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The distribution and trophic ecology of an introduced, insular population of red-necked wallabies (*Notamacropus rufogriseus*)

Paige Havlin, Anthony Caravaggi, and W. Ian Montgomery

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* (Desmarest, 1817)) 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 with those of the European hare (*Lepus europaeus* Pallas, 1778). The mean (±SE) population density was 26.4 ± 6.9 wallabies/km², the mean (±SE) population size was 1742 ± 455 individuals, and the species' range was 282 km², 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 understudied 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.

Key words: non-native species, population density, diet, activity, macropod, red-necked wallaby, *Notamacropus rufogriseus*, European hare, *Lepus europaeus*.

Résumé : Les mammifères non indigènes introduits peuvent avoir des effets négatifs sur le biote indigène, et il est important de quantifier leur écologie afin de comprendre ces impacts potentiels. Des wallabys à cou rouge (*Notamacropus rufogriseus* (Desmarest, 1817)) se sont établis dans l'île de Man (IOM), une réserve de biosphère de l'UNESCO, après s'être échappés de collections zoologiques au milieu du 20ᵉ siècle. Nous avons estimé l'activité circadienne et les densités de population des wallabys en utilisant des relevés au piège photographique et des modèles de rencontres aléatoires. Leur aire de répartition dans l'IOM a été établie à la lumière de signalements du public obtenus de médias sociaux. Le régime alimentaire et l'étendue de la niche des wallabys ont été quantifiés par l'examen microscopique de matières fécales et comparés à ceux du lièvre d'Europe (*Lepus europaeus* Pallas, 1778). La densité de population moyenne (±ET) était de 26,4 ± 6,9 wallabys/km², la taille de population moyenne (±ET) était de 1742 ± 455 individus et l'aire de répartition de l'espèce occupait 282 km², soit 49 % de l'île. Les régimes alimentaires des wallabys étaient dominés par des graminées, des carex et des joncs; les étendues de niche des wallabys et des lièvres (0,55 et 0,59, respectivement) et leur chevauchement (0,60) indiquent qu'il pourrait y avoir un potentiel de concurrence interspécifique et d'impacts synergiques sur des espèces de plantes rares ou vulnérables. La population de wallabys de l'IOM est sous-étudiée, et d'autres travaux sont nécessaires pour en décrire plus en détail les paramètres démographiques, les impacts potentiels sur les espèces d'intérêt pour la conservation et les coûts et avantages économiques directs et indirects. [Traduit par la Rédaction]

Mots-clés : espèce non indigène, densité de population, régime alimentaire, activité, macropode, wallaby à cou rouge, *Notamacropus rufogriseus*, lièvre d'Europe, *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 (i.e., the incursion of an alien species that threatens native biological diversity; Invasive Species Specialist Group 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 1976) 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 et al. 1997). Although mammals are among the most successful animal invaders, with rats (species of the genus *Rattus* Fischer, 1803), European rabbits (*Oryctolagus cuniculus* (Linnaeus, 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.

P. Havlin.* School of Biological Sciences, Queen's University Belfast, Belfast, BT9 7BL, United Kingdom.
A. Caravaggi. School of Biological Sciences, Queen's University Belfast, Belfast, BT9 7BL, United Kingdom; Quercus, School of Biological Sciences, Queen's University Belfast, Belfast, BT9 7BL, United Kingdom; School of Biological, Earth and Environmental Sciences, University College Cork, Distillery Field, N Mall, Cork, Ireland.
**W.I. Montgomery.** School of Biological Sciences, Queen's University Belfast, Belfast, BT9 7BL, United Kingdom; Quercus, School of Biological Sciences, Queen's University Belfast, Belfast, BT9 7BL, United Kingdom; Institute of Global Food Security, Queen's University Belfast, Belfast, BT9 5BN, United Kingdom.
Corresponding author: Paige Havlin (email: paigehavlin@gmail.com).
*Present address: 9 Derby House, 53-55 Derby Square, Douglas, IM1 3LP, Isle of Man.

