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Original Paper

The distribution and trophic ecology of an introduced, insular population of Red-Necked Wallabies, *Notamacropus rufogriseus*

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Abstract

Introduced non-native mammals can have negative impacts on native biota and it is important that their ecologies are quantified so that potential impacts can be understood. Red-necked wallabies (*Notamacropus rufogriseus* (Dawson and Flannery, 1985)) became established on the Isle of Man (IOM), an island with UNESCO Biosphere status, following their escape from zoological collections in the mid-1900s. We estimated wallaby circadial activity and population densities using camera trap surveys and Random Encounter Models. Their range in the IOM was derived from public sightings sourced via social media. Wallaby diet and niche breadth were quantified via microscopic examination of faecal material, and compared to those of the European hare (*Lepus europaeus* (Pallas, 1778)). The mean population density was 26.4 ± 6.9 wallabies/km^2, the population size was 1,742 ± 455 individuals, and the species' range was 282 km^2, comprising 49% of the island. Wallaby diets were dominated by grasses, sedges, and rushes; niche breadth of wallabies and hares (0.55 and 0.59 respectively) and overlap (0.60), suggest some potential for interspecific competition and/or synergistic impacts on rare or vulnerable plant species. The IOM wallaby population is under-studied and additional research is required to further describe population parameters, potential impacts on species of conservation interest, and direct and indirect economic costs and benefits.

Keywords: Non-native species, population density, diet, activity, macropod, red-necked wallaby, *Notamacropus rufogriseus,* European hare*, Lepus europaeus*

Introduction

Introduced non-native species can have significant negative effects on naïve native biota (Parker et al. 1999; Sakai et al. 2001; Rejmánek et al. 2002). Biological invasions (the incursion of an alien species which threatens native biological diversity; Invasive Species Specialist Group [ISSG] 2015) are a major driver of global loss of biodiversity (Sala et al. 2000). The impact of invasions is commonly, and disproportionately evident on islands, particularly those where ecological competitors (Lister 1979) and/or predators (Moors and Atkinson 1984; Diamond 1989) are absent, and/or there is a natural lack of species and functional diversity (Lodge 1993; Tilman 2001). Although mammals are amongst the most successful animal invaders, with rats (*Rattus* spp. (Fischer, 1803)), European rabbits (*Oryctolagus cuniculus* L., 1758), grey squirrels (*Sciurus carolinensis* (Gmelin, 1788)) and American mink (*Neovison vison* (Schreber, 1777)) being the most notorious (Veitch and Clout 2002), the impact of others is more equivocal. For example, high densities of muntjac deer (*Muntiacus reevesi* (Ogilby, 1839)) inhibit coppice regrowth, and, hence, have a negative economic impact, but have positive environmental benefits such as enhanced growth of ground flora species avoided by the deer, and increased invertebrate abundance (Cooke and Farrell 2001). The interactions between non-native species and the ecosystems to which they are introduced, thus, are often unpredictable. Researching all introduced species, their ecology and impacts, therefore, is important so as to elucidate their potential effects on native species, communities and ecosystems.

The red-necked wallaby (*Notamacropus rufogriseus* (Dawson and Flannery, 1985)) is a medium-sized marsupial native to south-east Australia including Tasmania. Broadly light brown or grey in colour, it has a characteristic patch of copper red fur on the nape and rump (Eldridge and Coulson 2015), but otherwise lacks distinctive markings. Males are considerably larger than females (Eldridge and Coulson 2015; Garnick, et al. 2016). Individuals are generally solitary, but may come together to form unstable, yet socially organised groups (Johnson 1989). In their native range, red-necked wallabies typically inhabit coastal scrub, heathlands, and sclerophyllous forest (Le Mar 2003; Jarman and Calaby 2008; Garnick et al. 2016). They prefer a heterogeneous landscape wherein they use long grass, shrubs and woodland for rest and refuge, before moving into the open to feed (Johnson 1989; Le Mar and McArthur 2005; Garnick et al. 2016). Most of the species' diet in their natural range is comprised of grass, with the remainder consisting of woody vegetation (Jarman and Phillips 1989; Sprent and McArthur 2002).

Red-necked wallabies have been introduced to several countries worldwide, including Scotland, England, France, Germany, and New Zealand (Gilmore 1977; Harris et al. 1995; Weir et al. 1995; Le Page et al. 2000). The species was brought to the Isle of Man (IOM), an island of 572 km^2 lying midway between Britain and Ireland (Fig. 1), as an addition to zoological collections from which they subsequently escaped. The oldest known record of red-necked wallabies on the island is from a pleasure park in 1957 (Isle of Man Examiner 1957). In 1965, Curraghs Wildlife Park purchased several individuals from Whipsnade Zoo (Isle of Man Weekly Times 1965), one of which escaped and evaded capture for a year (Isle of Man Weekly Times 1966). In July 1989, eight wallabies dug under a fence at the Wildlife Park, seven of which were eventually recaptured (Isle of Man Examiner 1989; Manx Independent 1989*a*; Manx Independent 1989*b*). The continued presence of the species in the wild was confirmed in 1994 (Isle of Man Examiner 1994) and the population was first studied in 2008 (Harby 2008). Other wild wallaby populations in the UK are ephemeral and restricted in distribution being affected adversely by limiting factors, including harsh winters, road traffic collisions and predation e.g. by foxes (*Vulpes vulpes* L., 1758) and dogs (*Canis lupus familiaris* L., 1758; Yalden 1999). However, the IOM is an island with limited space for population expansion, there are few if any foxes on the island (Reynolds and Short 2003), and the climate is maritime with mild winters (Kennington and Hisscott 2013). Factors affecting the expansion and impact of the red-necked wallaby population on the IOM may be less limiting than elsewhere in the British Isles.

