative analysis of the data is given at the end of section 3.2. A strength of association test could not be produced between solitary nesting bee and wasp species as no solitary nesting bee species were recorded over the study period. Exposure area of nesting surfaces for both nest activity sites and non-nest activity sites were purposefully selected to be of a similar size. This meant that grouping of exposure area data across nest activity and non-nest activity sites for the purpose of correlation testing to nesting species richness could not done. For this same reason variation testing of exposure area was also excluded.

Ten figure grid references of study site locations were recorded for the purpose of mapping using a Garmin GPSMAP 64s. Coordinates should have been accurate to within a meter squared radius of the recorded GPS location, however local vegetation may have distorted the locational accuracy, and has resulted in mapped sites deviating meters from their true location. This was identified as sites recorded along foot paths and vehicle tracks have migrated into stands of vegetation. Ultimately, this has affected the reliability of qualitative analysis for the distribution of nest activity and non-nest activity sites.

3.0 Data Results and Analysis:

3.1 Distribution of nest activity and non-nest activity sites:

Overall, nest activity sites appear to be aggregated regionally across Hartland moor NNR, Slepe heath NNR, and Godlingston NNR (See Figure 11 and Figure 13). Non-nest activity sites also follow this trend as they were selected within a 15 meter radius of nest activity sites (See Figure 12 and Figure 13). In Figure 13, sites 1, 2, 3 and 17 are aggregated in an area to the north west of Godlingston heath NNR, whereas in Figure 11 sites 3, 4, 5, 6, 7, and 12 are aggregated to the north east of Hartland moor NNR. In particular, sites 13 and 14 of Godlingston heath NNR are within 30 meters of each other (See Figure 13). Sites 14 and 18 of Slepe heath NNR are within 100 meters of each other, and sites 2 and 16 of Hartland moor NNR are within 50 meters of each other (See Figure 11).

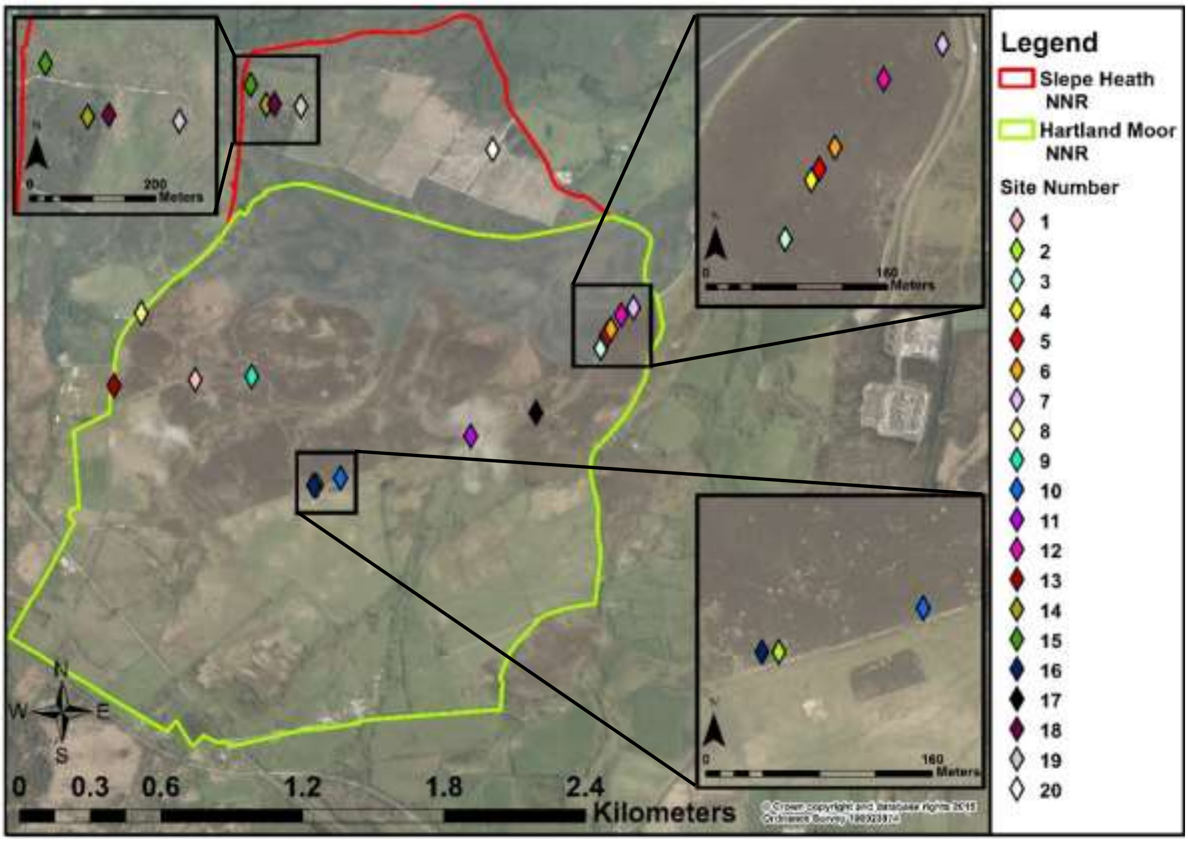


Figure 11: Nest activity map for Hartland moor NNR and Slepe heath NNR (Spiers, 2017b).

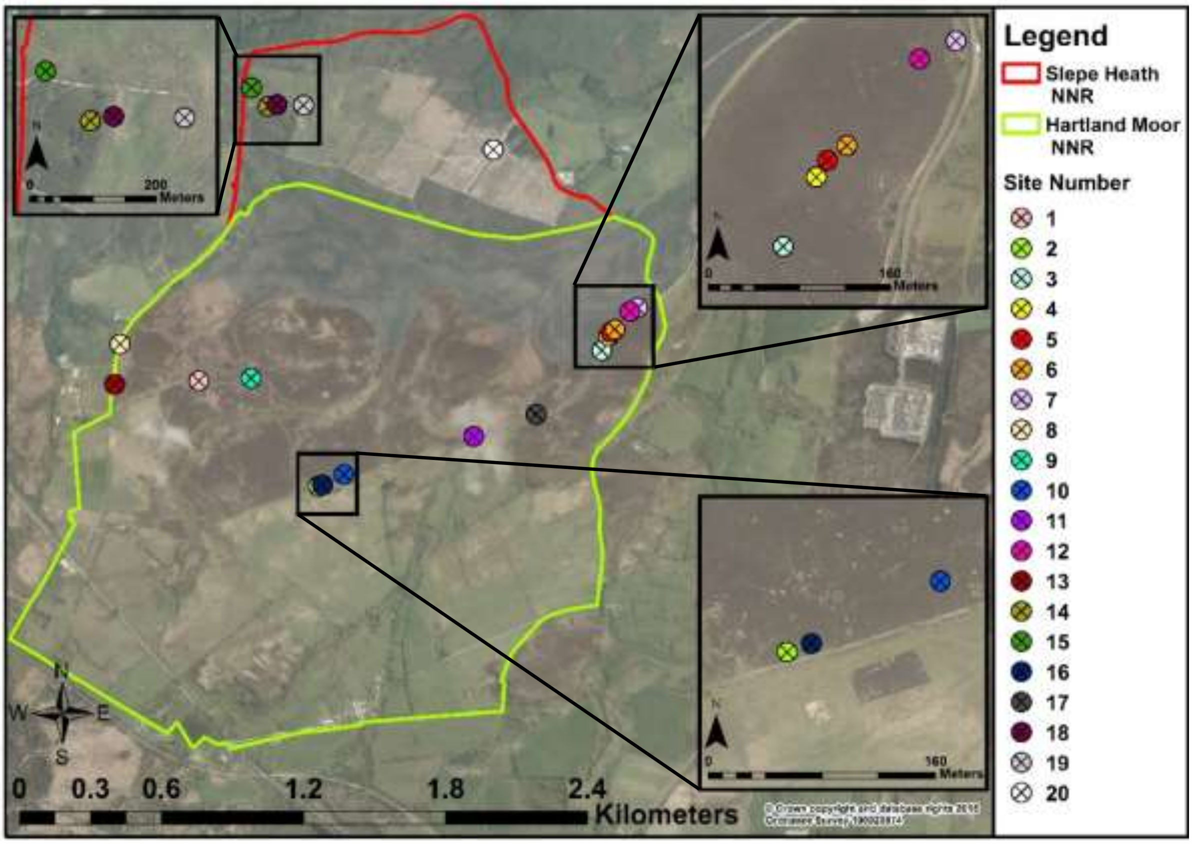


Figure 12: Non-nest activity map for Harltand moor NNR and Slepe heath NNR (Spiers, 2017c).

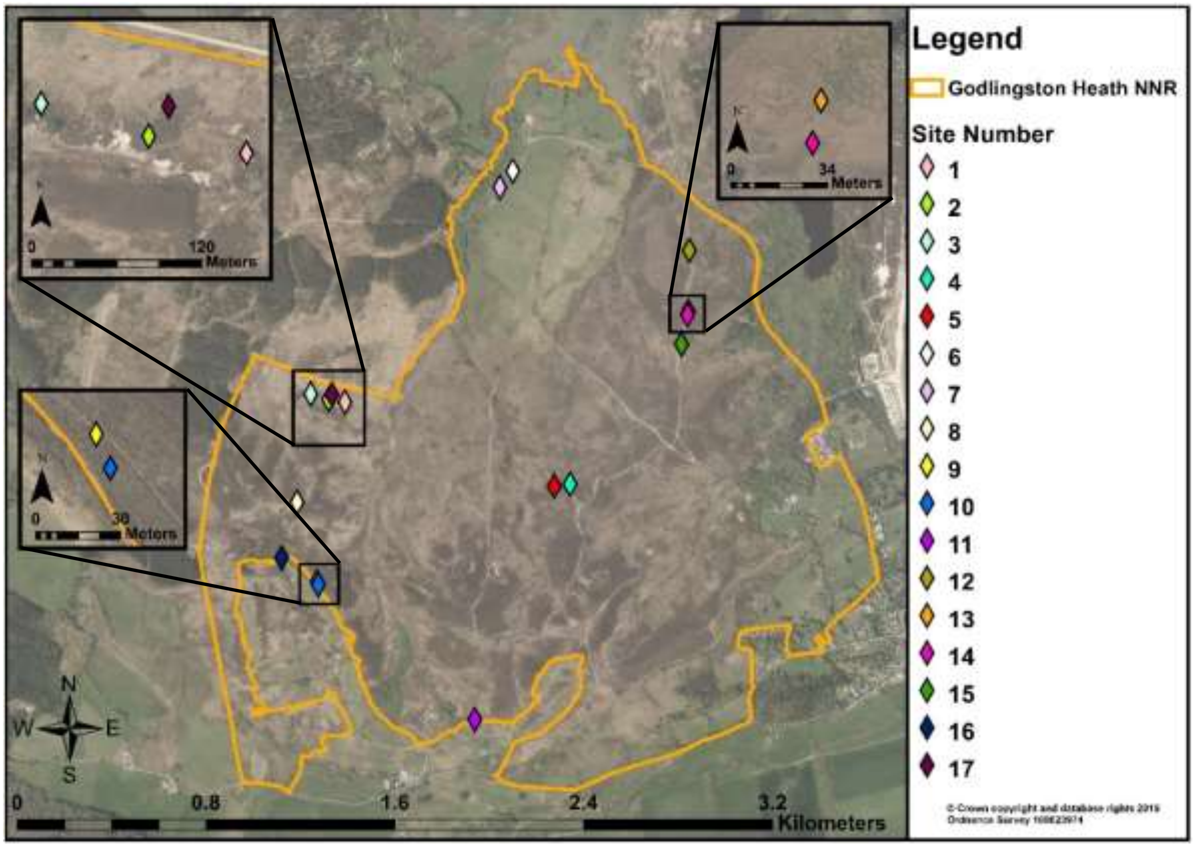


Figure 13: Nest activity map for Godlingston heath NNR (Spiers, 2017d).