Fig. 1. Map of the Isle of Man showing the study area (subsequently subsampled) for camera trap and faecal surveys of red-necked wallabies (*Notamacropus rufogriseus*).
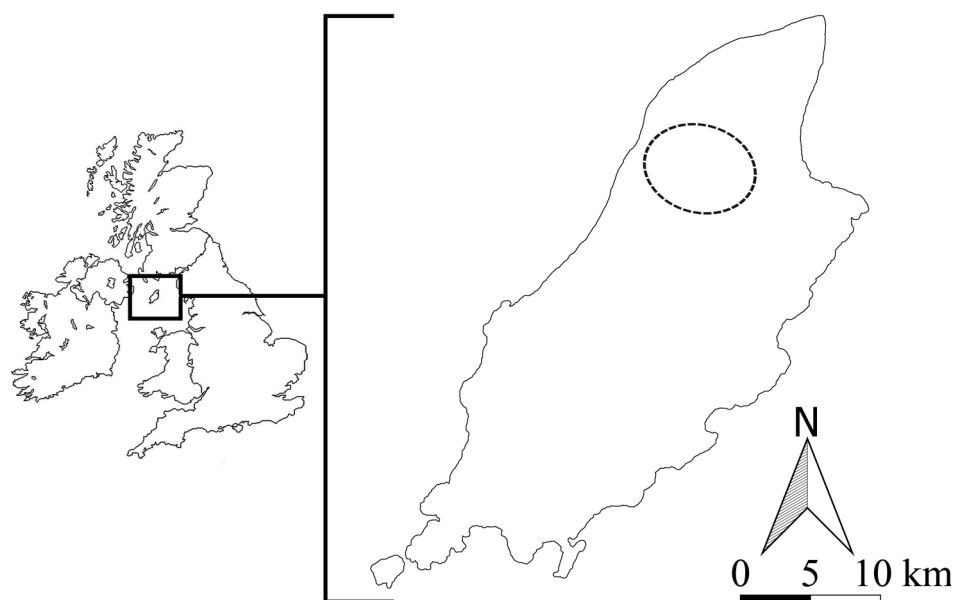
For example, high densities of Reeve's muntjac (*Muntiacus reevesi* (Ogilby, 1839)) deer inhibit coppice regrowth, and hence, have a negative economic impact, but have positive environmental benefits such as enhanced growth of ground flora species avoided by the deer and increased invertebrate abundance (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 their impacts, therefore, is important so as to elucidate their potential effects on native species, communities, and ecosystems.

The red-necked wallaby (*Notamacropus rufogriseus* (Desmarest, 1817)) is a medium-sized marsupial native to southeast 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 et al. 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). The majority of the species' diet in their natural range is composed 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 km² 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 1989a,

1989b). 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 because they are affected adversely by limiting factors, including harsh winters, road traffic collisions, and predation, e.g., by foxes (*Vulpes vulpes* (Linnaeus, 1758)) and dogs (*Canis lupus familiaris* Linnaeus, 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.

Materials and 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 composed of a characteristic mixture of bog and scrub, with many indicator species such as purple moor grass (*Molinia caerulea*) and bog myrtle (*Myrica gale* L.) (Department of Environment, Food and Agriculture 2006). (2) Close Sartfield (OS SC 358 955) is a 12 ha reserve owned by the Manx Wildlife Trust, incorporating open field, marsh grassland, and bog (Manx Wildlife Trust 2016a), and is 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 noncontact, low-impact means of quantifying the life-history traits (Silveira et al. 2003; Wegge et al. 2004) and estimating population parameters (Jenelle et al. 2002; Rowcliffe et al. 2008) 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; Silveira 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 that 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 that are not individually patterned (Rowcliffe et al. 2008). REMs have been successfully applied to several species including lowland tapir (*Tapirus terrestris* (Linnaeus, 1758)) (Oliveira-Santos et al. 2010), European pine marten (*Martes martes* (Linnaeus, 1758)) (Manzo et al. 2012), hares (species of the genus *Lepus* Linnaeus, 1758) (Caravaggi et al. 2016), and red-necked wallabies (Rowcliffe et al. 2008). The model is described by the equation:

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

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 the IOM wallabies. Here, r = 4 m, θ = 35° (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, nonconcurrently, between June and August 2015. The Curragh is large and bisected by a central public pathway, thus it was split into two subsites. Within each site, cameras were placed randomly, as required by the assumptions of 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 s, with a 2 min 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). Wal-

laby 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 Web sites) 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 (23 years since introduction; Johnson 1986); (*ii*) assuming a 10 year pre-expansion lag phase, as observed in a number of non-native mammals (15 years since introduction; e.g., Jeschke and Strayer 2005; Clout and Russell 2008).

Land-class polygons that coincided with wallaby occurrences, from both camera trap data and public sightings, were extracted from the 2012 Corine land-cover data set (Cole et al. 2015). Population estimates were calculated by multiplying the total area of resting habitat (i.e., forests, scrub) by the mean (±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 and 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 and September 2015. Dried samples were milled to a uniform size, around 2 mm fragments. One hundred millilitres of 0.05 mol/L 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., four from each sample) were produced. A reference plant collection was gathered from each site using a complete plant species list (Supplementary Table S1).[1] 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 ×400 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 ×400 magnification with the reference slide collection, along with images from previous studies (Dinkergus 1997; Hamilton 2006; George 2007). An eyepiece graticule with a 10 μm × 10 μm grid was used to generate 10 random coordinates for each slide, giving 40 records per faecal sample (i.e., a total of 1200 records from wallaby faecal material and 400 records from hare samples). Random coordinates were generated using a random number generator. Occurrence of each plant species in wallaby and hare fae-

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[1]Supplementary table is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0090.