We describe the ecology of wallabies on the IOM, establishing population status, distribution, potential ecosystem services, circadial activity, diet and trophic overlap with the European or brown hare (*Lepus europaeus* (Pallas, 1778)). We used analyses of faecal material to identify plants consumed and, hence, quantify wallaby diet and comparative niche breadth and overlap with that of sympatric European hares. Population surveys were conducted via remote-sensing camera traps at three sites to estimate population densities and island-wide distribution was based on records collected via a social-media-driven public appeal.

Methods

Three focal study areas were identified in the Ballaugh region of the IOM (Fig. 1), based on ease of access, regularity of wallaby sightings, landowner consent, and the location of the only previous wallaby population and impact survey (Harby 2008): (1) Ballaugh Curragh (referred to hereafter as Curragh; Ordinance Survey coordinates (OS): SC 362 951), is a 193 ha RAMSAR and ASSI site and was the focus of Harby (2008). This site has high levels of biological diversity in general and rare species of plants and birds in particular (Isle of Man Government 1990). The site is comprised of a characteristic mixture of bog and scrub, with many indicator species such as purple moor grass and bog myrtle (DEFA 2006). (2) Close Sartfield (OS SC 358 955), a 12 ha Manx Wildlife Trust-owned reserve, incorporating open field, marsh grassland and bog (Manx Wildlife Trust 2016*a*) and managed to maintain species rich hay meadows, orchids and wildflowers. (3) Goshen (OS SC 369 939), also owned by the Manx Wildlife Trust, covers 15 ha and is compositionally similar to Close Sartfield (Manx Wildlife Trust 2016*b*). All three sites are devoid of livestock or other large mammals.

Camera trap surveys

Remote-sensing camera traps are increasingly popular due to their improved efficacy through continued technological improvements and declining costs (Tobler et al. 2008). They provide a non-contact, low-impact means of quantifying the life history traits (Silveira and Jacomo 2003; Wegge, Pokheral and Jnwali 2004) and estimating population parameters (Rowcliffe et al. 2008; Jenelle and Runge 2002) for a wide range of species. Camera traps provide a range of data in wildlife surveys beyond establishing presence, including monitoring of focal populations and elucidating circadian activity without results biased by observer influence on animal behaviour (Cutler and Swann 1999; Silvera et al. 2003; Tobler et al. 2008). Population models based on camera trap data commonly employ capture-recapture methodologies (e.g. Karanth 1995; Karanth et al. 2003; Maffei et al. 2005). This approach, however, is only suitable for species which exhibit individual variation in pelage patterning or colouration. The Random Encounter Model (REM) is based on the principle of Brownian motion wherein animals are assumed to move randomly in the landscape, allowing the estimation of population densities for species which are not individually patterned (Rowcliffe et al. 2008). REMs have been successfully applied to several species including lowland tapir (*Tapirus terrestris* L., 1758; Oliveira-Santos et al. 2010), pine marten (*Martes martes* L., 1758; Manzo et al. 2011), hares (*Lepus* sp. L., 1758; Caravaggi et al. 2016) and red-necked wallabies (Rowcliffe et al. 2008). The model is described by the equation:

$$D = \frac{y}{t}\frac{\pi}{(vr(2+\theta))}$$

Equation 1

Where y = number of detections, t = survey effort in hours, v = speed of movement (distance travelled in 24 h), r = radial distance to the animal (in metres), and θ = zone of detection (i.e. the camera's effective field of view). Parameters relating to camera traps (r and θ) were defined via manual activation of cameras (Rowcliffe et al. 2008). Daily distance travelled (v) was extracted from Rowcliffe et al. (2008) as there are no movement data available for IOM wallabies. Here, r = 4m, θ = 35º (0.621 radians), and v = 710 m.

Twenty Bushnell Trophy Cam HD cameras (Model no: 119677) were deployed for 7 days at each of the three sites, non-concurrently, between June and August 2015. The Curragh is large and bisected by a central public pathway, thus was split into two sub-sites. Within each site, cameras were placed randomly, as required by the assumptions of the REM (Rowcliffe et al. 2008). Cameras were set approximately 75 cm from the ground, with no downward tilt, and were not baited. Cameras were set to capture video clips of 20 seconds, with a 2 minute delay between each trigger event mitigating against re-detection of the same individual. Successive triggers were interpreted as describing separate capture events unless there was compelling evidence to the contrary, e.g. an animal remaining in view for several successive triggers, in which case re-detections were removed to avoid false inflation of population estimates. Camera locations were recorded using a Garmin Oregon 600 handheld GPS unit. Population density estimates were calculated using REMs. Density estimates were calculated using the remBOOT package (Caravaggi 2017) in R (R Core Team 2016). Wallaby abundance was calculated as a function of the estimated population density relative to survey area.

Occurrence, range and population estimates

Conventional (i.e. local radio, community magazines and news websites) and social media (Facebook) were used to encourage the Manx public to submit wallaby sightings, thus facilitating an island-wide survey and elucidating the extent of their current range. The range of the red-necked wallaby in the IOM was described using a 100% Minimum Convex Polygon (MCP) and mapped using QGIS. Radial range expansion was taken as the distance between the point of introduction and the outermost record, divided by the time elapsed since introduction: i) assuming a delay of 2 years pre-expansion based on natal philopatry of (primarily male) offspring (Johnson 1986, 23 years since introduction); ii) assuming a 10-year pre-expansion lag phase, as observed in a number of non-native mammals (e.g. Jeschke and Strayer 2005; Clout and Russell 2007; 15 years since introduction).