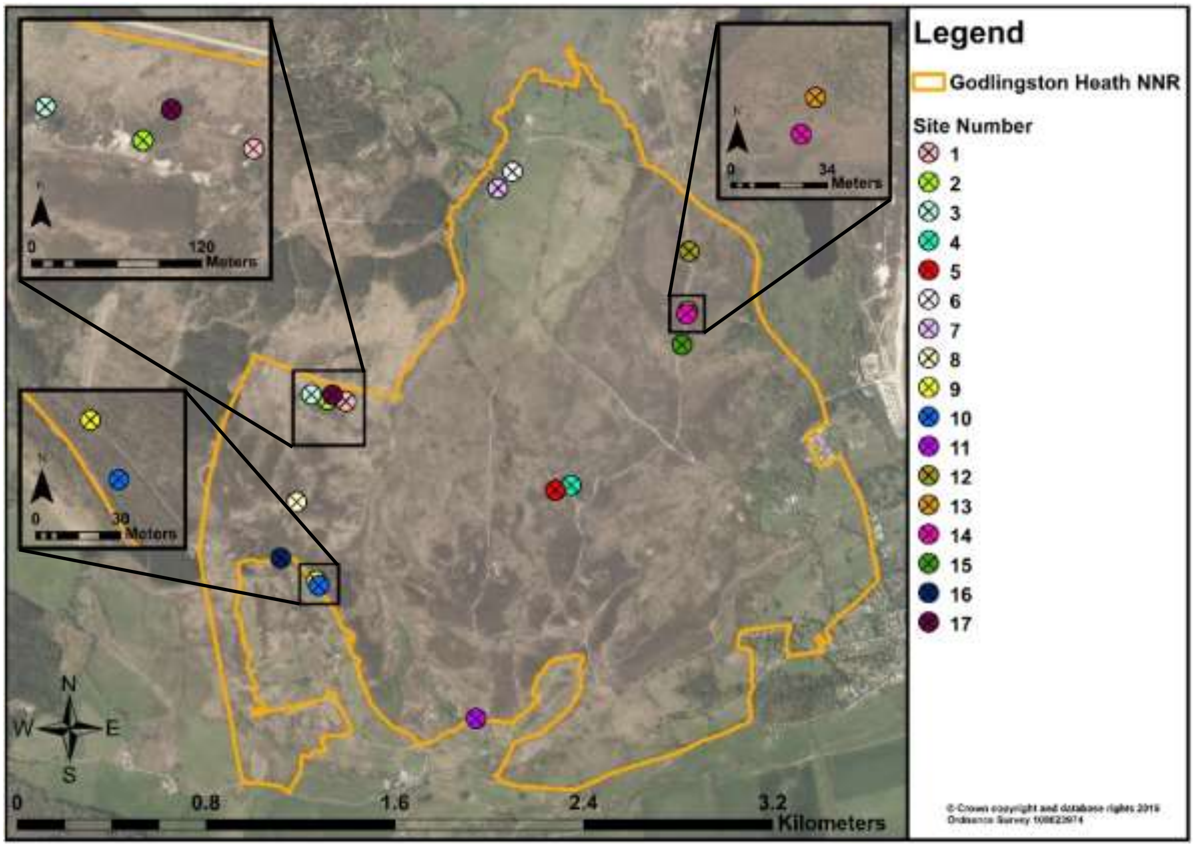


Figure 14: Non-nest activity map for Godlingston heath NNR (Spiers, 2017e).

3.2 Variation of variables between sites with and without nest activity:

Overall, there was no variation of average soil compaction between sites with and sites without nest activity (See Figure 15). Sites with nest activity had an average soil compaction of 2.22 Kg/cm², whereas sites without nest activity had an average soil compaction of 2.59 Kg/cm², a deviation of 0.37 Kg/cm² (See Figure 15).

There was a non-significant difference of average soil compaction between sites with nest activity and sites without nest activity (t-test, t = 1.33, d.f. = 71.72, p = 0.19). Therefore, soil compaction was not deterring nest excavation at non-nest activity sites.

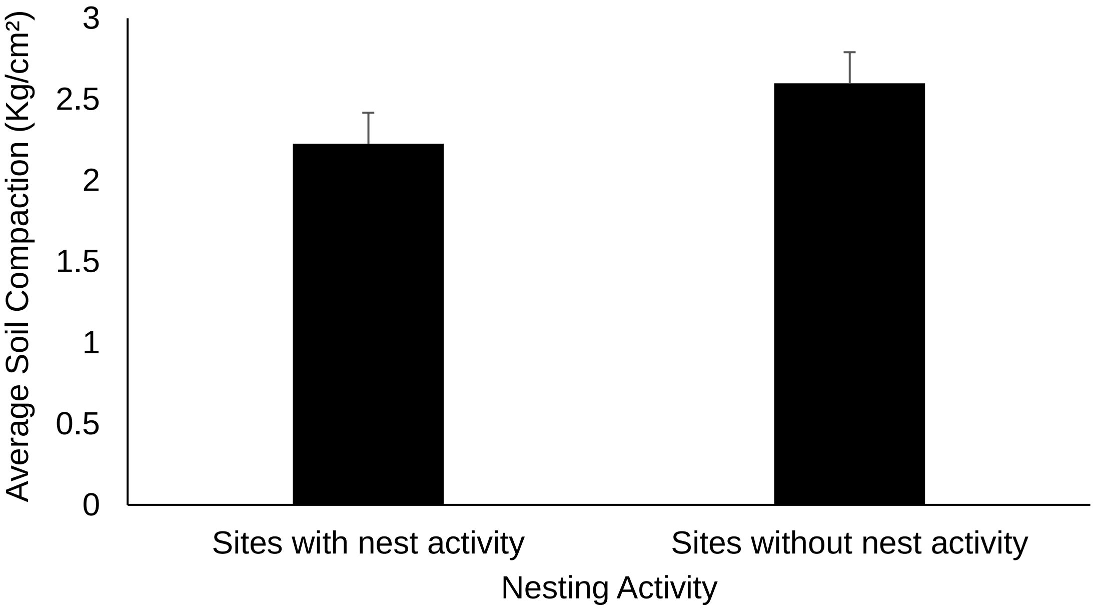


Figure 15: Variation of average soil compaction between sites with and sites without nest activity.

Overall, there was no variation of average inclination between sites with nest activity and sites without nest activity (See Figure 16). Sites with nest activity had an average inclination of 16°, whereas sites without nest activity had an average inclination of 15°, a deviation of 1° (See Figure 16).

There was a non-significant difference of average inclination between sites with nest activity and sites without nest activity (t-test, t = -0.48, d.f. = 71.49, p = 0.63). Therefore, average inclination was not deterring nest excavation at non-nest activity sites.

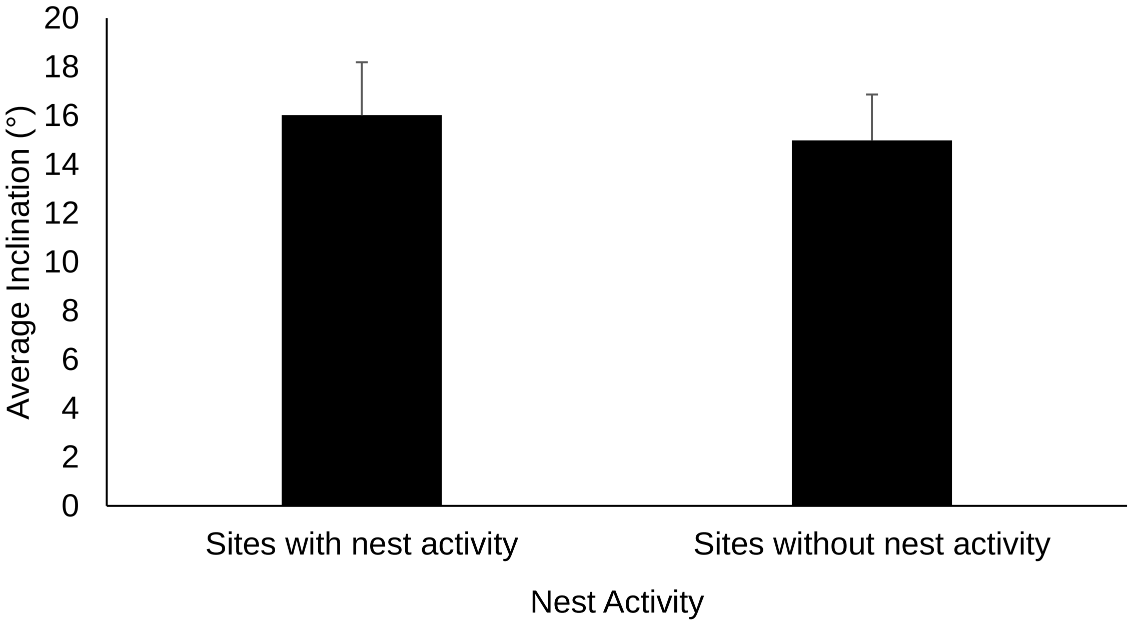


Figure 16: Variation of average Inclination between sites with and sites without nest activity.

Overall, there was no variation of average vegetation cover between sites with and sites without nest activity (See Figure 17). Sites with nest activity had an average vegetation cover of 26.1%, whereas sites without nest activity had an average vegetation cover of 29.9%, a deviation of only 3.8% (See Figure 17).

There was a non-significant difference of average vegetation cover between sites with nest activity and sites without nest activity (t-test, t = 0.87, d.f. = 72, p = 0.39). Therefore, average vegetation cover was not deterring nest excavation at non-nest activity sites.

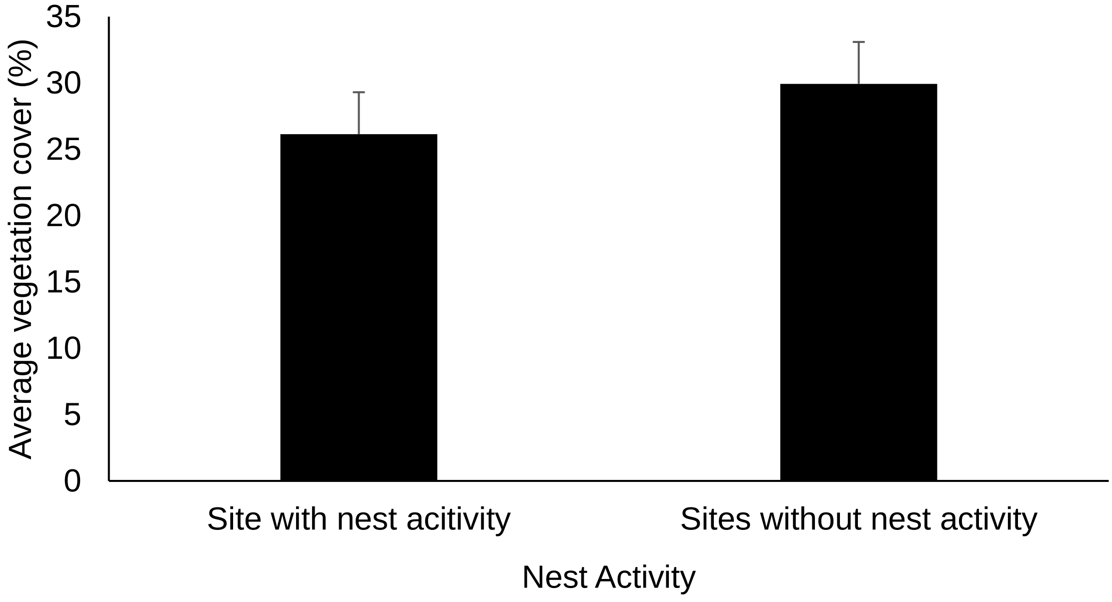


Figure 17: Variation of average vegetation cover between sites with and sites without nest activity.

There were some considerable differences in the frequency of occurring vegetation structure between sites with and sites without nest activity (See Figure 18). For example; the most frequently occurring vegetation structure for both sites with and without nest activity was pioneer vegetation structure, which occurred at 26 of the 37 nest activity sites and at 17 of the 37 non-nest activity sites respectively (See Figure 18). The least frequently occurring vegetation structure for sites with and sites without nest activity was that of a mature vegetation structure, which occurred at 1 of 37 nest activity sites and 8 of the 37 non-nest activity sites respectively (See Figure 18).

There was a significant difference between vegetation types found amongst those sites with nest activity and those without nest activity (kruskal wallis, Chi-squared = 7.33, d.f. = 1, p = 0.007). Therefore, vegetation structure did deter nest excavation at non-nest activity sites.