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 (no. of wallabies/km²)	Area (km²)
Curragh	5040	479	40.1	1.93
Close Sartfield	3360	147	18.6	0.12
Goshen	3192	115	20.5	0.15

ces 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 (*Notamacropus 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 (52 cm tall, compared with 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, 04°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 farthest point of the expansion wave front, then the radial expansion rate was 0.99 km/year given a 2 year pre-expansion delay or 1.52 km/year 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 km² (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 wallabies/km² (equating to 78 individuals), Close Sartfield had 18.6 wallabies/km² (2 individuals), and Goshen had 20.5 wallabies/km² (3 individuals) (Table 1). Intersections between wallaby occurrences and Corine land classes showed that wallabies were associated with arable land, pastures, heterogeneous agricultural areas, forests, and scrub; habitats that cover 423 km² (74%) of the IOM. Habitats that provide shelter during daylight hours (i.e., forests and scrub) covered 66 km², 12% of the IOM. The estimated wallaby population was 1742 ± 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%; Figs. 4a–4e) 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*), timothy grass (*Phleum pratense*), perennial rye grass (*Lolium perenne*), smooth meadow grass (*Poa pratensis*), and purple moor grass (*Molinia caerulea*). Sedges, including common sedge (*Carex nigra*) and oval sedge (*Carex ovalis*), comprised a mean of 19.7% of the faecal material; rushes, such as soft rush (*Juncus effusus*), comprised a mean of 10.6% of the faecal material. Forbs accounted for a mean of 6.7% of all plant material in wallaby faeces and included common dog violet (*Viola riviniana*), tormentil (*Potentilla erecta*), common daisy (*Bellis perennis*), and most commonly, Atlantic ivy (*Hedera helix*).The remainder of the

Fig. 2. Red-necked wallaby (*Notamacropus rufogriseus*) range (100% minimum convex polygon (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 by the ×.
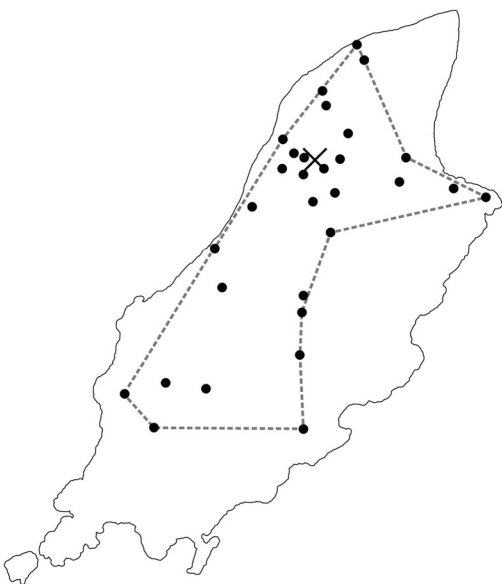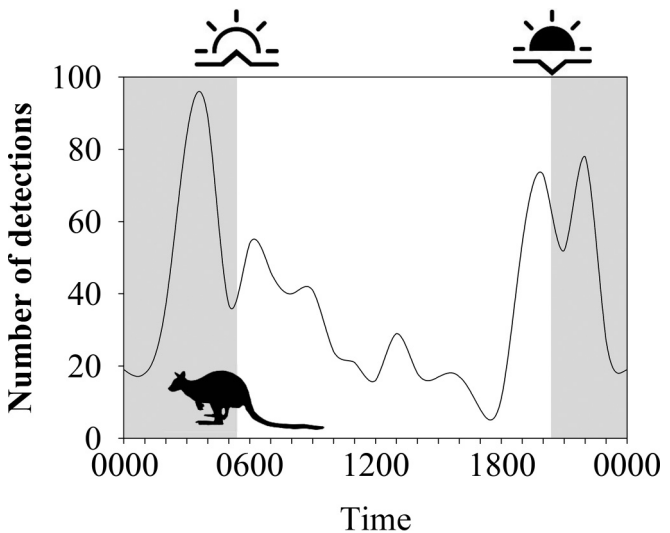

Fig. 3. Circadian activity of red-necked wallabies (*Notamacropus rufogriseus*) on the Isle of Man. Sun icons represent dawn and dusk, while shaded regions represent night time.

faecal material was composed of tree leaves from species such as willow (*Salix* sp.), birch (*Betula* sp.), and holly (*Ilex aquifolium* L.), and other unidentified species (Table 2).

Similarly, a mean of 70% of European hare faeces were composed of grasses (Figs. 4a–4e, Table 3). However, a mean of 21% of the hare's faeces were flowering plants, with common daisy as the most frequently recorded species. The remainder of the hare material was composed of rushes, sorrel, and sedges (family Cyperaceae). Wallaby niche breadth (0.59, Curragh; 0.60, Close Sartfield; 0.47 Goshen; mean = 0.55) was similar to that of European hares (0.60, Close Sartfield; 0.58, Goshen; mean = 0.59). Mean niche overlap between hares and wallabies across all sites was 0.60 (0.61, Close Sartfield; 0.59, Goshen).