Landclass polygons which coincided with wallaby occurrences, from both camera trap data and public sightings, were extracted from the 2012 Corine land cover dataset (Cole et al. 2012). Population estimates were calculated by multiplying the total area of resting habitat (i.e. forests, scrub) by the mean (± Standard Error [SE]) density derived from camera trap estimates. Spatial analyses were conducted using ArcGIS.

Faecal analyses

The identification and comparison of plant cuticle cells and stomata in dried faecal material via microscopic examination provides a simple inexpensive means of identifying food items and quantifying their contribution to the species diet (Holechek et al. 1982; Alipayo et al. 1992). Faecal material was collected from discrete piles of pellets found at each of the three study sites between June – September, 2015. Ten piles of wallaby pellets were sampled from each site, giving a total of 30 wallaby faecal samples. Hares were absent from Curragh and were infrequent on the other two sites; hence, 5 hare faecal samples were collected from each of Close Sartfield and Goshen (i.e. a total of 10 hare faecal samples). Pellets were identified to species based on overall size, shape, and colour. When there were conflicting results within or between criteria, identification was based on a match to at least two of the three characteristics. Samples were air dried outdoors in paper bags between June-September 2015. Dried samples were milled to a uniform size, around 2 mm fragments. 100 ml of 0.05 M Sodium hydroxide (NaOH) was added to the samples and left to settle for an hour; 300 ml distilled water was added, left to settle and the supernatant was removed. Glycerol was added to the sample prior to mounting on a microscope slide. A total of 120 wallaby and 40 hare faecal slides (i.e. 4 from each sample) were produced. A reference plant collection was gathered from each site using a complete plant species list (SI 1, Table S1). Sections of the upper epidermis, lower epidermis and stem of each species were created by scraping away layers with a scalpel. A reference slide was made for each plant species (120 in total). Images of each sample at x400 magnification were entered into a database. Plant species in faecal samples were identified by comparing the shape, colour and size of the cell and stomata at x400 magnification with the reference slide collection, along with images from previous studies (Dinkergus 1997; Hamilton 2006; George 2007). An eyepiece graticule with a 10x10µm grid was used to generate 10 random co-ordinates for each slide, giving 40 records per faecal sample (i.e. a total of 1,200 records from wallaby faecal material, and 400 records from hare samples). Random co-ordinates were generated using a random number generator. Occurrence of each plant species in wallaby and hare faeces was recorded as a percentage of all records at each site. Unidentified samples (two for all sites) were photographed and entered into the reference collection. Levins' measure of niche breadth (MacArthur and Levins 1967) and Pianka's measure of niche overlap (Pianka 1974) were calculated for both wallaby and hare at each site. Metrics were calculated using R (R Core Team 2016).

Results

A total of 741 individual detections of wallabies (4 Parma wallabies, *N. parma* (Waterhouse, 1846), and 737 red-necked wallabies) were recorded across 16,128 camera trap hours (Table 1). Parma wallabies are distinguished from red-necked wallabies by their smaller stature (52cm tall, compared to 150 cm in red-necked wallabies) and individuals typically have a white patch on their chest, cheek and upper mouth (Menkhorst and Knight 2001). Parma wallabies were detected only at the Curragh and likely also originated from the Curraghs Wildlife Park, as they shared an enclosure with the red-necked wallabies. All data, hereafter, refer only to red-necked wallabies.

The distance between the point of introduction (54°19'21.5"N, 4°30'49.6"W) and the most distant sighting was 22.87 km. If we assume that the population was established in 1989, and that the outermost record represents the furthest point of the expansion wave-front, the radial expansion rate was 0.99 $km.yr^{-1}$ given a 2 year pre-expansion delay, or 1.52 $km.yr^{-1}$ given a 10 year pre-expansion delay. The current range, based on records from the public in addition to camera trap and faecal surveys, covers approximately half of the island (49%), an area of approximately 282 km^2 (Fig. 2), with wallaby records being much scarcer on higher ground, in the east and south.

REM estimates suggested that the Curragh had a population density equivalent to 40.1 red-necked wallabies/km^2, equating to 78 individuals, Close Sartfield 18.6 wallabies/km^2 (2 individuals), and Goshen 20.5 wallabies/km^2 (3 individuals; Table 1). Intersections between wallaby occurrences and Corine landclasses showed that wallabies were associated with arable land, pastures, heterogeneous agricultural areas, forests, and scrub; habitats which cover 423 km^2 (74%) of the IOM. Habitats which provide shelter during daylight hours (i.e. forests and scrub) covered 66 km^2, 12% of the IOM. The estimated wallaby population was 1,742 ± 455. A plot of circadian activity showed that wallabies were largely crepuscular (active at dawn and dusk), with a strong bimodal signature. Diurnal detections occurred at substantially lower frequencies (Fig. 3).

Grasses comprised over half (57%; Fig. 4) of all plant material in wallaby faecal pellets, with some variation in the contents of faeces between sites (Table 2). The most common remains were Yorkshire fog (*Holcus lanatus* L.), timothy-grass (*Phleum pratense* L.), perennial ryegrass (*Lolium perenne* L.), smooth meadowgrass (*Poa pratensis* L.) and purple moor–grass (*Molinia caerulea* L.).