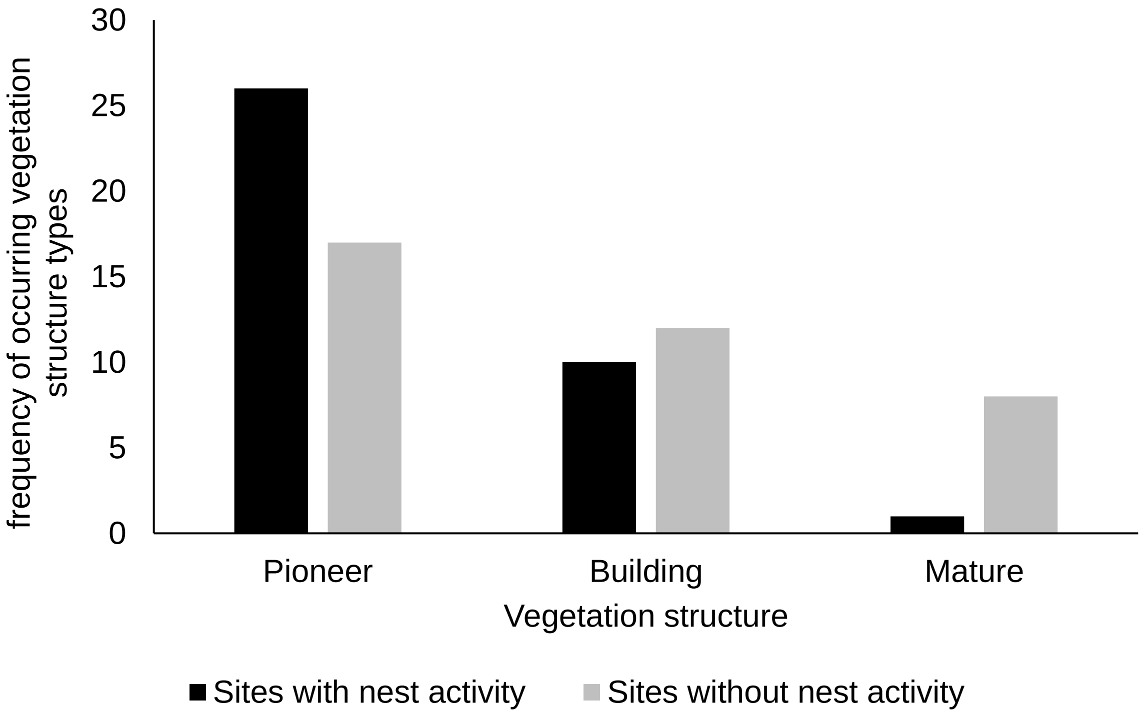


Figure 18: Frequency of occurring vegetation structures between sites with and sites without nest activity.

Data for the cobbles substrate type was not included in the statistical analysis for variation testing of substrate types across sites with and without nest activity. This was because the cobbles substrate type only occurred once throughout all of the study sites (See Figure 19). There were slight variations in the frequency of occurring substrate types between sites with and without nest activity (See Figure 19). For example; the most frequently occurring substrate type for both sites with and without nest activity was fine sand/clay, which occurred at 17 of 37 nest activity sites and 10 of the 37 non-nest activity sites respectively (See Figure 19). Sand occurred at 2 of the 37 nest activity sites, and 7 of the 37 non-nest activity sites (See Figure 19).

There was a non-significant difference between substrate types found amongst those sites with nest activity and those without nest activity (ANOVA, F = 0.09, d.f. = 1, p = 0.77). Therefore, substrate type did not deter nest excavation at non-nest activity sites.

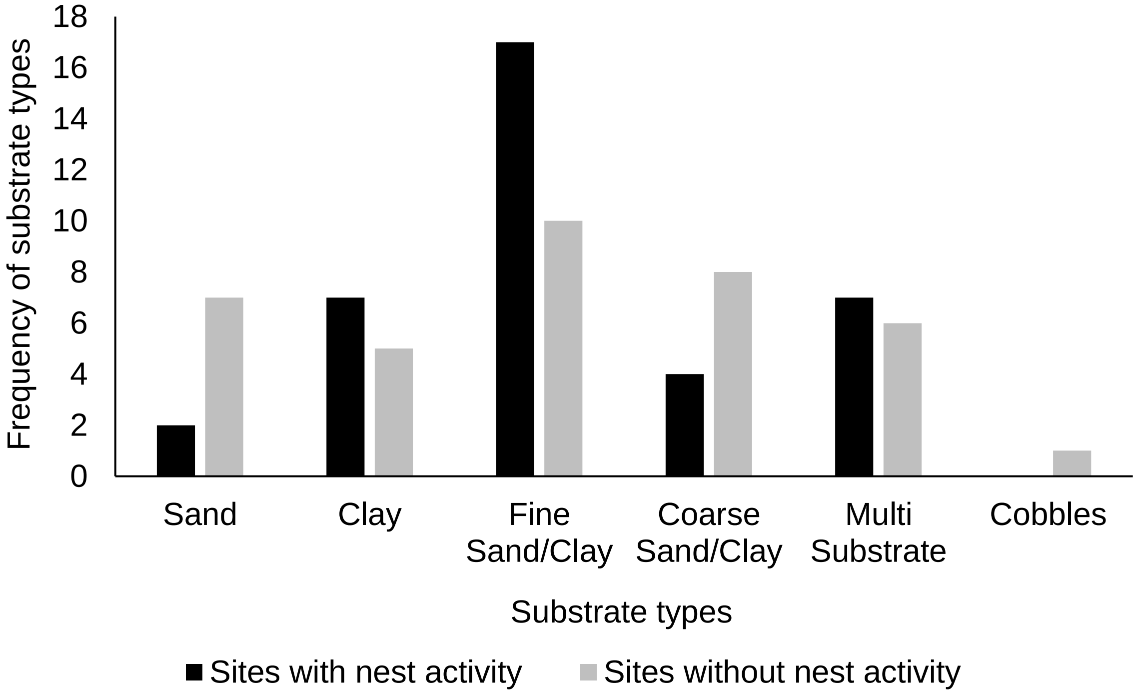


Figure 19: Frequency of occurring substrate types between sites with and sites without nest activity.

Across Hartland moor NNR, Slepe heath NNR, and Godlingston heath NNR, Sites with nest activity were mostly located on soil exposures with a south facing aspect (See Figure 20 and Figure 21). Seven nest activity sites had multiple aspects (See Figure 20 and Figure 21), and one nest site from Godlingston heath NNR had a north-westerly aspect (See Figure 21). Sites without nest activity were observed across a range of aspects and not strongly associated to any one aspect. Eleven of the non-nest activity sites had a northerly aspect, nine of the non-nest activity sites were multi-directional, and 17 of the non-nest activity sites were southerly facing (See Figure 22 and Figure 23). Therefore, nest activity does appear to have deterred nest excavation at non-nest activity sites.

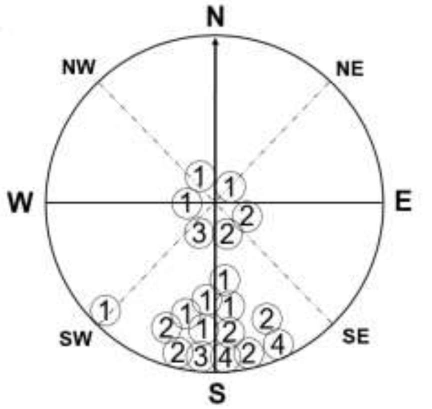


Figure 20: Species richness and aspect per nest activity site for Hartland moor NNR and Slepe heath NNR.

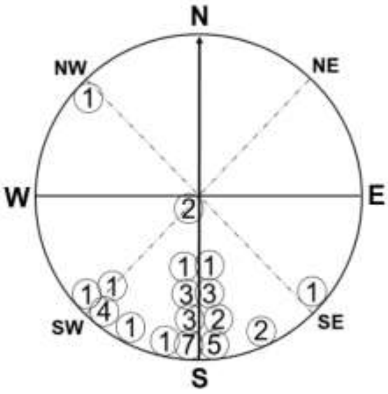


Figure 21: Species richness and aspect per nest activity site for Godlingston heath NNR.

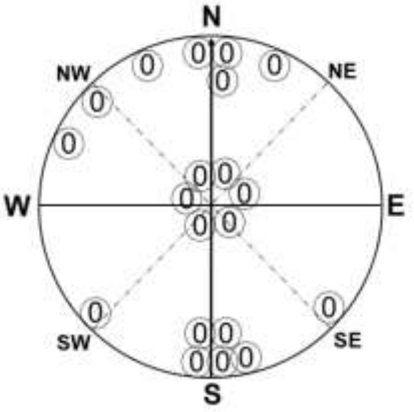


Figure 22: Species richness and aspect per non-nest activity site for Hartland moor NNR and Slepe heath NNR.

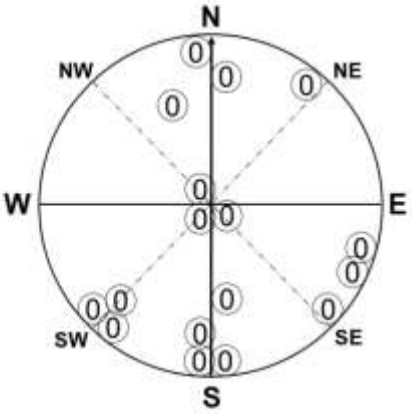


Figure 23: Species richness and aspect per non-nest activity site for Godlingston heath NNR.

3.3 Correlation of grouped data for sites with and without nest activity to nesting species richness:

Overall there is no correlation between average soil compaction and nesting species richness (See Figure 24). Sites with an average soil compaction of 2.27 Kg/cm² had the highest nesting species richness of 7 (See Figure 24). Multiple sites with average soil compaction ranging from 0.67 Kg/cm² to 4.5 Kg/cm² across non-nest activity sites had the lowest species richness values of 0 (See Figure 24).

There is a non-significant weak negative relationship between average soil compaction and nesting species richness across sites with and without nest activity (Spearman, rho = -0.15, N = 74, p = 0.19). Therefore, average soil compaction did not significantly affect nesting species richness across sites with and without nest activity.

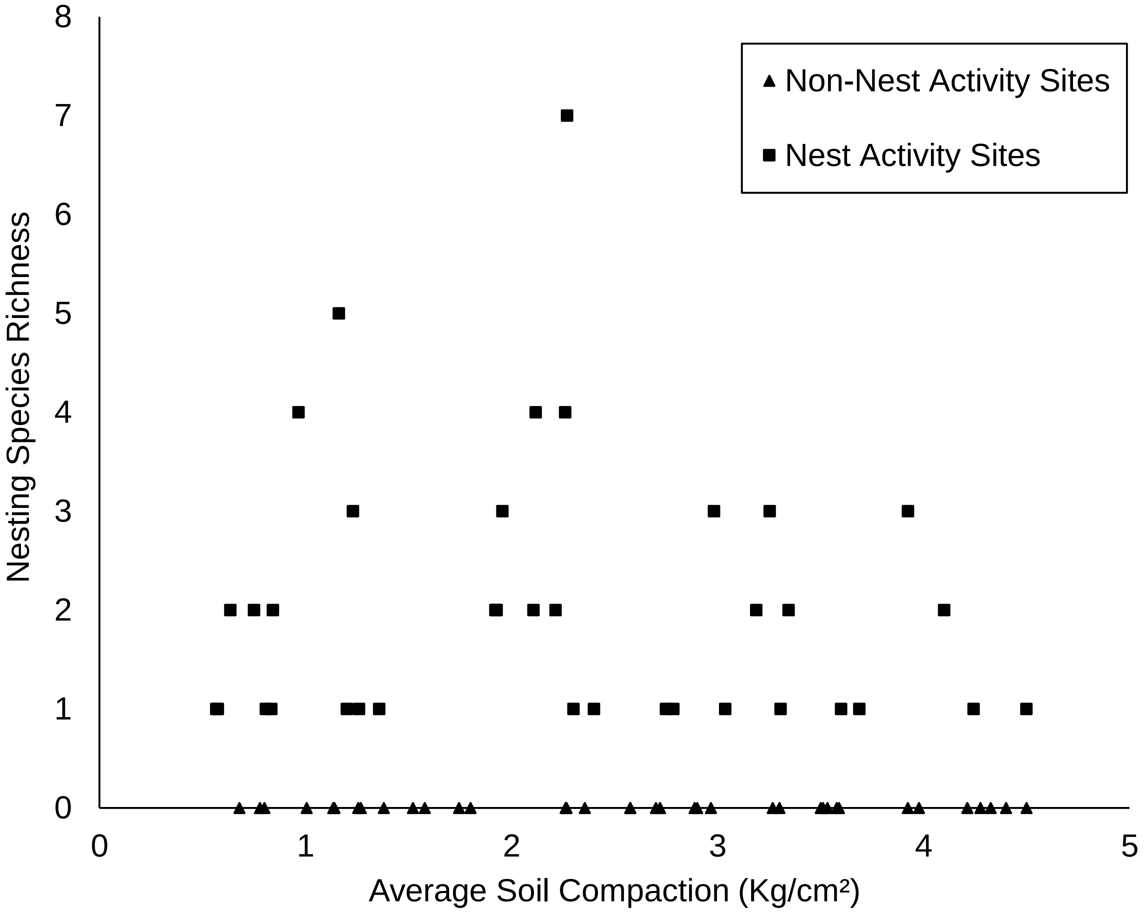


Figure 24: Average soil compaction and nesting species richness across sites with and sites without nesting activity.