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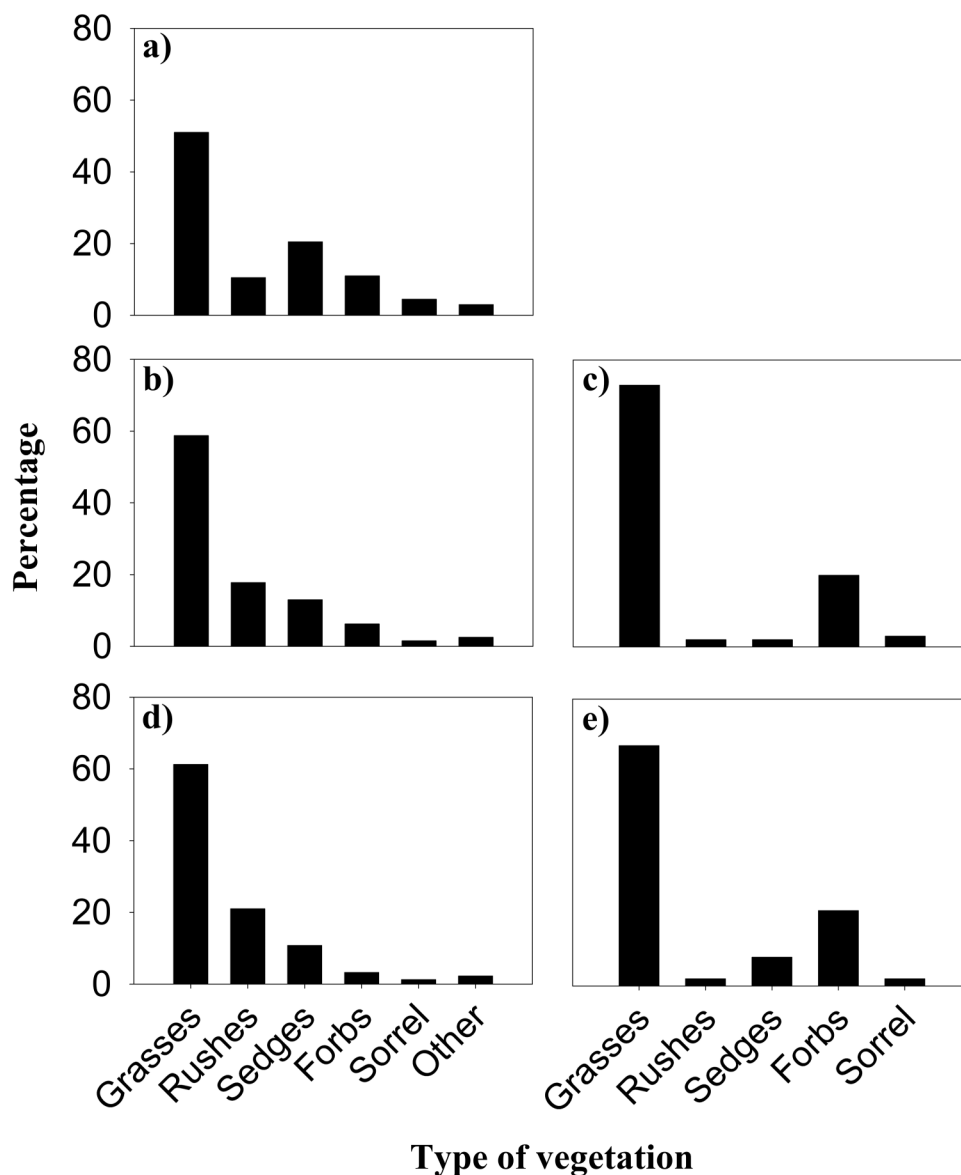
Discussion

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), as well as different methodological and observer biases (e.g., Harby (2008) used a line transect survey method for population estimation). Although 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 and 0.16 km², 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. 2012; Caravaggi et al. 2016) indicate that we can be reasonably confident of their accuracy. The limited temporal span of the current survey, however, suggests 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 scales. 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 that 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 to provide a more accurate picture of island-wide densities and abundance. Further population growth

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.

Common name	Latin name	Curragh	Close Sartfield	Goshen	Mean
False oat grass	*Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl	6.25	8.50	9.50	8.08
Soft rush	*Juncus effusus* L.	4.50	9.25	8.50	7.42
Common sedge	*Carex nigra* (L.) Reichard	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	*Anthoxanthum 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 pratense* L.	4.00	4.00	6.25	4.75
Purple moor grass	*Molinia caerulea* (L.) Moench	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* 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.	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.) Raeusch.	1.00	0.50	0.00	0.50
Ash	*Fraxinus 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 angustifolium* 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 viscosa* (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.	0.00	0.00	0.25	0.08

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 IOM that may act as potential ecological competitors for red-necked wallabies: European or brown hare, European rabbit, and the mountain hare (*Lepus timidus scoticus* Hilzheimer, 1906). Mountain hares are restricted to higher areas in the northern third of the island, in contrast to the European hare that is widespread on lower ground (Fargher 1977; Arnold 1993). European hares have been implicated in the displacement of native mountain hares (*Lepus timidus timidus* Linnaeus, 1758) in Sweden (Thulin 2003) and Northern Ireland (Irish hare, *Lepus timidus hibernicus* Bell, 1837) (Caravaggi et al. 2016), as well as Patagonian mara (*Dolichotis patagonum* (Zimmermann, 1780)) in Argentina (Puig et al. 2007). There are no data available, however, on interspecific population dynamics (e.g., spatial dis-

placement) between hares and wallabies. The degree of niche overlap observed between European hares and wallabies suggests that if resources become scarce, then 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 the 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, compared with 11.3% in the present study. This may be due to differences of scale and methodology, as well

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 (note that hares were not found on the Curragh site and therefore not enough samples could be taken), expressed as a percentage of the total number of samples of each species, in ascending order and according to mean abundance across all sites.