Sedges, including common sedge (*Carex nigra* L.) and oval sedge (*Carex ovalis* G.) comprised an average of 19.7% of the faecal material, and rushes such as soft rush (*Juncus effuses* L.) comprised an average of 10.6%. Forbs accounted for an average of 6.7% of all plant material in wallaby faeces, and included dog-violet (*Viola riviniana* Rchb.), tormentil (*Potentilla erecta* L. Raeusch.), common daisy (*Bellis perennis* L.) and, most commonly, common ivy (*Hedera helix* L.).The remainder of the faecal material was composed of tree leaves from species such as willow (*Salix* sp. L.), birch (*Betula* sp. L.), and holly (*Ilex aquifolium* L.) and other, unidentified species (Table 2).

Similarly, an average of 70% of European hare faeces were comprised of grasses (Fig. 4, Table 3). However, an average of 21% of the hare's faeces were flowering plants, with common daisy the most frequently recorded species. The remainder of the hare material was comprised of rushes, sorrel and sedges (*Cyperaceae* sp.). Wallaby niche breadth (0.59, Curragh; 0.60, Close Sartfield; 0.47 Goshen; $\bar{x}$ = 0.55) was similar to that of European hares (0.60, Close Sartfield; 0.58, Goshen; $\bar{x}$ = 0.59). Average niche overlap between hares and wallabies across all sites was 0.60 (0.61, Close Sartfield; 0.59, Goshen).

Discussion

Population density estimates derived from remote-sensing camera trap data using REMs varied considerably between sites. Although the abundance estimate for the Curragh population (78 individuals) was smaller than the 107 individuals reported by Harby (2008), this difference could be attributed to natural fluctuations in the population (McNab, 1980), and different methodological and observer biases (e.g. Harby 2008) used a line transect survey method for population estimation). While Close Sartfield and Goshen are small survey sites and wallabies are likely to be transient, the use of high density camera trap arrays (20 cameras in areas of 0.13 km^2 and 0.16 km^2 respectively) and the demonstrated capacity of REMs to produce accurate estimates (e.g. Rowcliffe et al. 2008; Oliveira-Santos et al. 2010; Manzo et al. 2011; Caravaggi et al. 2016) mean that we can be reasonably confident of their accuracy. The limited temporal span of the current survey, however, means that our estimates represent temporal snapshots; it is highly likely that wallaby abundance on the IOM is subject to considerable spatial and temporal variation.

Likewise, our population abundance estimates are likely to be subject to spatial variation in population density on the local and landscape scale. Over-extrapolation based on limited data can lead to false inferences regarding the likely size of a given population (Reynolds and Short 2003) and, hence, our abundance estimates should be cautiously interpreted as rough approximations based on incomplete data. Due to the lack of historical data regarding the distribution of red-necked wallabies on the IOM, it is not clear whether their range has increased in recent years or is temporally stable The range described here is likely to be an underestimate of their true distribution on the island, as it is based on opportunistic sightings over a short period of time. It is clear, however, that the wallaby population occupies at least half of the island, and its range extends well beyond the known point of origin. Similarly, expansion rates are likely to underestimate the rapidity of the colonisation process. Additional spatially-specific surveys should be undertaken to elucidate the true range of the species, and provide a more accurate picture of island-wide densities and abundance. Further population growth may be constrained by the carrying capacity of the environment(s) and the presence of potential ecological competitors.

There are three species of herbivore present on the Isle of Man which may act as potential ecological competitors for red-necked wallabies: European or brown hare; European rabbit; and the mountain hare (*L. timidus scoticus* (Hilzheimer, 1906)). Mountain hares are restricted to higher areas in the northern third of the island, in contrast to the European hare which is widespread on lower ground (Fargher 1977; Arnold 1993). European hares have been implicated in the displacement of native mountain hares (*L. t. timidus* L., 1758) in Sweden (Thulin 2003) and Northern Ireland (Irish hare, *L. t. hibernicus* (Bell, 1837); Caravaggi et al. 2016), and mara (*Dolichotis patagonum* (Zimmermann, 1780)) in Argentina (Puig et al. 2006). There are no data available, however, on inter-specific population dynamics (e.g. spatial displacement) between hares and wallabies. The degree of niche overlap observed between European hares and wallabies suggests that if resources become scarce, interspecific competition could occur. However, the diversity of the plant species found to be consumed by wallabies in the present study and that of Harby (2008) suggests that red-necked wallabies are adaptable and could potentially exploit a wider range of forage than hares. It is possible, therefore, that the forage activities of these two ecologically similar herbivores could have synergistic impacts on IOM flora.

There were some differences in terms of plant material recorded in wallaby faecal material, between the present study and that of Harby (2008) who estimated, for example, that rushes comprise 3.2% of wallaby diets, in comparison to 11.3% in the present study. This may be due to differences of scale and methodology, as well as variation between years. In contrast to feral wallabies in the Peak District, England, wallabies in IOM did not consume heather, bracken or pine (Weir et al. 2015; Yalden 1971), despite many of the plant species in the Peak District (Yalden 1971) being widespread on the IOM. Grasses have been observed to comprise up to 91% of the diet of wild wallabies (Sprent and McArthur 2002). The altitude, more clement conditions, and consequent longer growing season on the IOM may provide a greater abundance of more digestible food (high in protein, carbohydrates, and sugars), allowing red-necked wallabies to be more selective.