Overall, there is no correlation between average inclination and nesting species richness (See Figure 25). Sites with an average inclination of 26.6° across nest activity sites and non-nest activity sites have the highest nesting species richness of 7 (See Figure 25). Multiple sites with an average inclination ranging from 0.88° and 51° across nest activity and non-nest activity sites have the lowest species of 0 (See Figure 25).

There is a non-significant relationship between average inclination and nesting species richness across sites with and without nesting activity (Spearman, rho = -0.02, N = 74, p = 0.89). Therefore, average inclination did not have a significant effect on nesting species richness across sites with and sites without nest activity.

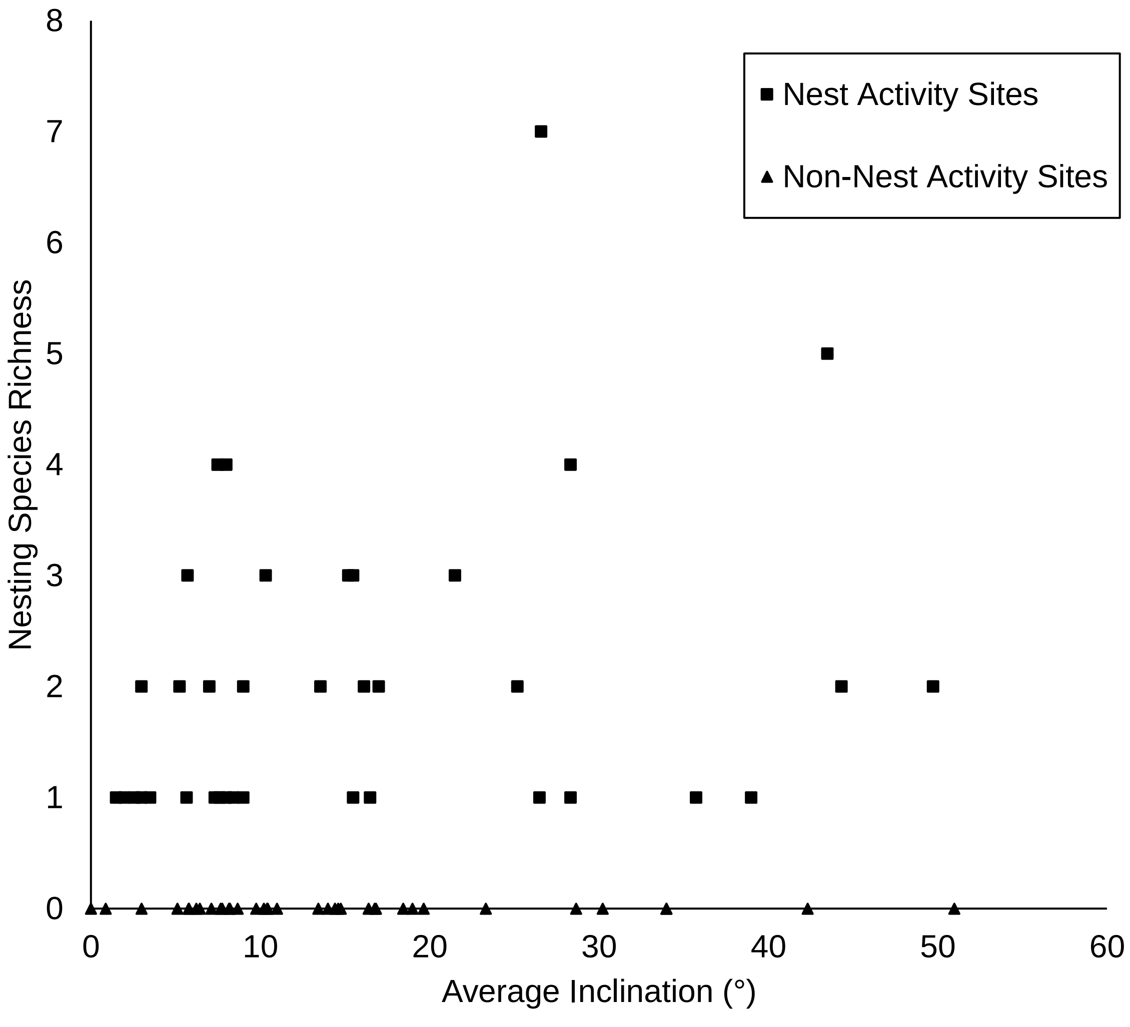


Figure 25: Average inclination and nesting species richness across sites with and sites without nesting activity.

Overall there is a weak negative correlation between average vegetation cover for nest activity sites and non-nest activity sites and nesting species richness (See Figure 26). Sites with an average vegetation cover of 0% had the highest nesting species richness of 7, however these sites also have nesting species richness values as low as 0 and 1 (See Figure 26). Multiple sites with an average vegetation cover ranging from 0% to 72.66% had the lowest nesting species richness values of 0 (See Figure 26).

There is a non-significant moderate negative relationship between average vegetation cover and nesting species richness across nest activity and non-nest activity sites (Spearman, rho = - 0.12, N = 74, p = -0.31). Therefore, average vegetation cover did not have a significant effect upon nesting species richness across sites with and sites without nest activity.

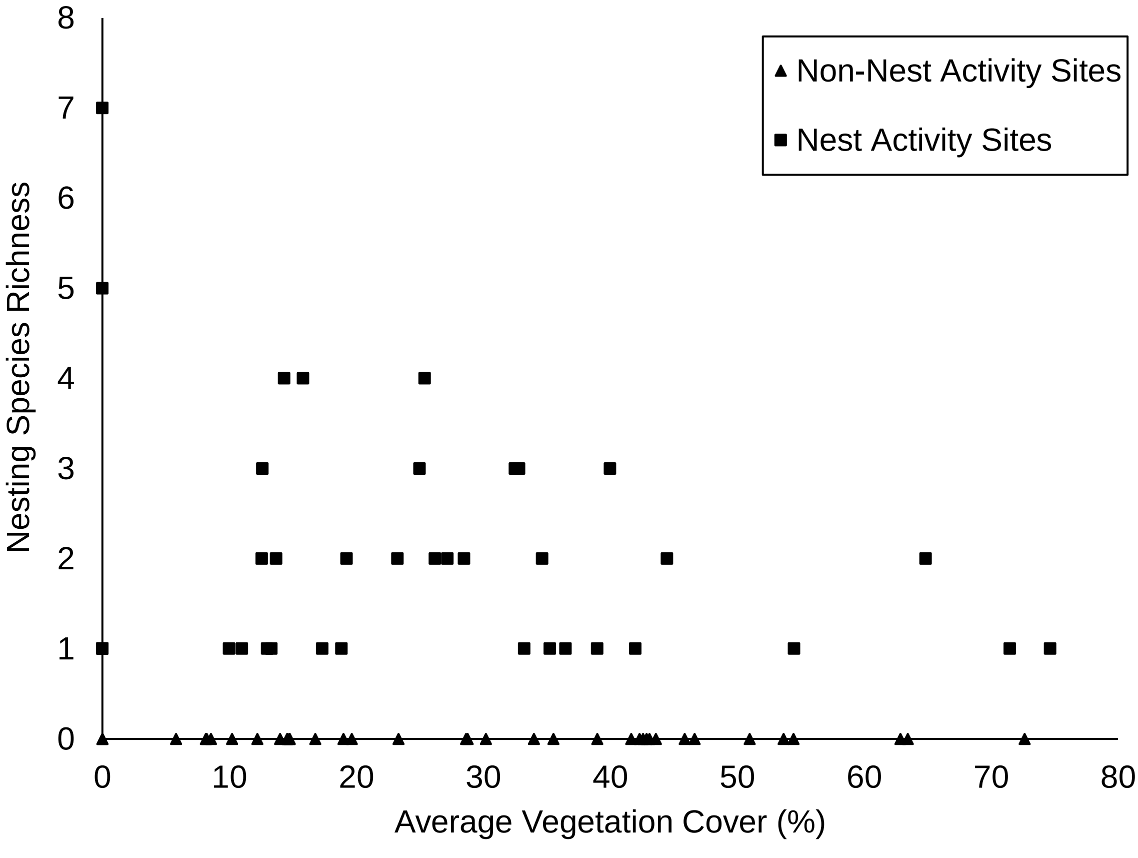


Figure 26: Average vegetation cover and nesting species richness across sites with and sites without nest activity.

3.4 Correlations of data across sites with nest activity to species richness:

There is a moderate positive correlation between exposure area of nesting surfaces and nesting species richness, however this is dependent on an outlier data sample which has an exposure area of 8m² and a nesting species richness of 7 (See Figure 27). Sites with an exposure area of 8m² had the highest nesting species richness of 7, however these sites also had nesting species richness values as low as 1 and 2 (See Figure 27). Multiple sites with exposure areas ranging from 0.19m² to 12m² had the lowest nesting species richness values of 1 (See Figure 27).

There is a significant moderate positive relationship between exposure area of nesting surface and nesting species richness across sites with nest activity (Spearman, rho = 0.38, N = 37, p = 0.02). Therefore, exposure area of nesting surface did have a significant effect on nesting species richness across active nest sites.

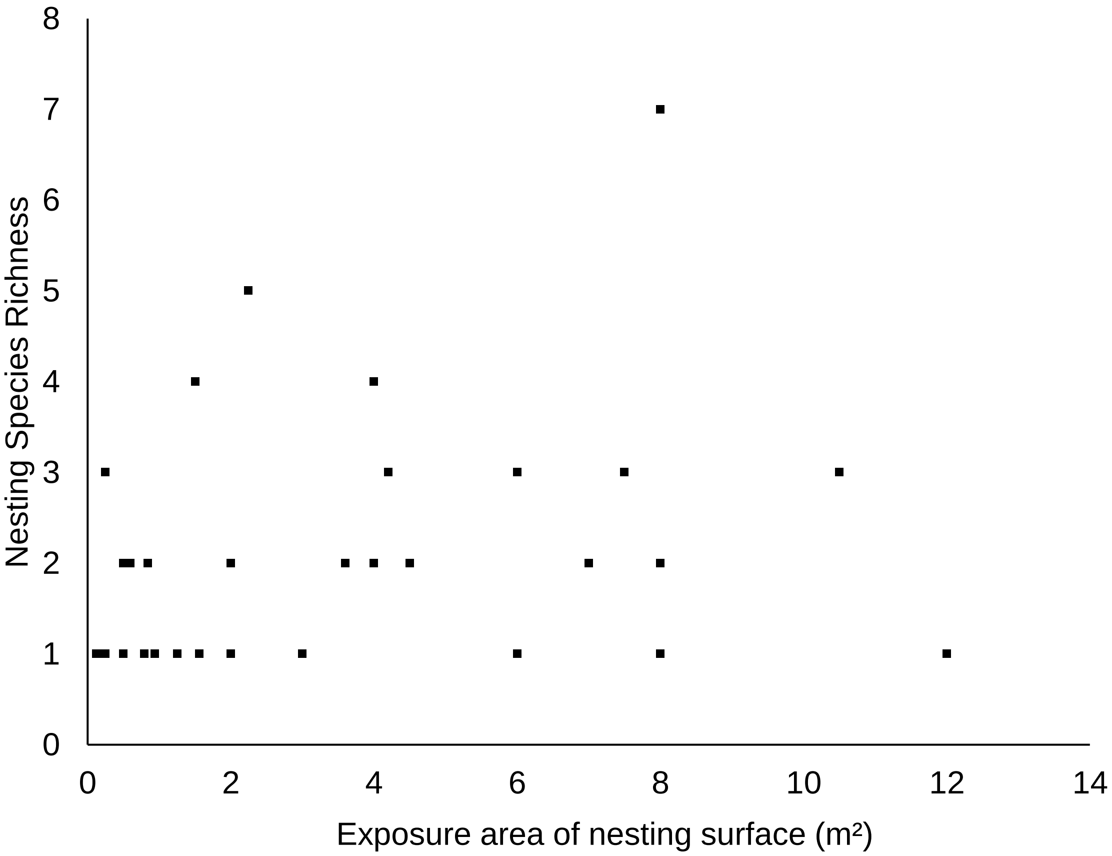


Figure 27: Exposure area of nesting surface and nesting species richness across active nest sites.