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

as variation between years. In contrast to feral wallabies in the Peak District, England, wallabies in the IOM did not consume heather, bracken, or pine (Yalden 1971; Weir et al. 1995), 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 plant species eaten by the wallabies on the IOM are common. However, the floating club rush (*Isolepis fluitans*) is a protected species (Isle of Man Government 1990; Charter 2011) and was identified in Curragh and Close Sartfield wallaby samples. Although 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* (Linnaeus, 1766)) and Corn Crakes (*Crex crex* (Linnaeus, 1758)) in the IOM (Hayhow et al. 2013; Wotton et al. 2015; Department of Environment, Food and Agriculture, personal communication, 2016). 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, owing to their grazing habits and use of open areas for feeding, wallabies disturb ground-nesting birds, including Hen Harriers and Corn Crakes, 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 (Sim 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 Corn Crakes across Britain is generally very low but increasing locally, while population estimates for the IOM are regarded as unreliable (Wotton et al. 2015). The interaction between wallabies and vul-

nerable ground-nesting birds on the IOM should be considered 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 because of the presence of wallabies (Manx Wildlife Trust 2016b). Furthermore, wallabies are charismatic animals that may be popular with tourists. Thus, they may confer economic benefits to the IOM residents and organisations. The IOM wallaby population remains understudied and should be monitored at regular intervals, and further research should be conducted to establish their range and population size, impacts on the wider ecosystem, and their direct and indirect economic costs and benefits.

Acknowledgements

References

Alipayo, D., Valdez, R., Holechek, J.L., and Cardenas, M. 1992. Evaluation of microhistological analysis for determining ruminant diet botanical composition. J. Range Manage. **45**: 148–152. doi:10.2307/4002773.

Arnold, H.R. 1993. Atlas of mammals in Britain. HMSO, London, UK.

Caravaggi, A. 2017. remBOOT: an R package for estimating animal densities and variance from camera trap data using Random Encounter Modelling. J. Open Source Softw. **2**(10): 176. doi:10.21105/joss.00176.

Caravaggi, A., Zaccaroni, M., Riga, F., Schai-Braun, S.C., Dick, J.T.A., Montgomery, W.I., and Reid, N. 2016. An invasive-native mammalian species replacement process captured by camera trap survey random encounter models. Remote Sens. Ecol. Conserv. **2**: 45–58. doi:10.1002/rse2.11.

Charter, E. 2011. Isle of Man: Appendices. *In* UK Overseas Territories and Crown Dependencies: 2011 Biodiversity snapshot. *Edited by* T. Pelembe and G. Cooper. The Joint Nature Conservation Committee, Peterborough, UK. Available from http://jncc.defra.gov.uk/page-5759 [accessed 4 August 2016].

Clout, M.N., and Russell, J.C. 2008. The invasion ecology of mammals: a global perspective. Wildl. Res. **35**: 180–184. doi:10.1071/WR07091.

Cole, B., King, S., Ogutu, B., Palmer, D., Smith, G., and Balzter, H. 2015. Corine land cover 2012 for the UK, Jersey and Guernsey. NERC Environmental Information Data Centre, UK. Available from https://doi.org/10.5285/32533dd6-7c1b-43e1-b892-e80d61a5ea1d [accessed 14 February 2017].

Cooke, A.S., and Farrell, L. 2001. Impact of muntjac deer (*Muntiacus reevesi*) at Monks Wood National Nature Reserve, Cambridgeshire, eastern England. Forestry, **74**(3): 241–250. doi:10.1093/forestry/74.3.241.

Cutler, T.L., and Swann, D.E. 1999. Using remote photography in wildlife ecology: a review. Wildl. Soc. Bull. **27**: 571–581.

Department of Environment, Food and Agriculture. 2006. Ballaugh Curragh Area of Scientific Interest (ASSI). Department of Environment, Food and Agriculture, St John's, Isle of Man. Available from https://www.gov.im/media/1040166/05_-_211kb_ballaugh_curragh_assi_and_ramsar_site_designation_documents.pdf [accessed 5 April 2016].

Diamond, J. 1989. Overview of recent extinctions. *In* Conservation for the Twenty-First Century. *Edited by* D. Western and M.C. Pearl. Oxford University Press, New York. pp. 37–41.

Dinkergus, S.K. 1997. The distribution and ecology of the Irish hare *Lepus timidus hibernicus* in Northern Ireland. Ph.D. thesis, Queen's University Belfast, Belfast, UK.