Most of the plant species eaten by the wallabies on IOM are common. However, the floating club-rush (*Isolepis fluitans* L. R. Br.) is a protected species (Isle of Man Government 1990; Charter 2011), and was identified in Curragh and Close Sartfield wallaby samples. While prevalence was low (1.5 – 2%), the current distribution and abundance of this species on the island is unknown. No orchids were identified in wallaby faeces during either the present study, or previously (Harby 2008), suggesting that the impact of wallabies may be negligible. However, rare species are inherently unlikely to be detected in faecal samples as their scarcity precludes frequent consumption. Further investigation is required to truly ascertain the presence or absence of orchids from wallaby diets. In contrast, orchid fragments were found in two hare samples. Hares are known to consume orchids (Reichlin et al. 2006), which grow in abundance in several locations on the island. It is reasonable to assume, therefore, that hares may present a greater threat to Manx orchid populations than do wallabies.

Wallabies have been implicated in the decline of Hen harriers (*Circus cyaneus* L., 1766) and corncrakes (*Crex crex* L., 1758) in the IOM (Department of Environment, Food and Agriculture [DEFA] personal communication 2016.; Hayhow et al. 2013; Wotton et al. 2015). Indeed, the IOM hen harrier population has declined by 49% between 2004 and 2010 (Hayhow et al. 2013). There is growing public concern regarding hen harriers in particular, as wallabies may disturb their nests (Hayhow et al. 2013). A nesting pair were present at the Curragh study site in 2013 (Manx BirdLife personal communication 2016). It is possible that, due to their grazing habits and use of open areas for feeding, wallabies disturb ground-nesting birds, including hen harriers and corncrakes, during the breeding season, thus impacting the number of young successfully reared to fledging. However, hen harrier populations are also in decline elsewhere in the UK and Ireland due to illegal persecution and habitat destruction (Innes et al. 2007; Hayhow et al. 2013), and Manx populations are likely to be affected by habitat loss or food depletion (Sim et al. 2001; Hayhow et al. 2013; Manx BirdLife personal communication 2016). The population of corncrakes across Britain is generally very low but increasing locally, whilst population estimates for the IOM are regarded as unreliable (Wotton et al. 2015). The interaction between wallabies and vulnerable ground-nesting birds on the IOM should be considered as a priority research area.

Red-necked wallabies are widespread and abundant on the IOM and, hence, should be considered an established, non-native species. Wallabies may be effective natural exponents of scrub control; the Manx Wildlife Trust, for example, report that they no longer graze some reserves with sheep or cattle due to the presence of wallabies (Manx Wildlife Trust 2016*b*). Furthermore, wallabies are charismatic animals which may be popular with tourists. Thus, they may confer economic benefits to IOM residents and organisations. The IOM wallaby population remains under-studied and should be monitored at regular intervals, whilst further research required to establish their range and population size, impacts on the wider ecosystem, and their direct and indirect economic costs and benefits.

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Figure 1. Map of the Isle of Man showing the study area (subsequently sub-sampled) for camera trap and faecal surveys of red-necked wallabies (*Notamacropus rufogriseus*).

Figure 2. Red-necked wallaby (*Notamacropus rufogriseus*) range (100% MCP) on the Isle of Man during 2014, with points indicating sightings reported by the public. The likely point of introduction (i.e. escapees from the Curraghs Wildlife Park) is indicated (X).

Figure 3. Circadian activity of red-necked wallabies (*Notamacropus rufogriseus*) on the Isle of Man. Sun icons represent dawn and dusk, and shaded regions represent night time.

Figure 4. Frequency of vegetation types identified from faecal material of red-necked wallaby (*Notamacropus rufogriseus*) **(a, b, d)** and European hare (*Lepus europaeus*) **(c, e)** at three sites in the Isle of Man: **(a)** Curragh; **(b, c)** Close Sartfield; **(d, e)** Goshen. See Tables 2 and 3 for a comprehensive list of plant species identified, along with their relative abundances.

Table 1. Survey effort data and red-necked wallaby (*Notamacropus rufogriseus*) population estimates derived from camera trap surveys in the Isle of Man in 2014.

Site	Camera hours	Number of captures	Density (wallabies/km^2)	Area (km^2)
Curragh	5,040	479	40.1	1.93
Close Sartfield	3,360	147	18.6	0.12
Goshen	3,192	115	20.5	0.15

Table 2. Frequency of epidermal fragments of plant species identified in the faecal material of red-necked wallabies (*Notamacropus rufogriseus*) at each of three sites on the Isle of Man, expressed as a percentage of the total number of samples of each species, in ascending order and according to mean abundance across all sites.

