The importance of host plant-habitat substrate in the maintenance of a unique isolate of the Sandhill Rustic: disturbance, shingle matrix and bare ground indicators

Adrian Spalding, Mark Young & Roger L. H. Dennis

Journal of Insect Conservation

An international journal devoted to the conservation of insects and related invertebrates

ISSN 1366-638X Volume 16 Number 6

J Insect Conserv (2012) 16:839-846 DOI 10.1007/s10841-012-9470-7





Your article is protected by copyright and all rights are held exclusively by Springer Science+Business Media B.V.. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.



ORIGINAL PAPER

The importance of host plant-habitat substrate in the maintenance of a unique isolate of the Sandhill Rustic: disturbance, shingle matrix and bare ground indicators

Adrian Spalding · Mark Young · Roger L. H. Dennis

Received: 19 July 2011/Accepted: 9 February 2012/Published online: 3 March 2012 © Springer Science+Business Media B.V. 2012

Abstract The Sandhill Rustic moth *Luperina nickerlii* leechi is an isolate restricted to the beach of Loe Bar in Cornwall UK; it is a UK Priority taxon because of its unique status and small, declining population. The larval foodplant is Sand Couch-grass Elytrigia juncea; the larvae feed at first inside the stems and then on the rhizomes underground. The distribution of the moth and E. juncea were investigated in this study in relation to substrate conditions and other plants. E. juncea has an above-ground clumped distribution; near the sea the plants are linked by rhizomes, but away from the sea the apparent clumping is a probable historic record of previous connectivity where the rhizomes have disappeared. The adult moths were found to be associated with more vigorous E. juncea plants growing in sparsely vegetated, more disturbed ground near the sea, especially those plants with large rhizome systems along which later instar larvae can travel between plants. Emerging moths were associated with areas of extensive E. juncea surrounded by bare ground, where there was a substantial variation of shingle particles between 125 μ m and 8 mm. The absence of vegetation and associated roots apart from *E. juncea*, and a coarse particle mix, may allow larvae to move through the shingle and the moths to push their way upwards from their subterranean pupae. We conclude that management should aim to create areas of bare ground with extensive patches of *E. juncea* growing in coarser shingle, with extensive underground connectivity and few other plants.

Keywords Beach · *Elytrigia juncea* · Lepidoptera · *Luperina nickerlii* · Management · Particle size · Rhizomes

Introduction

Although larval host plants are the key habitat resource of phytophagous Lepidoptera (Thomas et al. 2011), the latter are not always found where their larval host plants are located, and when present may be in very small numbers (Dennis 2010). Subsidiary resources accounting for ability to exploit the host plant by the adult when egg laying, and by the larvae when feeding and developing, typically limit the host areas used (Dennis et al. 2003). These are often described as host quality factors. There may be variations in food plant quality over space (Dempster and Pollard 1981) and food plant suitability can change over time (Feeny 1970; Haukioja 1980; Barbour and Young 1993; Stevenson et al. 1993; Choong 1996) and after management (Fowles et al. 2004). In addition, Lepidoptera may prefer a particular food plant growing in one biotope and not in others (Spalding and Parsons 2004).

The amount of bare ground in the vicinity of host plants may be an important 'resource'. It is frequently an important habitat component for Lepidoptera in a resource-based sense

A. Spalding · M. Young

School of Biological Sciences, University of Aberdeen, Zoology Building, Aberdeen AB24 2TZ, Scotland, UK

e-mail: m.young@abdn.ac.uk

A. Spalding (⊠)

Spalding Associates (Environmental Ltd), Norfolk House, 16-17 Lemon Street, Truro TR1 2LS, Cornwall, UK e-mail: a.spalding@spaldingassociates.co.uk

R. L. H. Dennis

Department of Biological and Medical Sciences, Oxford Brookes University, Headington, Oxford OX3 0BP, UK e-mail: rlhdennis@aol.com

R. L. H. Dennis

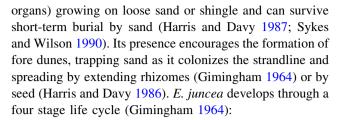
Institute for Environment, Sustainability and Regeneration, Staffordshire University, Mellor Building, College Road, Stoke-on-Trent ST4 2DE, UK