Eldridge, M.D.B., and Coulson, G.M. 2015. Family Macropodidae (kangaroos and wallabies). *In* Handbook of the mammals of the world. Vol. 5. Monotremes and marsupials. *Edited by* D.E. Wilson and R.A. Mittermeier. Lynx Edicions, Barcelona, Spain. pp. 630–735.

Fargher, S.E. 1977. The distribution of the Brown hare (*Lepus capensis*) and the Mountain hare (*Lepus timidus*) in the Isle of Man. J. Zool. **182**: 164–167. doi:10.1111/j.1469-7998.1977.tb04151.x.

Garnick, S., Di Stefano, J., Elgar, M.A., and Coulson, G. 2016. Ecological specialisation in habitat selection within a macropodid herbivore guild. Oecologia, **180**: 823–832. doi:10.1007/s00442-015-3510-4. PMID:26621691.

George, S. 2007. Winter diet selection of single-species populations of deer. Honours thesis, Queen's University Belfast, Belfast, UK.

Gilmore, P. 1977. The success of marsupials as an introduced species. *In* The biology of marsupials. *Edited by* B. Stonehouse and D. Gilmore. Macmillan Education, London, UK. pp. 169–178.

Hamilton, N. 2006. Winter diet in three species of deer. Honours thesis, Queen's University Belfast. Belfast, UK.

Harby, A. 2008. An assessment of the Ballaugh Curragh wallaby population. M.Sc. thesis, University College London, London, UK.

Harris, S., Morris, P., Wray, S., and Yalden, D.W. 1995. A review of British mammals: population estimates and conservation status of British mammals other than cetaceans. The Joint Nature Conservation Committee, Peterborough, UK.

Hayhow, D.B., Eaton, M.A., Bladwell, S., Etheridge, B., Ewing, S., Ruddock, M., Saunders, R., Sharpe, C., Sim, I.M.W., and Stevenson, A. 2013. The status of the Hen Harrier, *Circus cyaneus*, in the UK and Isle of Man in 2010. Bird Study, **60**: 446–458. doi:10.1080/00063657.2013.839621.

Holechek, J.L., Vavra, M., and Pieper, R.D. 1982. Botanical composition determination of range herbivore diets: a review. J. Range Manage. **35**(3): 309–315. doi:10.2307/3898308.

Invasive Species Specialist Group. 2015. About invasive species. Global Invasive Species Database. Invasive Species Specialist Group, Species Survival Commission, International Union for the Conservation of Nature, Gland, Switzerland. Available from http://www.issg.org/database/welcome/content.asp [accessed 5 August 2016].

Isle of Man Examiner. 1957. 'Special zoo club competition'. Isle of Man Examiner, 23 August 1957. p. 11.

Isle of Man Examiner. 1989. 'Wally spotting in the north of the Island'. Isle of Man Examiner, 1 August 1989.

Isle of Man Examiner. 1994. 'Wayward wallaby'. Isle of Man Examiner, 5 July 1994. p. 1.

Isle of Man Government. 1990. Wildlife Act 1990. Isle of Man Government, Douglas, Isle of Man. Available from http://www.legislation.gov.im/cms/images/LEGISLATION/PRINCIPAL/1990/1990-0002/WildlifeAct1990_2.pdf [accessed 3 April 2016].

Isle of Man Weekly Times. 1965. 'Opening feature'. Isle of Man Weekly Times, 2 July 1965.

Isle of Man Weekly Times. 1966. 'Wanda returns "fat and healthy"'. Isle of Man Weekly Times, 28 October 1966.

Jarman, P.J., and Calaby, J.H. 2008. Red-necked wallaby, *Macropus rufogriseus*. *In* The mammals of Australia. *Edited by* S. Van Dyck and R. Strahan. 3rd ed. Reed New Holland, Sydney, N.S.W., Australia. pp. 349–351.

Jarman, P.J., and Phillips, C.M. 1989. Diets in a community of macropod species. *In* Kangaroos, wallabies and rat-kangaroos. Vols. 1 and 2. *Edited by* G.C. Grigg, P.J. Jarman, and I.D. Hume. Surrey Beatty and Sons, Sydney, N.S.W., Australia. pp. 143–149.

Jennelle, C.S., Runge, M., and MacKenzie, D.I. 2002. The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. Anim. Conserv. **5**: 119–120. doi:10.1017/S1367943002002160.

Jeschke, J.M., and Strayer, D.L. 2005. Invasion success of vertebrates in Europe and North America. Proc. Natl. Acad. Sci. U.S.A. **102**: 7198–7202. doi:10.1073/pnas.0501271102. PMID:15849267.

Johnson, C.N. 1986. Philopatry, reproductive success of females, and maternal investment in the red-necked wallaby. Behav. Ecol. Sociobiol. **19**(2): 143–150. doi:10.1007/BF00299949.

Johnson, C.N. 1989. Grouping and the structure of association in the red-necked wallaby. J. Mammal. **70**: 18–26. doi:10.2307/1381665.