Plant species		Site			
Common name	Latin name	Curragh	Close Sartfield	Goshen	$\bar{x}$
False oat grass	*Arrhenatherum elatius* L. P.	6.25	8.50	9.50	8.08
Soft rush	*Juncus effuses* L.	4.50	9.25	8.50	7.42
Common sedge	*Carex nigra* L.	5.50	6.50	9.00	7.00
Smooth meadow grass	*Poa pratensis* L.	5.50	7.00	8.00	6.83
Yorkshire fog	*Holcus lanatus* L.	4.00	7.50	7.00	6.17
Sweet vernal grass	*Anthorranthum odoratum* L.	3.50	7.25	7.5	6.08
Oval sedge	*Carex ovalis* Gooden.	5.25	5.75	7.00	6.00
Annual meadow grass	*Poa annua* L.	5.25	5.25	5.00	5.17
Timothy grass	*Phleum pratensis* L.	4.00	4.00	6.25	4.75
Purple moor grass	*Molinia caerulea* L.	6.00	4.00	3.75	4.58
Perennial rye grass	*Lolium perenne* L.	4.00	4.00	4.50	4.17
Atlantic ivy	*Hedera helix spp.* L.	4.50	4.25	2.50	3.75
Tufted hair grass	*Deschampsia cespitosa* L. P. Beauv.	2.50	2.25	3.50	2.75
Yellow sedge	*Carex flava* L.	4.00	2.75	1.50	2.75
Bottle sedge	*Carex rostrata Stokes.*	2.50	2.25	3.00	2.58
Red fescue	*Festuca rubra* L.	1.50	2.00	3.25	2.25
Cock's foot	*Dactylis glomerata* L.	1.50	3.50	1.00	2.00
Rough meadow grass	*Poa trivialis* L.	1.50	2.50	1.00	1.67
Sharp flowered rush	*Juncus acutiflorus* Enrh. Ex Hoffm.	1.75	1.25	1.75	1.58
Sheep's sorrel	*Rumex acetosella* L.	2.75	0.75	0.75	1.42
Willow	*Salix spp.* L.	0.75	1.75	1.00	1.17
Floating club rush	*Isolepis fluitans* L. R. Br.	1.50	1.75	0.00	1.08
Star sedge	*Carex echinata* Murray.	2.75	0.25	0.25	1.08
Common sorrel	*Rumex acetosa* L.	1.75	0.75	0.50	1.00
Creeping bent	*Agrostis stolonifera* L.	1.75	1.00	0.25	1.00
Compact rush	*Juncus conglomeratus* L.	1.50	0.75	0.25	0.83
Crested dog's tail	*Cynosurus cristatus* L.	2.50	0.00	0.00	0.83
Daisy	*Bellis perennis* L.	1.00	1.25	0.25	0.83
Tufted forget-me-not	*Myosotis laxa* Lehm.	1.50	0.00	0.25	0.58
Holly	*Ilex aquifolium* L.	0.75	0.00	0.75	0.50
Toad rush	*Juncus bufonius* L.	1.00	0.00	0.25	0.50
Tormentil	*Potentilla erecta* L.	1.00	0.50	0.00	0.50
Ash	*Frartinus excelsior* L.	1.00	0.00	0.25	0.42
Carnation sedge	*Carex panicea* L.	0.50	0.25	0.25	0.33
Dandelion	*Taraxacum officinale* F.H. Wigg.	0.50	0.25	0.00	0.33
Hawthorn	*Crataegus monogyna* Jacq.	0.25	0.75	0.00	0.33
Honeysuckle	*Lonicera periclymenum* L.	1.00	0.00	0.00	0.33
Common cotton grass	*Eriophorum angustigfolium* Honck.	0.75	0.00	0.00	0.25

Creeping buttercup	*Ranunculus repens* L.	0.50	0.00	0.25	0.25
Sheep's fescue	*Festuca ovina* L.	0.00	0.00	0.75	0.25
Alder	*Alnus glutinosa* L. Gaertn.	0.50	0.00	0.00	0.17
Floating sweet grass	*Glyceria fluitans* L. R. Br.	0.50	0.00	0.00	0.17
Yellow bartsia	*Parentucellia liriscosa* L. Caruel.	0.50	0.00	0.00	0.17
Unidentified		0.00	0.25	0.25	0.17
Common dog violet	*Viola riviniana* Rchb.	0.25	0.00	0.00	0.08
Birch	*Betula sp.* L.	0.00	0.00	0.25	0.08

Table 3. Frequency of epidermal fragments of plant species identified in the faecal material of European hares (*Lepus europaeus*) at each of three sites on the Isle of Man, expressed as a percentage of the total number of samples of each species, in ascending order and according to mean abundance across all sites.

Plant species		Site		
Common name	**Latin name**	**Close Sartfield**	**Goshen**	$\bar{x}$
False oat grass	*Arrhenatherum elatius* L. P.	8.95	10.31	19.26
Daisy	*Bellis perennis* L.	6.32	11.34	17.66
Yorkshire Fog	*Holcus lanatus* L.	10.00	4.12	14.12
Annual meadow grass	*Poa annua* L.	9.47	4.12	13.59
Timothy grass	*Phleum pratensis* L.	6.84	6.70	13.54
Perennial rye grass	*Lolium perenne* L.	7.89	5.15	13.04
Tufted hair grass	*Deschampsia cespitosa* L. P. Beauv.	4.74	8.25	12.99
Purple moor grass	*Molinia caerulea* L.	8.42	4.12	12.54
Tufted forget-me-not	*Myosotis larta Lehm.*	5.26	4.64	9.90
Rough meadow grass	*Poa trivialis* L.	3.68	4.64	8.32
Tormentil	*Potentilla erecta* L.	4.74	2.58	7.32
Sweet vernal grass	*Anthorranthum odoratum* L.	2.11	5.15	7.26
Creeping bent	*Agrostis stolonifera* L.	2.63	4.12	6.75
Crested dog's tail	*Cynosurus cristatus* L.	3.68	2.58	6.26
Cock's foot	*Dactylis glomerata* L.	1.58	4.12	5.70
Sheep's sorrel	*Rumex acetosella* L.	1.58	2.58	4.16
Red fescue	*Festuca rubra* L.	1.58	2.06	3.64
Bottle sedge	*Carex rostrate* Stokes.	1.05	2.58	3.63
Yellow sedge	*Carex flava* L.	0.53	3.09	3.62
Common dog violet	*Viola riviniana* Rchb.	2.11	1.03	3.14
Common cotton grass	*Eriophorum angustigfolium* Honck.	1.58	-	1.58
Sharp flowered rush	*Juncus acutiflorus* Enrh. Ex Hoffm.	1.58	-	1.58
Soft rush	*Juncus effuses* L.	1.05	0.52	1.57
Common sorrel	*Rumerr acetosa* L.	1.05	-	1.05
Heath spotted orchid	*Dactylorhiza maculate* L. Soó.	1.05	-	1.05
Bog bean	*Menyanthes trifoliate* L.	-	1.03	1.03
Common sedge	*Carex nigra* L.	-	1.03	1.03
Compact rush	*Juncus conglomeratus* L.	-	1.03	1.03
Sheep's fescue	*Festuca ovina* L.	-	1.03	1.03
Lesser spearwort	*Ranunculus flammula* L.	0.53	-	0.53
Carnation sedge	*Carex panicea* L.	-	0.52	0.52
Common mouse ear	*Cerastium fontanum* Baumg.	-	0.52	0.52
Oval sedge	*Carex ovalis* Gooden.	-	0.52	0.52
Smooth meadow grass	*Poa pratensis* L.	-	0.52	0.52