of habitat (Dennis 2010) and used for thermoregulation (Dennis and Shreeve 1988) and mate location (Dennis and Sparks 2005), as well as associated with substrate disturbance and the quality of consumer resources such as larval host plants (e.g. Lycaena phlaeas, Dempster 1971; Pieris napi, Dennis 1985). Other invertebrates (e.g. solitary wasps, Hymenoptera) use bare ground sites for burrows for inserting their eggs and food for hatchlings, and as areas for obtaining food (hunting) (e.g. Carabidae, Cicindelinae; Diptera, Asilidae) (Key 2000). In particular, the UK Priority Habitat of coastal vegetated shingle (JNCC 2011) supports in places extensive areas of bare ground where the shingle may be used by insects as a place of concealment during the day e.g. by the Scaly Cricket Pseudomogoplistes vicentae (Sutton 1999) and by moth larvae (e.g. Coast Dart Euxoa cursoria, Portland Moth Actebia praecox and Sand Dart Agrotis ripae (Skinner 2009)) or for nesting (e.g. by the Short-haired Bumblebee Bombus subterraneus).

Although bare earth may be related to disturbance and observed to be an essential component of the larval host plant resource where it occurs, it is often not known just what is important about the nature of the bare substrate that may be limiting the population of a phytophagous Lepidoptera. This paper investigates the distribution of the Sandhill Rustic moth Luperina nickerlii Freyer, 1845 ssp. leechi Goater and Sand Couch-grass Elytrigia juncea (Viviani) Runemark ex Melderis, its host plant, on Loe Bar in Cornwall. L. nickerlii is a medium sized noctuid moth occurring in Europe mainly on dry xerothermic slopes, but in Britain and Ireland is found only in coastal locations (Skinner 2009), where it can be found from the sea's edge to several hundred metres inland (Spalding 2002). The moth is univoltine, the eggs being laid in parallel rows in August and September on various grasses, inside the stems of which the larvae feed during warm spells in winter before moving down in early spring to feed on the crowns and roots; on softer substrates the larvae are subterranean, pushing through the sand as they feed on the rhizomes of the larval foodplant. The moth is nocturnal, emerging through the sand in late summer. The present study concerns subspecies leechi Goater which is restricted to Loe Bar, in Cornwall. Loe Bar is a narrow sandy shingle beach which is occasionally washed over by waves in major storm events. L. nickerlii is a UK BAP Priority species because of its small, declining population (Spalding 1997; Spalding and Young 2011). The adults, especially the females, move very little within the habitat (Spalding and Young 2011) and the moths can easily be found resting on the grass stems of the larval foodplant.

Sand Couch-grass *Elytrigia juncea* is a characteristic grass of early successional biotopes and persistent in established foredune biotopes as one of the primary colonizers of dune succession (Harris and Davy 1986). It is a geophyte (an herbaceous plant with underground storage



- 1. juvenile establishment phase in which colonising plants form small rosettes;
- adolescent dynamic phase in which plants develop horizontal rhizomes;
- stabilizing mature phase in which clumps are connected by extensive rhizomes;
- 4. senile degenerative phase in which interconnecting rhizomes die leaving plants isolated.

Elytrigia juncea is commonly found on foredunes in suitable biotopes throughout Britain, but on Loe Bar it occurs both extensively within reach of the waves and in small, less vigorous patches on the hind zone, which is about 200 m from the sea. Disturbance (which can be identified by particle size variation and lack of vegetation, and/or burial by shingle) can bring renewed vigour to E. juncea (Harris and Davy 1987); otherwise the plants gradually become moribund and out-competed by other plants.

Elytrigia species are not generally preferred foodplants for Lepidoptera. Only three Elytrigia species are used in Britain as butterfly or moth larval foodplants: the widespread Elytrigia repens is fed on by at least three butterflies and five Noctuid moths (Emmet 1991); the coastal Elytrigia atherica is fed on by one species only (Emmet and Langmaid 2002); two moth species (L. nickerlii and E. cursoria) feed primarily or regularly on E. juncea (Emmet 1991). The lack of moths feeding on E. juncea may be partly due to its narrow coastal distribution. The geographical range of a plant has been found to have a considerable effect on the total number of insects associated with it (Lawton and Schroder 1977; Strong and Levin 1979).

The objectives of this study were to discover the habitat requirements of *E. juncea* on Loe Bar and the factors influencing the selection by Sandhill Rustics of particular patches of *E. juncea* as foodplant. The key questions addressed are why *E. juncea* grows more abundantly in some areas and not others and why the Sandhill Rustic does not occur everywhere *E. juncea* occurs. Recommendations for management are made on the basis of the requirements of the moth and its host plant.