Karanth, K.U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture–recapture models. Biol. Conserv. **71**(3): 333–338. doi:10.1016/0006-3207(94)00057-W.

Karanth, K.U., Nichols, J.D., Seidensticker, J., Dinerstein, E., Smith, J.L.D., McDougal, C., Johnsingh, A.J.T., Chundawat, R.S., and Thapar, V. 2003. Science deficiency in conservation practice: the monitoring of tiger populations in India. Anim. Conserv. **6**: 141–146. doi:10.1017/S1367943003003184.

Kennington, K., and Hisscott, A. 2013. Hydrology, weather and climate, climatology. *In* Manx marine environmental assessment. *Edited by* L.J. Hanley, F.G. Gell, K. Kennington, E. Stone, E. Rowan, P. McEvoy, M. Brew, K. Milne, L. Charter, M. Gallagher, and K. Hemsley. Isle of Man Marine Plan, Isle of Man Government, Douglas. pp. 45.

Le Mar, K., and McArthur, C. 2005. Comparison of habitat selection by two sympatric macropods, *Thylogale billardierii* and *Macropus rufogriseus rufogriseus*, in a patchy eucalypt-forestry environment. Austral Ecol. **30**: 674–683. doi:10.1111/j.1442-9993.2005.01510.x.

Le Mar, K., McArthur, C., and Statham, M. 2003. Home ranges of sympatric red-necked wallabies, red-bellied pademelons and common brushtail possums in a temperate eucalypt forestry environment. Aust. Mammal. **25**(2): 183–191. doi:10.1071/AM03183.

Le Page, S.L., Livermore, R.A., Cooper, D.W., and Taylor, A.C. 2000. Genetic analysis of a documented population bottleneck: introduced Bennett's wallabies (*Macropus rufogriseus rufogriseus*) in New Zealand. Mol. Ecol. **9**: 753–763. doi:10.1046/j.1365-294x.2000.00922.x. PMID:10849291.

Lister, B. 1976. The nature of niche expansion in West Indian *Anolis* lizards I: ecological consequences of reduced competition. Evolution, **30**: 659–676. doi:10.1111/j.1558-5646.1976.tb00947.x. PMID:28563323.

Lodge, D.M. 1993. Biological invasions: lessons for ecology. Trends Ecol. Evol. **8**: 133–137. doi:10.1016/0169-5347(93)90025-K. PMID:21236129.

MacArthur, R., and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. **101**(921): 377–385. doi:10.1086/282505.

Maffei, L., Noss, A.J., Cuellar, E., and Rumiz, D.I. 2005. Ocelot (*Felis pardalis*) population densities, activity and ranging behaviour in the dry forests of eastern Bolivia: data from camera trapping. J. Trop. Ecol. **21**: 349–353. doi:10.1017/S0266467405002397.

Manx Independent. 1989*a*. 'Caught on the hop'. Manx Independent, 21 July 1989. p. 9.

Manx Independent. 1989*b*. 'Beware: Wallabies crossing!' Manx Independent, 24 October 1989.

Manx Wildlife Trust. 2016*a*. Close Sartfield. Manx Wildlife Trust, Peel, Isle of Man. Available from http://www.manxwt.org.uk/reserves/close-sartfield [accessed 5 April 2016].

Manx Wildlife Trust. 2016*b*. Goshen. Manx Wildlife Trust, Peel, Isle of Man. Available from http://www.manxwt.org.uk/reserves/goshen [accessed 5 April 2016].

Manzo, E., Bartolommei, P., Rowcliffe, J.M., and Cozzolino, R. 2012. Estimation of population density of European pine marten in central Italy using camera trapping. Acta Theriol. **57**: 165–172. doi:10.1007/s13364-011-0055-8.

McNab, B.K. 1980. Food habits, energetics, and the population biology of mammals. Am. Nat. **116**(1): 106–124. doi:10.1086/283614.

Menkhorst, P., and Knight, F. 2001. A field guide to the mammals of Australia. Oxford University Press, Melbourne, Vic., Australia.

Moors, P.J., and Atkinson, I.A.E. 1984. Predation on seabirds by introduced animals, and factors affecting its severity. *In* Status and conservation of the world's seabirds. *Edited by* J.P. Croxall, P.G.H. Evans, and R.W. Schreiber. ICBP Tech. Publ. No. 2, Cambridge, UK. pp. 667–690.

Oliveira-Santos, L.G.R., Zucco, C.A., Antunes, P.C., and Crawshaw, P.G. 2010. Is it possible to individually identify mammals with no natural markings using camera-traps? A controlled case-study with lowland tapirs. Mamm. Biol. **75**: 375–378. doi:10.1016/j.mambio.2009.08.005.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., and Goldwasser, L. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biol. Invasions, **1**: 3–19. doi:10.1023/A:1010034312781.

Pianka, E.R. 1974. Niche overlap and diffuse competition. Proc. Natl. Acad. Sci. **71**(5): 2141–2145. doi:10.1073/pnas.71.5.2141. PMID:4525324.