Figure 1

97x62mm (300 x 300 DPI)

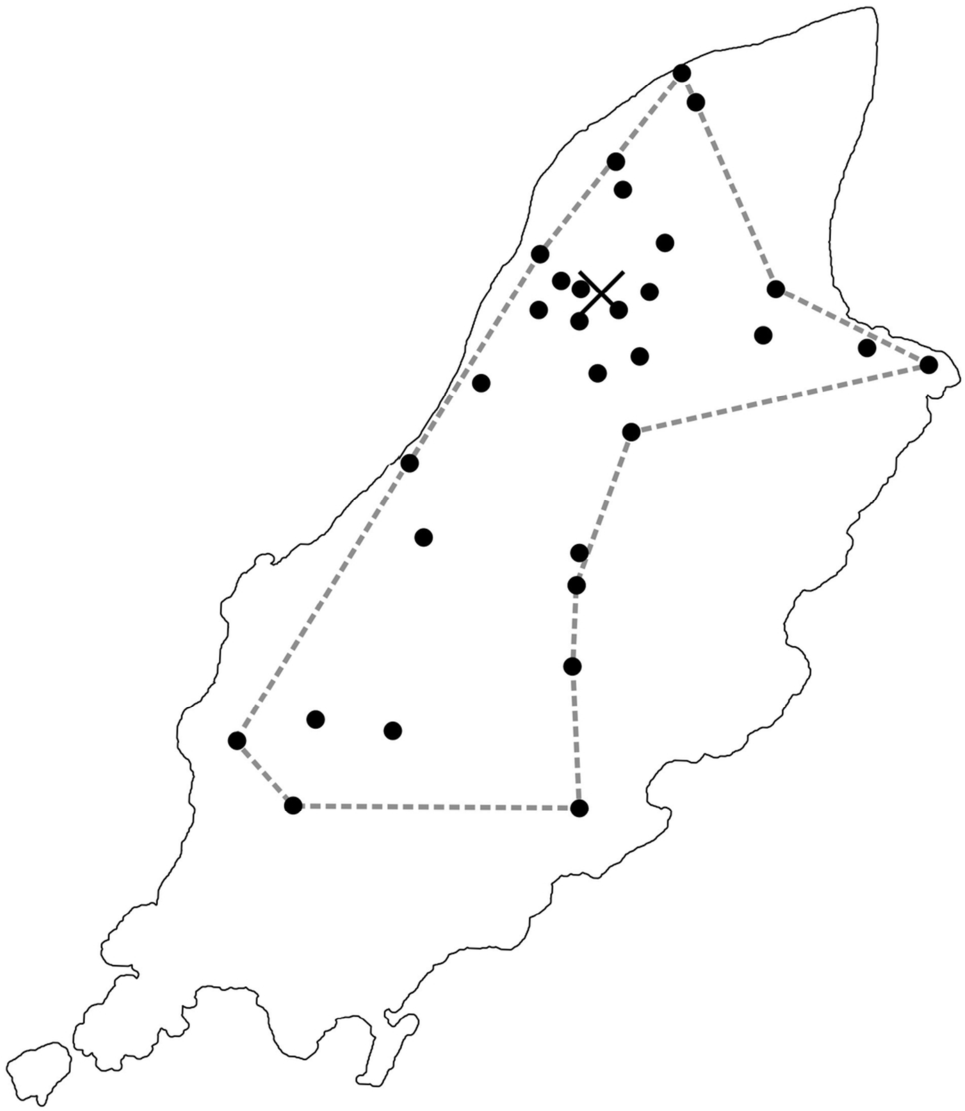


Figure 2

95x108mm (300 x 300 DPI)