Overall there was no correlation between average soil compaction and nesting species richness (See Figure 28). Sites with an average soil compaction of 2.27 Kg/cm² had the highest nesting species richness of 7, whilst sites with average soil compaction ranging from 0.575 Kg/cm² and 4.5 Kg/cm² had the lowest nesting species richness of 1 (See Figure 28).

There was no significant relationship between average soil compaction and species richness (Spearman, rho = -0.07, N = 37, p = 0.68). Therefore, average soil compaction did not have a significant effect upon nesting species richness across nest activity sites.

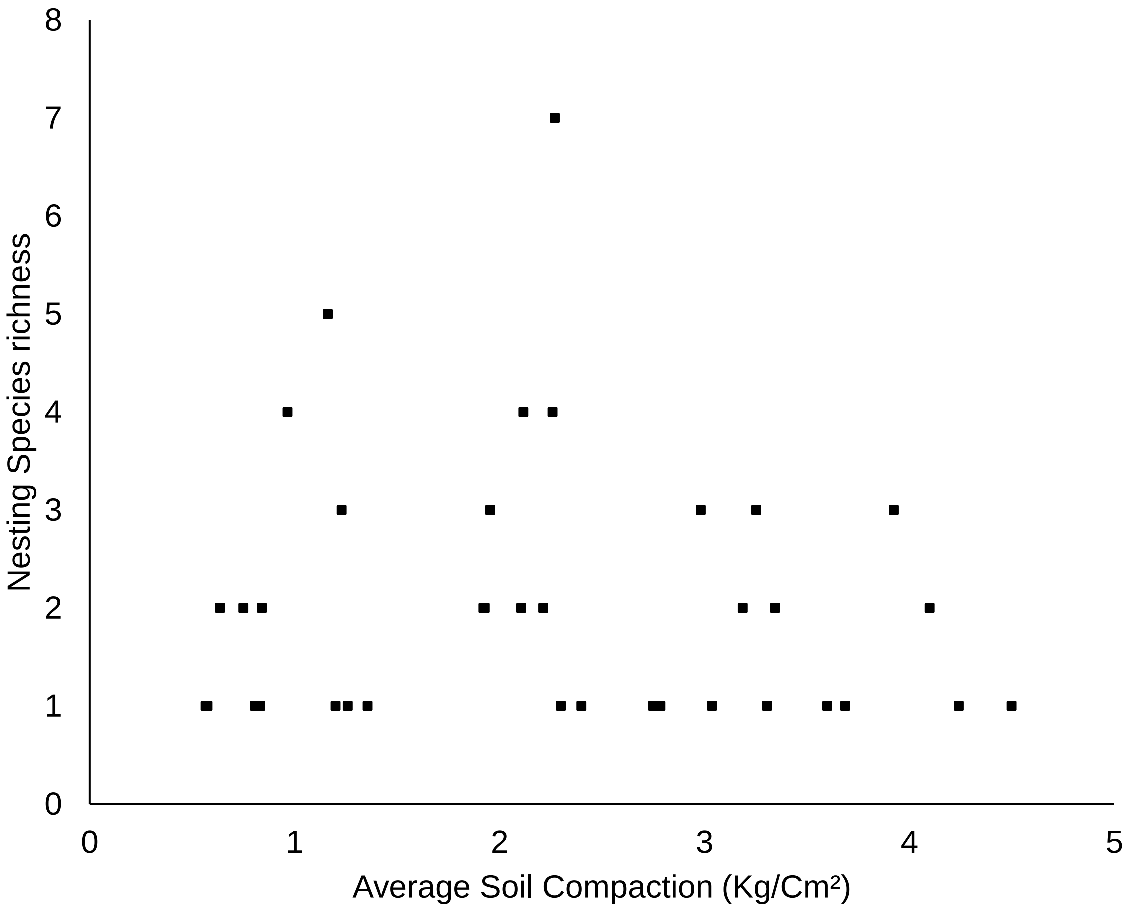


Figure 28: Average soil compaction and nesting species across active nest sites.

Overall there is a weak positive correlation between average inclination and nesting species richness (See Figure 29). Nest sites with an average inclination of 26.6 degrees had the highest nesting species richness of 7, whereas nest sites with an average inclination ranging from 1.5 degrees to 39 degrees had the lowest nesting species richness of 1 (See Figure 29).

There is a non-significant weak positive relationship between mean inclination and nesting species richness across active nest sites (Spearman, rho = 0.28, N = 37, p = 0.09). Therefore, average inclination did not have a significant effect on nesting species richness across nest activity sites.

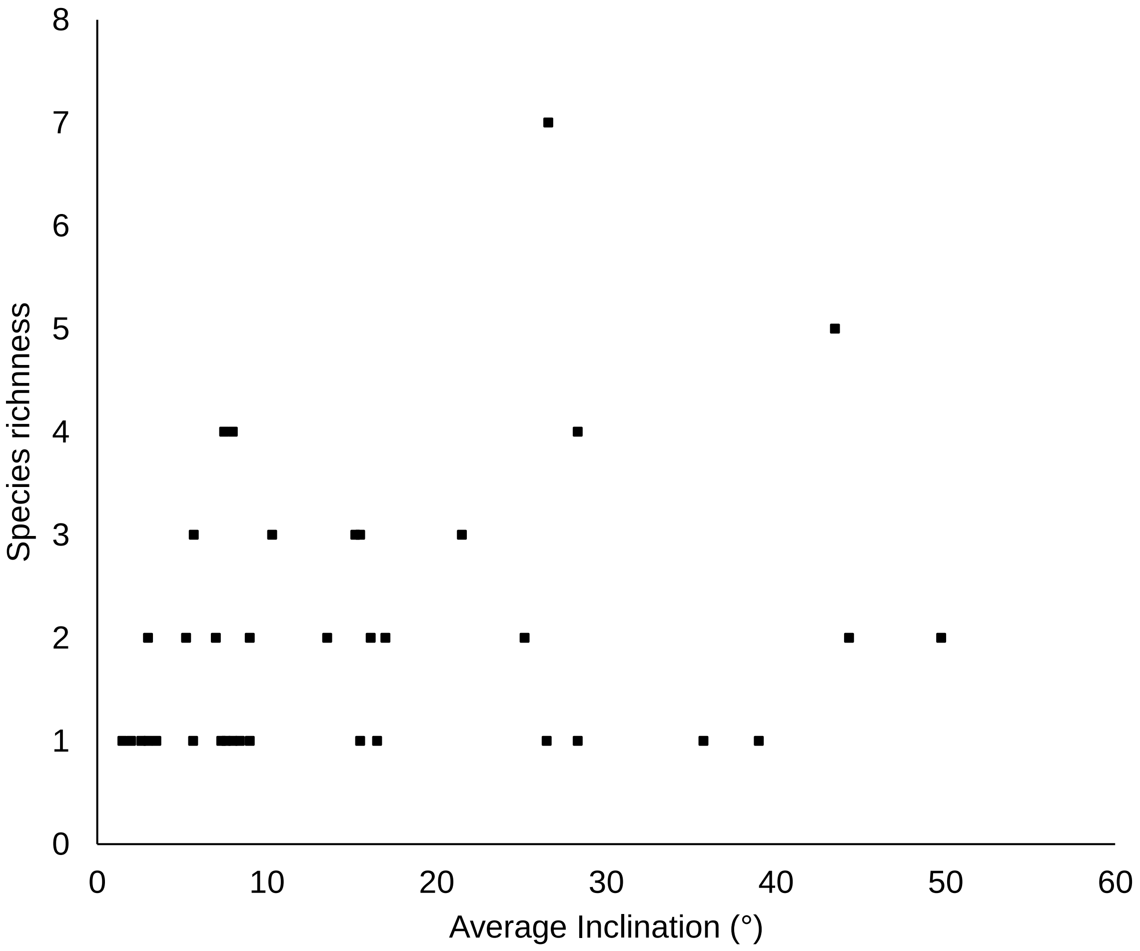


Figure 29: Average Inclination and nesting species richness across nest activity sites.

Overall there is a weak negative correlation between average vegetation cover and nesting species richness (See Figure 30). Sites with an average vegetation cover of 0% had the highest nesting species richness of 7, however these sites were also recorded as having a nesting species richness as low as 1 (See Figure 30). Multiple sites with an average vegetation cover ranging from 0% to 80% exhibited the lowest nesting species richness of 1 (See Figure 30).The largest variation of nesting species richness is between 1 and 5, which can be observed for sites with an average vegetation cover of 0% (See Figure 30).

There is a non-significant weak negative relationship between average vegetation cover and nesting species richness (Spearman, rho = - 0.13, N = 37, p = 0.45). Therefore, average vegetation cover did not have a significant effect on nesting species richness across sites with nest activity.

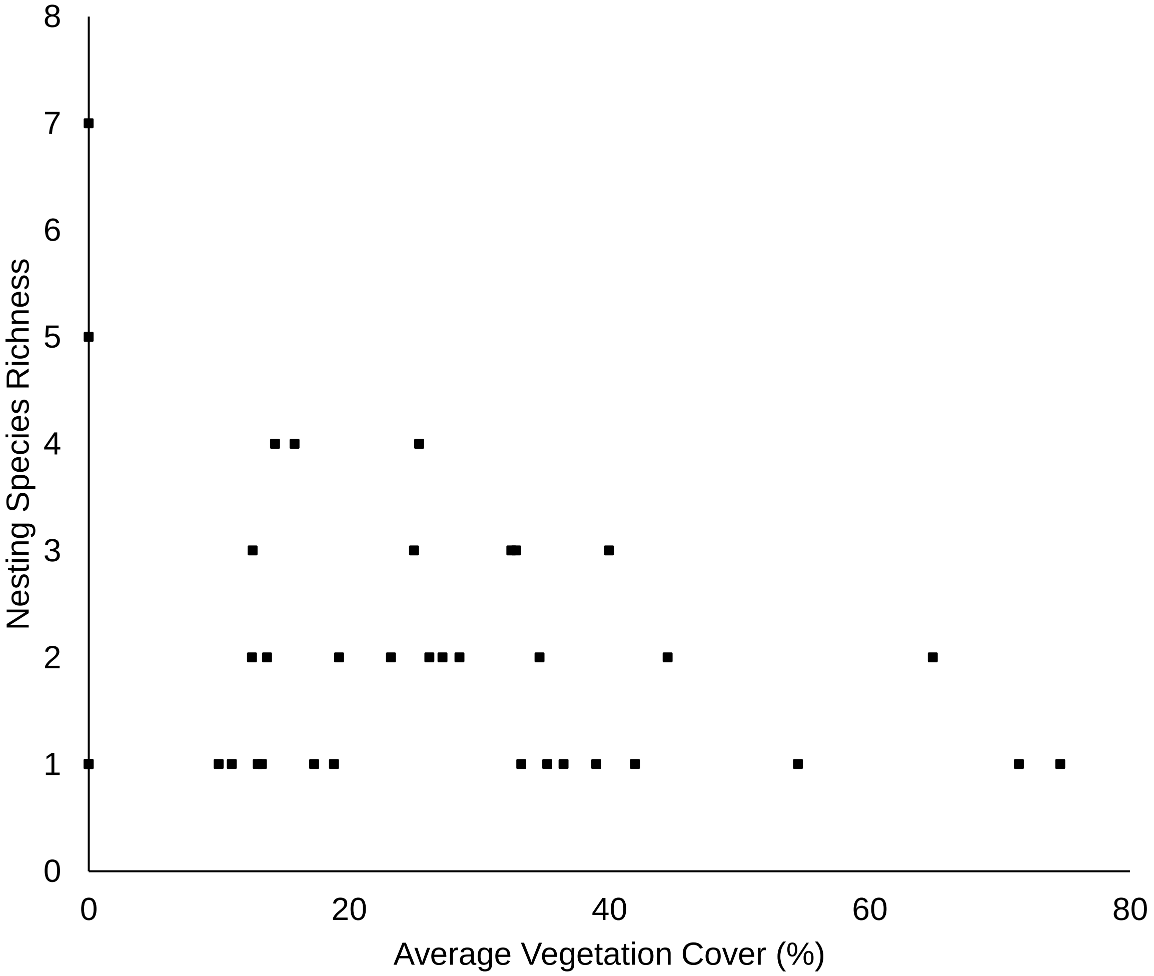


Figure 30: Average vegetation cover and nesting species richness across active nest sites.