Methods

All work was carried out on Loe Bar between 2003 and 2007. Loe Bar is the sole location of *L. nickerlii leechi* in



the British Isles and comprises a shingle barrier beach enclosing a lagoon, The Loe, near Porthleven, Cornwall, UK (50.08 N, 5.31 W). It is a marine depositional landform subject to perpetual disturbance but with distinctive zonation and gradients in material and in the overlying vegetation. Although subject to occasional overtopping by the sea, this did not occur during the study period. Loe Bar is divided into four zones inwards from the sea: an un-vegetated beach zone, a vegetated crest zone where Elytrigia was abundant, a more closely vegetated mid-zone where Elytrigia was very sparse, and a partially-vegetated hind zone where Elytrigia was again abundant. Sandhill Rustics were searched for at night during the flight periods in each year using a high powered torch and the position of each individual found was recorded. Newly emerged and older adults were distinguished, with the former being identified by their habitat of drying their wings whilst quiescent immediately following emergence. The distribution of E. juncea was established using a systematic sampling pattern to identify the different contrasting areas followed by random sampling within these areas to measure percentage vegetation cover and percentage bare ground using 118 1×1 m quadrats (49 in autumn 2005 and 69 in autumn 2006). (It was impractical to count the numbers of individual plants as many on the beach reproduce from rhizomes and therefore may be connected underground). The Bar was sub-divided into areas where moths had been found (the with-moth areas) and those areas where moths had never been seen over 22 years of study (the withoutmoth areas). Quadrats were placed at random within the main patches of Elytrigia at the coastal edge of Loe Bar and on the hind dune in areas with moths and without moths in order to investigate percentage vegetation cover and Elytrigia stem density in occupied and unoccupied areas. More detailed observations were made in 15 places where moths were seen freshly emerged; 0.25×0.25 m quadrats were centered on the position for each moth, and vegetation cover data recorded. The Bar was stable over this period and the distribution of *Elytrigia* changed very little during these surveys.

Elytrigia swards appear to consist of an evenly-distributed pattern of shoots, but this pattern may conceal clumping at various scales. Clumping pattern was investigated using a method outlined in Kershaw (1957, 1973), a transect 0.05 m wide and 0.512 m long, within areas of Elytrigia (avoiding the edges). The number of emergent Elytrigia stems was then counted in block lengths doubled each time, i.e. 0–0.01, 0–0.02, to 0–0.512 m (many of these stems will be derived from a single plant). In 2007, 6 transects (3 sets of 2 transects at right angles) were surveyed; 3 in areas with the Sandhill Rustic, and 3 in areas without it. The total number of stems for each transect was calculated and the variance around the mean calculated for

each block length; a steady increase in variance around the mean indicates an increase in clump size as the block size increased; declines in variance indicate the end of the clump. Potential clumps below 0.002–0.004 m have been omitted from this analysis due to the possibility of sampling error at this small scale; they provide less compelling evidence of clumping than for the larger clumps.

Underground connectivity was investigated by surveying 100 individual *Elytrigia* plants (choosing larger plants with more than one stem) in 12 areas (6 with moths and 6 without moths) by digging around each plant. The clumps were divided into two classes: plants with attached rhizomes and plants lacking rhizomes, having only small roots.

Eighty samples of sand were collected to a depth of 8 cm (the maximum depth at which larvae are usually found) in May 2003 in each of the four zones of Loe Bar, with 20 samples from each zone. Samples were riffled several times to reduce each one to about 400–500 g in weight. Sand was also collected in 1 L plastic bottles from 10 quadrats in 2002–2004, where moths had been recorded emerging, or where pupae were found. All samples were oven dried and sieved in a standard sieve tower, ranging from <125 μ m to >8 mm mesh size, for 5 min to produce a series of classes in finite increments. All sub-samples were weighed and the percentage for each sub-sample of the total sample calculated.

Data analysis

Kruskal-Wallis ANOVA was used to test for differences in median beach particle size by location; it was also used to determine any significant differences of particle sizes for samples of beach material taken from locations where emerging moths were found, compared to the zone samples. Differences between beach zones (and samples where emerging moths were located) for particle size classes were determined using non-metric scaling (NMS) using STAT-ISTICA 9 (Statsoft Inc.) based on Euclidean distances between proportions for particle size grades. Two measures of stress (alienation and Kruskal's stress) are used to assess the reliability of the solution. Comparisons for vegetation cover were calculated using Spearman rank order correlations, for Elytrigia clump size Wilcoxon Matched Pair test and for rhizome abundance and Elytriga variables the Mann-Whitney U test.