Puig, S., Videla, F., Cona, M.I., and Monge, S.A. 2007. Diet of the brown hare (*Lepus europaeus*) and food availability in northern Patagonia (Mendoza, Argentina). Mammal. Biol. **72**: 240–250. doi:10.1016/j.mambio.2006.08.006.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Reichlin, T., Klansek, E., and Hacklander, K. 2006. Diet selection by hares (*Lepus europaeus*) in arable land and its implications for habitat management. Eur. J. Wildl. Res. **52**(2): 109–118. doi:10.1007/s10344-005-0013-3.

Rejmánek, M., Richardson, D.M., Barbour, M.G., Crawley, M.J., Hrusa, G.F., Moyle, P.B., Randall, J.M., Simberloff, D., and Williamson, M. 2002. Biological invasions: politics and the discontinuity of ecological terminology. ESA Bull. **83**: 131–133.

Reynolds, J.C., and Short, M.J. 2003. The status of foxes *Vulpes vulpes* on the Isle of Man in 1999. Mammal Rev. **33**(1): 69–76. doi:10.1046/j.1365-2907.2003.00002.x.

Rowcliffe, J.M., Field, J., Turvey, S.T., and Carbone, C. 2008. Estimating animal density using camera traps without the need for individual recognition. J. Appl. Ecol. **45**(4): 1228–1236. doi:10.1111/j.1365-2664.2008.01473.x.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., and Weller, S.G. 2001. The population biology of invasive species. Annu. Rev. Ecol. Syst. **32**: 305–332. doi:10.1146/annurev.ecolsys.32.081501.114037.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R., Kinzig, A., Leemans, R., Lodge, D., Mooney, H.A., Oesterheld, M., Poff, L., Sykes, M.T., Walker, B.H., Walker, M., and Wall, D. 2000. Global biodiversity scenarios for the year 2100. Science, **287**: 1770–1774. doi:10.1126/science.287.5459.1770. PMID:10710299.

Silveira, L., Jacomo, A.T.A., and Diniz-Filho, J.A.F. 2003. Camera trap, line transect census and track surveys: a comparative evaluation. Biol. Conserv. **114**: 351–355. doi:10.1016/S0006-3207(03)00063-6.

Sim, I.M.W., Gibbons, D.W., Bainbridge, I.P., and Mattingley, W.A. 2001. Status of the Hen Harrier *Circus cyaneus* in the UK and the Isle of Man in 1998. Bird Study, **48**(3): 341–353. doi:10.1080/00063650109461233.

Sim, I.M.W., Dillon, I.A., Eaton, M.A., Etheridge, B., Lindley, P., Riley, H., Saunders, R., Sharpe, C., and Tickner, M. 2007. Status of the Hen Harrier *Circus cyaneus* in the UK and Isle of Man in 2004, and a comparison with the 1988/89 and 1998 surveys. Bird Study, **54**: 256–267. doi:10.1080/00063650709461482.

Sprent, J.A., and McArthur, C. 2002. Diet and diet selection of two species in the macropodid browser–grazer continuum: do they eat what they "should"? Aust. J. Zool. **50**: 183–192. doi:10.1071/ZO01043.

Thulin, C.G. 2003. The distribution of mountain hares *Lepus timidus* in Europe: a challenge from brown hares *L. europaeus*? Mamm Rev. **33**: 29–42. doi:10.1046/j.1365-2907.2003.00008.x.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. Science, **277**: 1300–1302. doi:10.1126/science.277.5330.1300.

Tobler, M.W., Carrillo-Percastegui, S.E., Leite Pitman, R., Mares, R., and Powell, G. 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Anim. Conserv. **11**: 169–178. doi:10.1111/j.1469-1795.2008.00169.x.

Veitch, C., and Clout, M. (*Editors*). 2002. Turning the tide: the eradication of invasive species. *In* Proceedings of the International Conference on Eradication of Island Invasives. Occasional Paper of the IUCN Species Survival Commission. No. 27. pp. 1–3. Available from http://www.issg.org/pdf/publications/turning_the_tide.pdf.

Wegge, P., Pokheral, C.P., and Jnawali, S.R. 2004. Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. Anim. Conserv. **7**: 251–256. doi:10.1017/S1367943004001441.

Weir, A., McLeod, J., and Adams, C.E. 1995. The winter diet and parasitic fauna of a population of red-necked wallabies *Macropus rufogriseus* recently introduced to Scotland. Mamm. Rev. **25**(3): 111–116. doi:10.1111/j.1365-2907.1995.tb00450.x.

Wotton, S.R., Eaton, M., Ewing, S.R., and Green, R.E. 2015. The increase in the Corncrake *Crex crex* population of the United Kingdom has slowed. Bird Study, **62**(4): 486–497. doi:10.1080/00063657.2015.1089837.

Yalden, D.W. 1971. Feral wallabies in the Peak District. J. Zool. (Lond.), **165**(4): 513–520. doi:10.1111/j.1469-7998.1971.tb02203.x.

Yalden, D.W. 1999. The history of British mammals. T & AD Poyser, London, UK.