Overall, there was no variation of species richness between vegetation structural types (See Figure 31). There was an average nesting species richness of 2 amongst sites with pioneer vegetation structure, whereas average nesting species richness amongst sites with a building vegetation structure was 2.2 (See Figure 31). Only one site over the study period was recorded as having a mature vegetation structure and was consequently removed from statistical analysis.

There is a non-significant difference of average nesting species richness amongst pioneer and building vegetation structures (ANOVA = F = 0.145, d.f. = 1, p = 0.71). Therefore, vegetation structure did not have a significant effect on average nesting species richness across sites with nest activity.

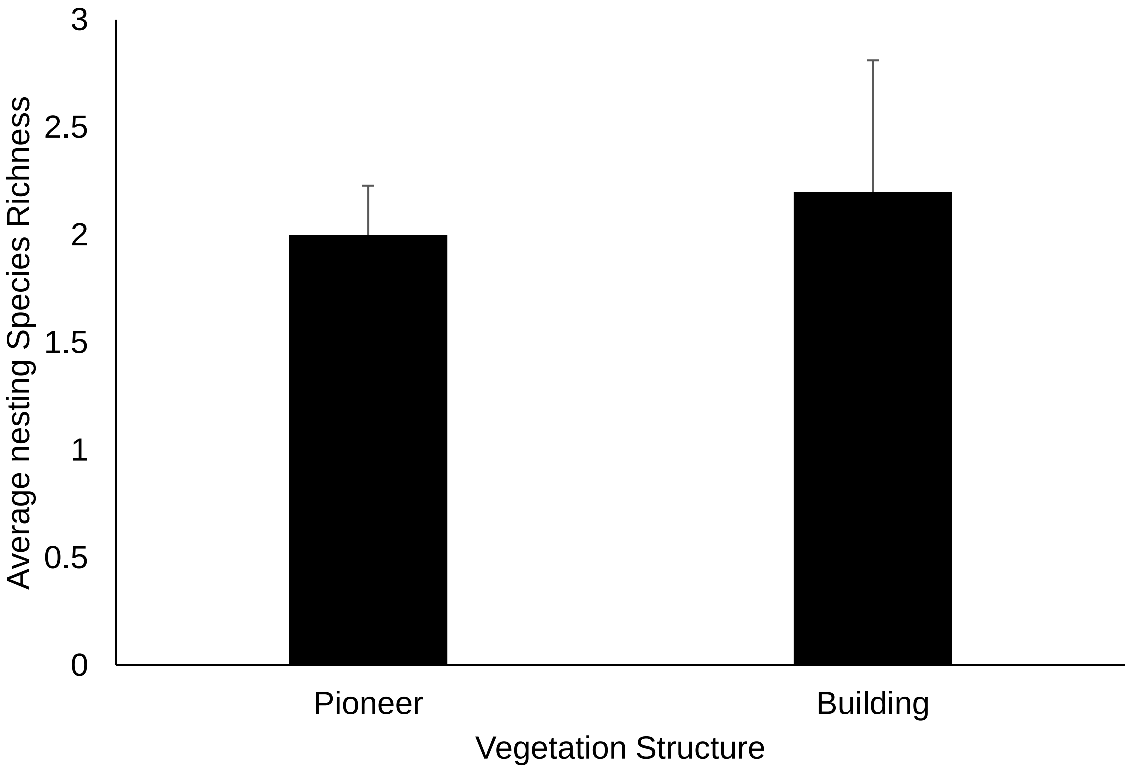


Figure 31: Average nesting species richness per vegetation structural type across active nest sites.

Overall, there was considerable variation of species richness amongst substrate types (See Figure 32). The group for multiple-substrates yielded the highest average nesting species richness of 3.6, whereas the sand substrates yielded the lowest average nesting species richness of 1 (See Figure 32). Fine sand/clay substrates yielded the second highest average nesting species richness of 2.1 (See Figure 32). Clay substrates and coarse sand/clay substrates yielded average nesting species richness values of 1.3 (See Figure 32).

There is not a significant difference of the average nesting species richness between sand, clay, and coarse sand/clay substrates, however there is a significant difference between average nesting species richness of those substrate types and sites with fine sand/clay substrates and multiple substrates (See Figure 32). There is also a significant difference of the average nesting species richness between fine sand/clay and multiple substrates (See Figure 32).

There is a significant difference of average nesting species richness amongst sand, clay, fine sand/clay, coarse sand/clay and multi-substrate groups (Kruskal wallis, chi-square = 12.19, d.f. = 4, p = 0.16). Therefore, substrate type did have a significant effect on nesting species richness across nest activity sites.

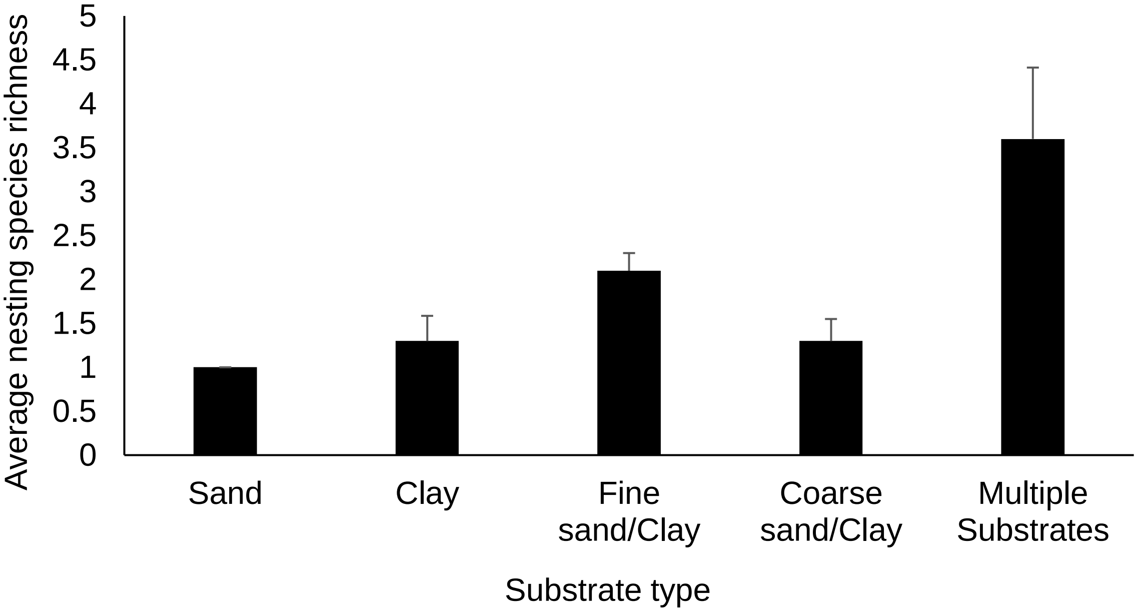


Figure 32: Average nesting species richness per substrate type across active nest sites.

Sites with an aspect between south west and south east had the highest nesting species richness values which range from 1 to 7, whereas sites with a north-westerly aspect has nesting species richness values of 1 (See Figure 33 and Figure 34). Therefore, aspect did appear to have an effect on nesting species richness across nest activity sites.

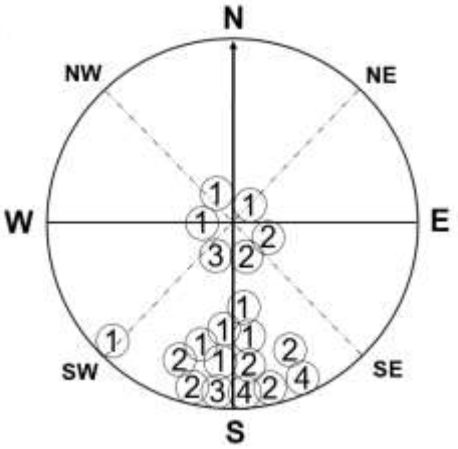


Figure 33: Species richness and aspect per nest activity site for Hartland moor NNR and Slepe heath NNR.

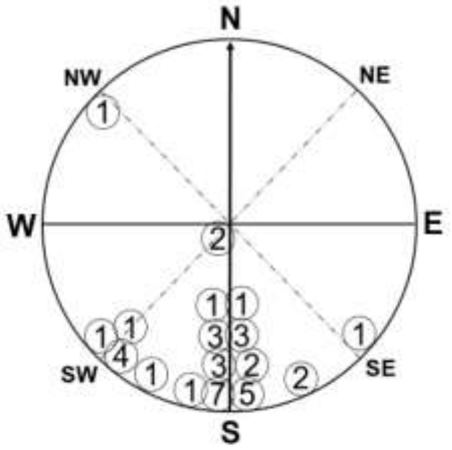


Figure 34: Species richness and aspect per nest activity site for Godlingston heath NNR.

3.5 Strength of association between social nesting types:

Overall, gregarious nesting and solitary nesting species have preferences for seperate nesting. Across the 37 study sites 11 were inhabited by both gregarious nesting species and solitary nesting species (See Figure 35 and Figure 36). 7 of the 37 study sites were inhabited exclusively by solitary nesting species, and 19 of the 37 study sites were inhabited exclusively by gregarious nesting species (See Figure 35 and Figure 36).

There is a significant negative association between gregarious nesting species and solitary species in their nesting environments (Chi-squared = 9.112, p = 0.003). Therefore, solitary nesting and gregarious nesting species had preferences for nesting in isolation to one another, rather than communally.

Overall, gregarious nesting wasps and gregarious nesting bees have preferences for separate nesting (See Figure 35 and Figure 36). Across the 37 study sites 2 of these were inhabited by both gregarious nesting wasp species and gregarious nesting bee species (See Figure 35 and Figure 36). 13 of the 37 study sites were inhabited exclusively by gregarious nesting wasp species, 15 of the 37 study sites were inhabited exclusively by gregarious nesting bee species, and 7 of the 37 study sites were absent of gregarious nesting bee and wasp species (See Figure 35 and Figure 36).

There is a significant negative association between gregarious nesting wasps and gregarious nesting bees in their nesting environments (Chi-squared = 10.803, p = 0.0001). Therefore, gregarious nesting bees and gregarious nesting wasps have preferences for nesting in isolation to one another, rather than communally.