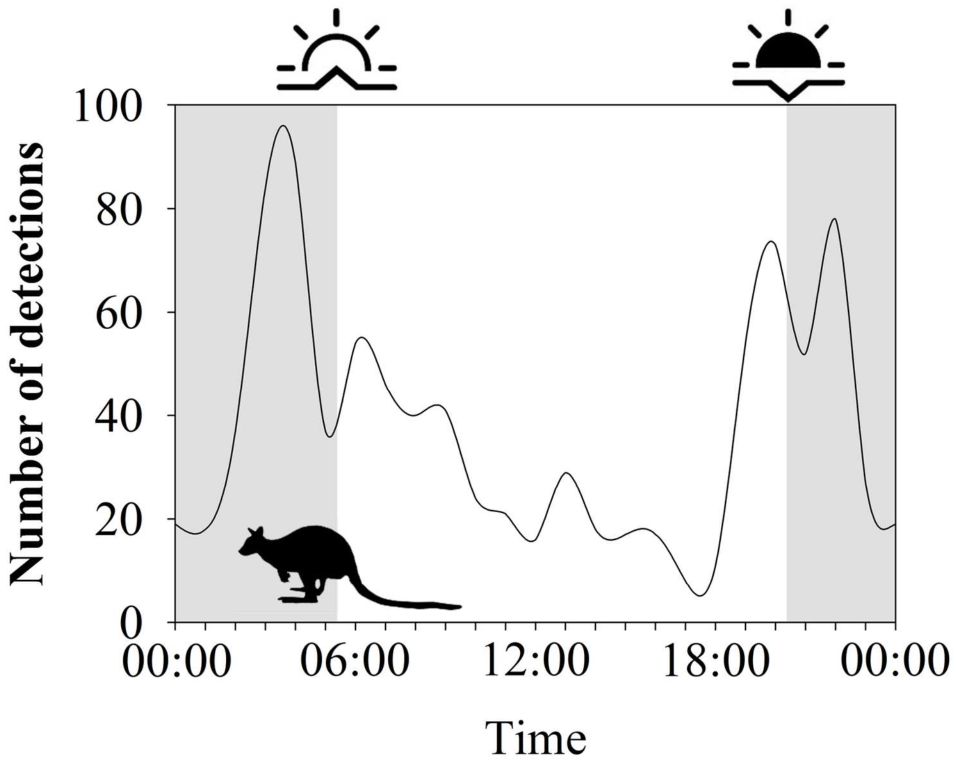
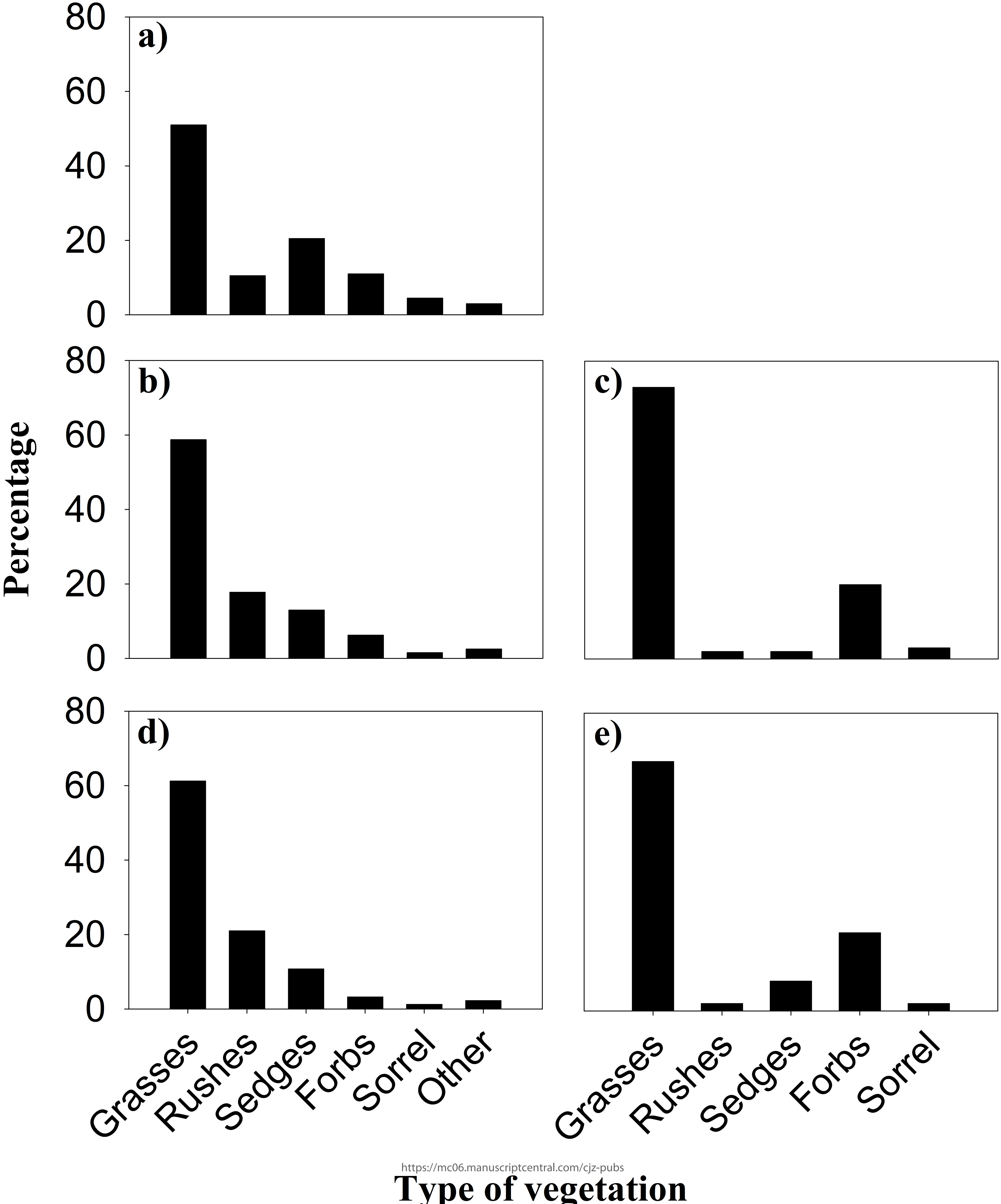


Figure 3

134x104mm (300 x 300 DPI)



a)
b)
c)
d)
e)
80
60
40
20
0
Percentage
Grasses
Rushes
Sedges
Forbs
Sorrel
Other
Type of vegetation