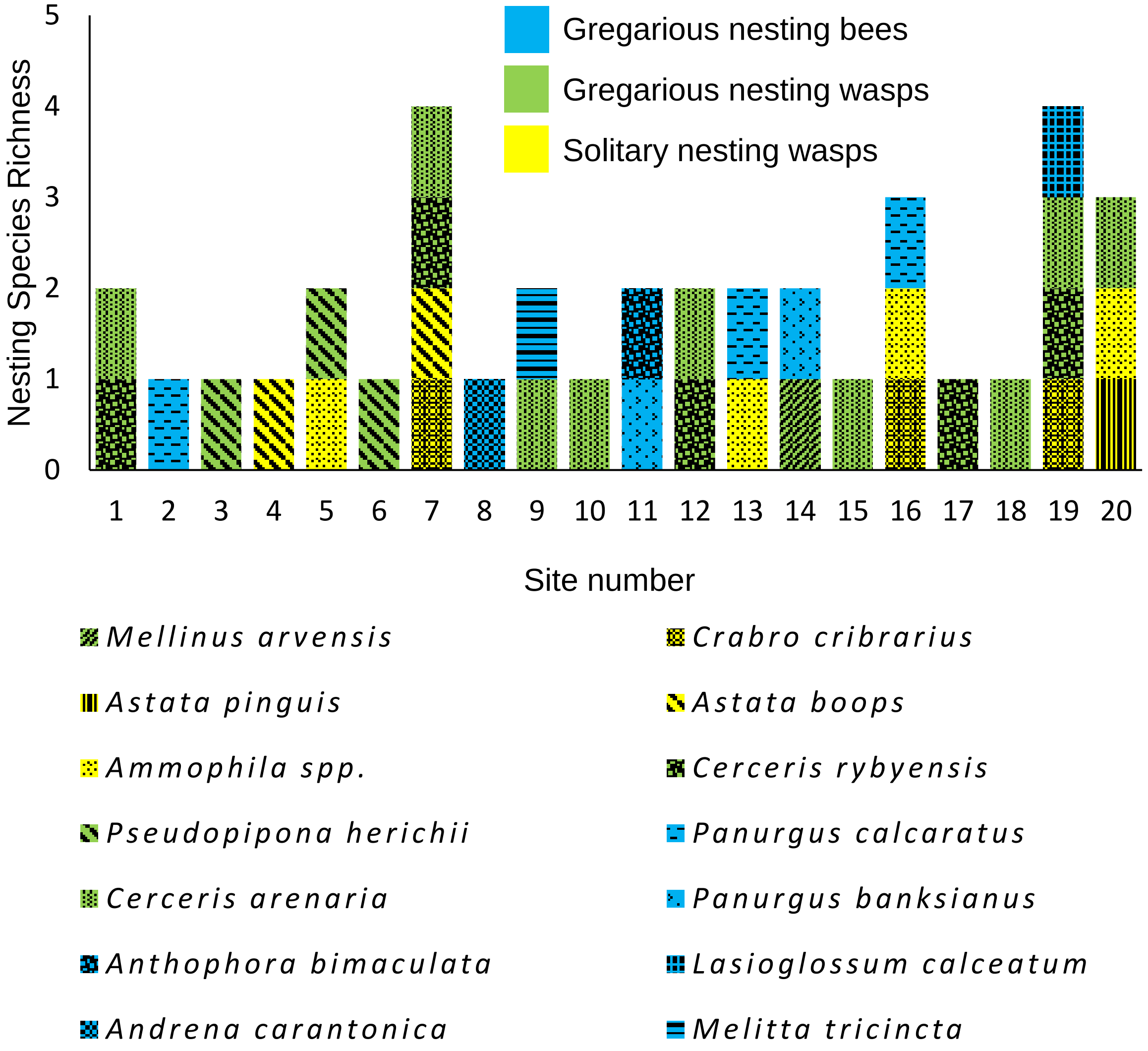


Figure 35: Nesting species richness per site across Hartland moor NNR and Slepe heath NNR.

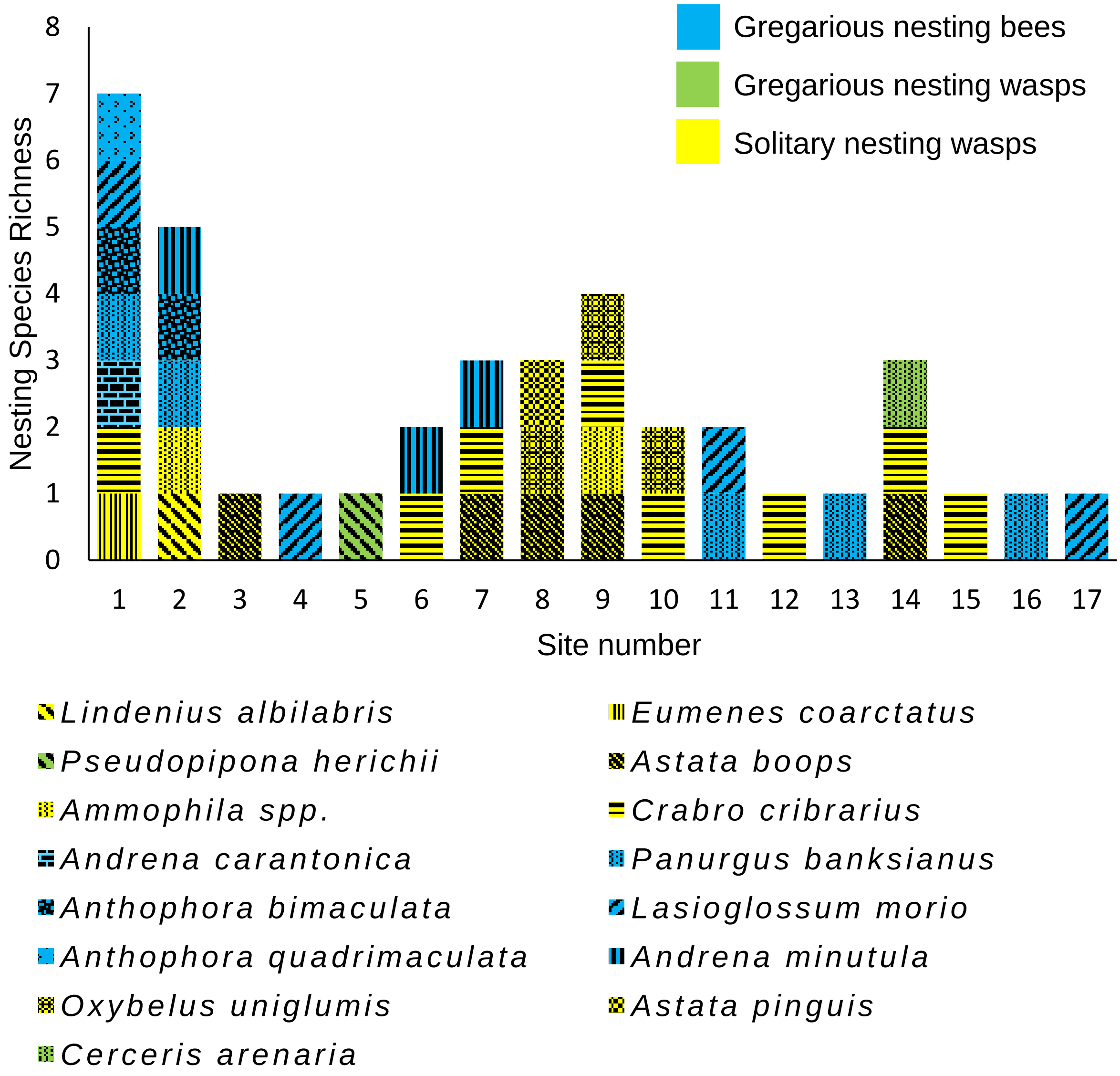


Figure 36: Nesting species richness per site across Godlingston heath NNR.

3.6 Morphological burrow richness as an indicator of nesting species richness:

There is an overall moderate positive correlation between morphological burrow richness and species richness, although this is heavily dependent on the existence of the outlier which reads a morphological burrow richness of 5 and a species richness of 7 (See Figure 37). Nest sites with a morphological burrow richness of 5 had the highest species richness of 7, whereas those nest sites with a morphological burrow richness of 1 had the lowest average species richness ranging from 1 to 3 (See Figure 37). Nest sites with a morphological burrow richness of 2 had the largest variation in relation to species richness, ranging from 1 to 5 species (See Figure 37).

There is a significant relationship between morphological burrow richness and nesting species richness at nest sites (Pearson, r = 0.68, N= 37, p = 0.0001). Therefore, it is highly likely that a high morphological burrow richness indicates a high nesting species richness.

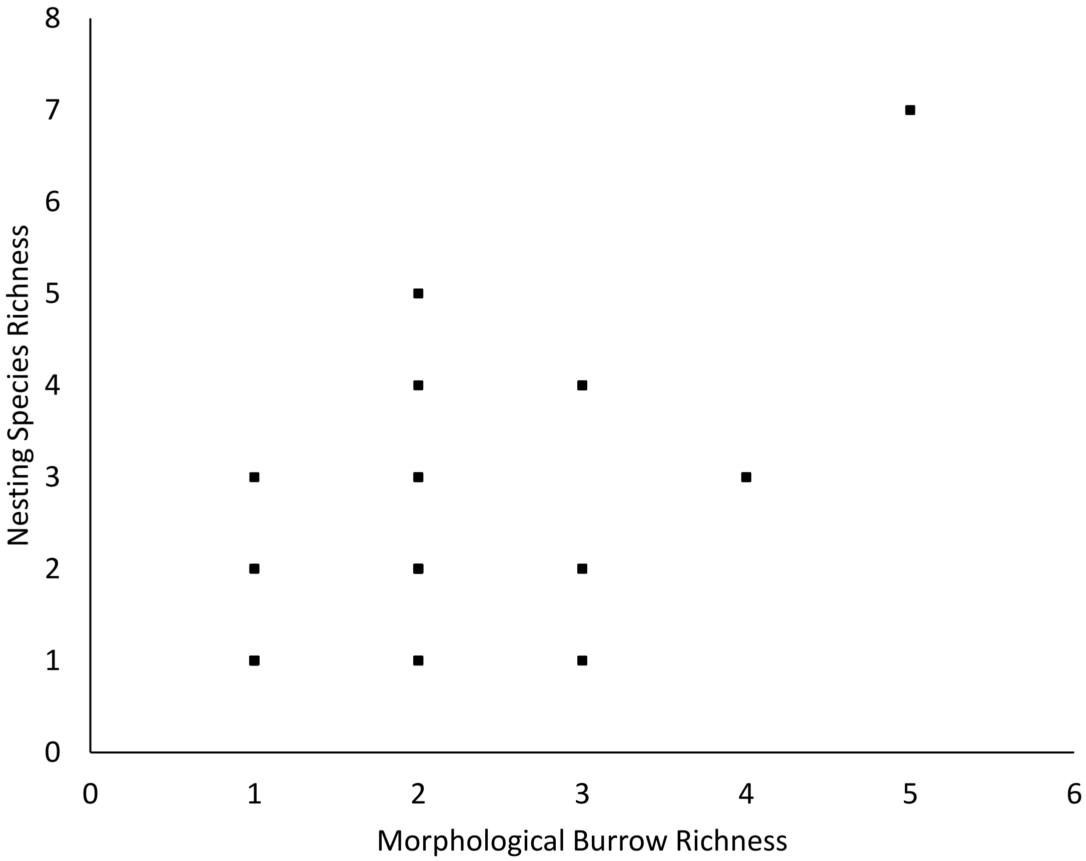


Figure 37: Burrow morphological richness and nesting species richness per active nest site.

4.0 Discussion:

4.1 Distribution of nest sites:

Nest sites exhibited spatial clustering across the study sites. This may have been a result of pure chance, or through bias of site selection along foot paths and vehicle tracks. Nevertheless, spatial clustering of nest sites may be indicative of regionally optimal habitat conditions within the home ranges of the species discovered at those sites (Michener et al, 1958). For example; Westrich (1996) claims that in order for ground nesting bees to reproduce, their habitats must contain suitable nesting sites, particular nest building materials, and a sufficient amount of food plants. The same can be applied to ground nesting wasps, although these are dependent on the availability of prey. Therefore, regions surrounding spatially clustered sites have a good chance of providing the basic requirements needed for reproduction, thus explaining local aggregation of nest activity sites. Spatial clustering of nests may be caused by conspecific attraction, whereby the presence of conspecifics indicates optimal environmental conditions (Stamps, 1988). Spatial clustering might also be explained by breeding philopatry to nest sites as is seen in *Halictus rubicundus* and *Cerceris arenaria* (Yanega, 1990; Polidori et al, 2006).

4.2 Variables effecting nest site suitability and nesting species richness:

Overall, variables such as vegetation structure and aspect did vary across nest activity and non-nest activity sites, thus indicating that vegetation structure and aspect do effect nest site suitability. Soil compaction, inclination, vegetation cover, vegetation structure and substrate type had no significant effect on nesting species richness across sites with and without nest activity. However, when tested exclusively against nest activity sites, exposure area of nesting surface and substrate type did significantly affect nesting species richness. A qualitative analysis of aspect appears to show some effect on nesting species richness also.

Literature investigating the effects of nesting variables upon nesting species richness of ground nesting hymenoptera is extremely lacking. This promoted a significant challenge to comparing results of this study to the known literature. However, the findings of this research are comprehensively explained and recommendations for further research are given.

4.2.1 Vegetation structure:

Vegetation structure was the only variable to significantly differ across nest activity and non-nest activity sites. This suggests that vegetation structure does effect nest site suitability. Nest activity sites and non-nest activity sites were both dominated by the occurrence of pioneer vegetation structure, however, non-nest activity sites had a significantly higher proportion of building and mature vegetation structure. This indicates that ground nesting hymenoptera prefer nest sites with a locally homogeneous pioneer vegetation structure. Similar to these findings, Wuellner (1999) acknowledged that soil surfaces with tall vegetation were avoided as nest sites by the ground nesting bee *Dieunomia triangulifera*. Possible reasons for this are; the growth of deep roots into nest cells thus causing larval mortality, hindered larval development as a result of interrupted soil temperature regimes by shade, and an increased risk of parasitism by natural enemies from perches of tall standing vegetation (Wuellner, 1999).

As a means to locate nest entrances, ground nesting hymenoptera perform circled orientation flights using landmark features to indicate the whereabouts of nest entrances (Zeil, 1992; Wuellner, 1999; Brünnert, Kelber and Zeil, 1994). It can be hypothesised that tall dense stands of vegetation surrounding nest sites may obstruct the visual orientation of these landmarks and nest entrances, potentially leading to abandonment of nests which cannot be easily identified. In this case, reproductive ability is effected and so, tall dense stands of vegetation surrounding soil exposures act as a deterrent to nesting in these locations. Furthermore, nesting activity may be more prevalent at sites with a pioneer vegetation structure as this is associated with floral diversity, covering a greater range of the food plants specific to bee taxa and prey species of wasp taxa (Calvo et al 2007).

Vegetation structure did not have an effect on nesting species richness across nest activity sites. The likeness of species richness data experienced between pioneer and building groups was expected as these structural types are morphologically quite similar. The statistical power of identifying effect between pioneer and building groups was less than might be observed for pioneer and mature vegetation structural groups. This is because pioneer and mature age stage vegetation structures are morphologically different in height and density respectively. Only one sample was recorded over the study period for the mature vegetation group and was therefore excluded from variation testing. Crucially, this meant that opposing structural vegetation types were not compared in their average nesting species richness data. As only two of the three groups could be tested, this explains why average nesting species richness was not significantly different. In all, a much greater quantity of data for mature vegetation structure was needed to improve the statistical power of identifying variation.

4.2.2 Substrate type:

Substrate types across nest sites with and without nest activity did not significantly differ. This implies that sites without nest activity contained substrate types just as suitable for nest excavation as those sites without nest activity. Therefore, other factors at non-nest activity sites were deterring nest excavation.

Substrate type did affect nesting species richness. Those nest sites with multiple substrate types had the highest average nesting species richness whereas sand, clay, fine sand/clay and coarse sand/clay substrates had invariably lower average nesting species richness. As various species of ground nesting hymenoptera have preferences for nesting in different substrate types, this explains why those sites with multiple substrates experienced communal nesting of various species (Potts and vulliamy et al, 2005). Clay substrates were species poor, which is supported by Julier and Roulston (2009) whom found that clay-rich soil were not the preferred nesting medium for *Peponapis pruinosa*. Similarly, Cane (1991) reported that of the various ground nesting bee species in their study, none were recorded as nesting in clay type substrates. However, Roberts (2001) reports the Purbeck mason wasp (*Pseudepipona herichii*) as requiring clay type substrates for nest excavation. This may explain why clay type substrates in this research exhibited low average nesting species richness, whereas sites with multiple substrates had the highest average nesting species richness.

4.2.3 Aspect:

A qualitative analysis of aspect shows that nest activity sites were mostly south facing, whereas non-nest activity sites were varied in orientation. Nest site suitability is likely effected by aspect as ground nesting hymenoptera occurred more frequently at south facing nest sites. Literature produced by Potts and Willmer (1997) also found the ground nesting bee *Halictus rubicundus* preferred nest sites with a southern aspect as these locations presented thermal advantages.

A south facing nest site in the northern hemisphere may be particularly important for ground nesting hymenoptera as this maximises solar insolation, passively warming the underground nest cells and maintaining consistent temperature gradients needed for larval development (Jones and Oldroyd, 2007; Jeanna and Morgan, 1992; Potts and Willmer, 1997). South facing nest sites exhibiting consistent temperature gradients might might require little brood incubation and wing cooling by host species, the likes of which is often seen in cavity nesting Hymenoptera such as *Bombus bifarius nearcticus* (Jones and Oldroyd, 2007; O'Donnell and Foster, 2001). This is supported by the findings produced by Weissel et al, (2006) whom linked nest sites with a warmer soil temperature to increased brood sizes, and also decreased brood development periods. Therefore, south facing nest sites may be chosen as a strategy to maximise reproductive output (Jones and Oldroyd, 2007).

Aspect also appeared to effect species richness. Those sites with a southerly aspect had the highest nesting species richness values, which may be explained by the thermal advantages of south facing slopes to larval development described above. This might suggest that species with overlapping temperature requirements are more likely to co-occur at south facing nest sites.

4.2.4 Exposure area of nesting surface:

Sites with a large exposure area of nesting surface were marginally more suitable than small exposures for supporting high nesting species richness. Larger exposures may be more attractive as nest sites to dispersing species as these are more visible in the landscape. Furthermore, larger nesting surfaces may allow gregarious nesting species to aggregate in large numbers, which might aid the detection and active group defence of nests against natural enemies such as parasites (Rosenheim, 1990; Evans et al, 1990). Another hypothesis is that large nesting surfaces offer a range of edaphic conditions required by multiple species for nesting, which are not reciprocated by small nesting surfaces. For example, Nest sites with a mixture of substrates ranging from loose to compact, and fine grained to coarse grained sediments offer a greater diversity of nesting medium types which may be preferred by multiple species.

4.2.5 Soil compaction:

Soil compaction did not significantly affect nest site suitability or nesting species richness. In support of this study’s findings, Potts and Willmer (1997) determined that soil compaction and inclination were broad ranging for nest site suitability of the ground nesting bee *Halictus rubicundus*, which can nest in soft and hard soils. However, some species are limited in their tolerance of soil compactness. McCorquodale, (1989) states the sphecid wasp *Cerceris antipodes* is challenged by nest construction in hard soils, whereas Srba and Heneberg (2011) found that *Ammophila pubescens* utilises highly compact soils. As data was recorded across nest sites occupied by species with diverse nesting requirements in terms of soil compaction, this may explain overlap of data variation for nest activity and non-nest activity sites, and also for the non-significant relationship to species richness.

4.2.6 Inclination:

Inclination did not significantly affect nest site suitability or nesting species richness. In support of this study’s findings, Potts and Willmer (1997) determined that preferences for the inclination of nesting surfaces were broad ranging for the ground nesting bee *Halictus rubicundus*, which was recorded nesting in surfaces that range from horizontal, to almost vertical. Yeo and Corbet (1995) state that many of the aculeate solitary wasps nest in sunny situations of horizontal or vertical banks of soil. Falk and Lewington (2015) state that various bee species nest in flat ground, slopes, and vertical banks. As various bee and wasp species are tolerant of flat, sloping and even vertical nesting situations, this explains why there was little variation of inclination between nest activity and non-nest activity sites, and also why no significant relationship was identified to nesting species richness.

4.2.7 Vegetation Cover:

Vegetation cover did not significantly affect nest site suitability or nesting species richness. Therefore, levels of vegetation cover at sites without nest activity were as suitable for nest excavation as they were for sites with nest activity. This implies that other factors were deterring nest excavation at sites without nest activity.

Nest sites may have been occupied by species that were both tolerant and intolerant of vegetation in their nesting environment. Evidence to support this is provided by Yanega (1990) whom observed a colony of the bee *Halictus rubicundus* nesting in surfaces with up to 60-80% vegetation cover, whereas, Steffen-Dewenter and Tscharntke (2000) found a negative correlation between the number nest entrances of numerous ground nesting bees to vegetation cover. The variance of vegetation cover between nest activity and non-nest activity sites, and the non-significant relationship to nesting species richness might be explained by the presence of vegetation tolerant species at nest sites with a high vegetation cover.

4.3 Social typing:

A negative association between gregarious and solitary nesting species indicates preferences for these social types to nest separately, rather than communally. These findings are unique in so much as no literature could be found investigating this phenomenon. However, there are plausible reasons why solitary and gregarious types might nest separately.

Theories for the evolution of aggregated nesting behaviours are comprehensive. Aggregated nesting may result in thorough nest defence and parasite detection, predator dilution effect, increased mate availability, enhanced foraging efficiency, and lessened energy expense of nest construction via the habitation of pre-existing ones (Michener et al, 1958; Rosenheim, 1990; Evans et al, 1990; Coster-Longman et al, 2002; Hamilton, 1971). These factors may act as ques for attraction between gregarious nesting species (Stamps, 1988).

When individuals of the same species nest in close proximity, they experience competition for resources (West-Eberhard, 1978). Here it is inferred that solitary nesting species may have evolved spatially isolated nesting behaviours in response to diminished abundance of a shared food resource when nesting amongst gregarious species. Effectively, solitary nesting species are outcompeted in their foraging ability by gregarious nesting species. Also, as nest building is time and energy intensive, the risks associated with nest usurpation, and raiding by gregarious nesters may have led to the derived behaviour of isolated nesting.

Gregarious nesting bees and gregarious nesting wasps were also found to have a strong negative association across nest sites. This also implies that gregarious nesting bees and gregarious nesting wasps have preferences for isolated nesting.

Potentially, spatial competition and antagonistic interactions for nest space may exist at sites where gregarious wasp and gregarious bee species co-occur. Although this has not been reported between wasps and bees, Ghazoul (2001) demonstrates that aggressive behaviours take place between conspecifics of the wasp *Mellinus arvensis*, which is explained may be as a result of nest usurpation, raiding of nest provisions, or nest ownership confusion (Tepadino and Torchio, 1994). This is merely speculation for the reasons why gregarious bees and wasps were found to nest separately, and further research is needed to strengthen these findings.

4.4 Morphological burrow types:

The reliability of using morphological burrow richness as a tool to indicate the nesting species richness has been proven by the significant and moderately strong relationship observed between the two variables. Although replicate studies should be undertaken to fully assess the reliability of this tool, the findings are nonetheless informative for conservation managers. For example; those sites with a high morphological burrow richness have been shown to indicate high nesting species richness. Those sites with a high nesting species richness must therefore cover the habitat requirements of those species and are consequently of priority conservation status for monitoring and management.

4.5 Recommendations:

In the discussed literature, factors affecting nest site suitability for the ground nesting hymenoptera are countless and appear to be interspecific with their effect. For this reason, it is recommended that this study be replicated on a species specific basis to better the understanding of the detailed habitat preferences for species of interest.

Also, the findings of this research raise the question; are the separate nesting preferences of gregarious and solitary nesting species explained by varying nesting requirements? This question might be answered by investigating variations in substrate type, inclination, and soil temperature across sites with solitary nesting species and sites with gregarious nesting species. Further research might strengthen the case for conservation based management of social types rather than individual species.

Soil temperature is repeatedly mentioned in the literature as a limiting factor to nest site suitability. Therefore, it is strongly recommended that soil temperature is incorporated into replications of this study. Potts and Willmer (1997) found soil temperature of nest sites of the bee *Halictus rubicundus* to be a good indicator of the temperature of the nest cells deeper within the sediment, and Weissel et al (2006) linked soil temperature to the speed of physiological development in larvae of the halictid bee *Lasioglossum malachurum*. In this instance, temperature variability of nesting surfaces is a key limiting factor of nest site suitability as it affects reproductive output and fitness of developing larvae.

5.0 Conclusion:

Overall, spatial clustering of nest sites can be attributed to factors ranging from conspecific attraction, to breeding philopatry and possibly even chance. South facing nest sites with a large nesting surfaces, multiple substrate types and a locally pioneer vegetation structure are deemed to be the most suitable nest sites chosen by diverse groups of ground nesting hymenopteran bee and wasp species. This research discovered evidence to suggest that semi-social gregarious nesting species and solitary nesting species have preferences for nesting in isolation from one another, as do gregarious nesting wasps and gregarious nesting bees. Finally, data suggests morphological burrow richness to be a competent indicator of nesting species richness and thus nest site suitability.

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