Results

Distribution of Sandhill Rustic moths and *E. juncea* on Loe Bar

The majority (733) of moths was found in the crest zone; 62 were found in the hind zone (the crest zone was 1.174



Table 1 Comparison of plant and substrate variables for random quadrats with *Elytrigia* in areas with moths and without moths on Loe Bar in 2005 and 2006; Mann–Whitney *U* test results

2005, n = 49, 30 with moths, 19 without moths; 2006, n = 69, 40 with moths, 29 without moths

	Median in with-moth areas	Median in without-moth areas	U	P
Number of Elytrigia stems (2005)	154	102	164.00	0.013
Number of Elytrigia stems (2006)	215	148	293.00	0.0005
% Elytrigia cover (2005)	15	10	144.00	< 0.004
% Elytrigia cover (2006)	20	10	160.50	< 0.000000
% Bare ground (2005)	75	65	235.00	0.31
% Bare ground (2006)	75	60	281.00	0.0003

times larger than the hind zone). *E. juncea* was found extensively on Loe Bar, mainly in the crest zone near the sea and in the hind zone on the inland edge of the Bar. There were extensive areas of *E. juncea* where no moths were found, especially in the hind zone. A comparison of the areas with and without moths, in both 2005 and 2006, indicated that there were significantly more *Elytrigia* stems in the with-moth areas and a greater percentage cover of *Elytrigia* (Table 1). There was significantly more bare ground in the with-moth areas than the without moth areas in 2006, but not in 2005.

Elytrigia was found growing mainly with Honkenya peploides (found with Elytrigia in 47% of the quadrats in 2005/2006; mean 3.9%) and Eryngium maritimum (found with Elytrigia in 63% of the quadrats in 2005/2006; mean 2.5%). Bare ground was always abundant (Table 1). A significant negative correlation was found between the abundance of Elytrigia and several other plants including Festuca rubra, Plantago lanceolata, Leontodon saxatilis, Silene uniflora, Daucus carota and Ononis repens (Spearman $r_s = -0.22$ to -0.40, P = 0.02 to <0.001). H. peploides was more common in the with-moth areas. No moths were found where L. saxatilis, S. uniflora, F. rubra, Cirsium arvense, Achillea millefolium, Trifolium repens, Glaucium flavum and Triplospeurnum maritimum occurred.

Fifteen moths were seen emerging 2003–2005. The only vegetation present where moths were seen emerging consisted of *E. juncea*, *H. peploides* and *E. maritimum*. Percentage bare ground ranged from 15 to 95% (mean = 66.8%; n = 15); percentage cover for *Elytrigia* ranged from 5 to 50% (mean = 18%), for *Honkenya* 0–60% (mean = 9.4%) and *Eryngium* 0–30% (mean = 3.1%).

Characteristics of E. juncea on Loe Bar

Elytrigia juncea exhibited different growth patterns in the four zones of Loe Bar, growing in thick clumps in some areas and more sparsely in other areas. 76 clumps were detected within the 36 transects sampled (mean = 2.11 clumps per transect) (Table 2). There appeared to be a significant difference (Wilcoxon Matched Paired test,

Table 2 Surface *E. juncea* clump size in areas with and without moths on Loe Bar 2007, as recorded in 6 transects from each area

Clump length (cm)	Number of clumps in the with moth areas	Number of clumps in the without moth areas
2–4	2	4
4–8	6	6
8–16	3	5
16-32	4	5
32-64	7	4
64–128	5	4
128-256	11	10

Z=3.75, P=0.0002, valid n=16) between *Elytrigia* clump size in the areas where moths occurred (median = 64) and those areas where no moths were found (median = 32) and there was a significant difference (Mann–Whitney U=0, Z=2.80, P=0.005, n=6 and 6) in the number of *Elytrigia* clumps with rhizomes in the areas with moths (median = 89.5) and the areas without moth (median 57.5) (Table 3).

Particle size across Loe Bar

Particle size analysis in 2003 of the four main zones (Beach, Crest, Mid and Hind) across the Bar, defined by their proximity to the sea, showed a steady decrease in particle size variation away from the sea (Table 4). The crest zone had a relatively high percentage of both larger and smaller particles; in comparison, the sand in the hind zone showed less variation, with a greater concentration of mid-range particles between 250 µm and 2 mm.

The two-dimensional NMS plot (Fig. 1) had low stress and is suitable for displaying relationships between beach samples. Particle size samples in each zone grouped according to distance from the sea (i.e. from beach to hind zone). Particle size in the beach quadrats revealed a high level of variation with samples being more widely scattered across the ordination than for the other zones. There are



Table 3 The number of *E. juncea* clumps with and without rhizomes in areas with moths and areas without moths on Loe Bar 2007

With rhizomes	Without rhizomes		
With moths			
Total = 527 (median = 89.5)	Total = 73 (median = 10.5)		
Without moths			
Total = 328 (median = 57.5)	Total = 272 (median = 42.5)		

Table 4 Percentage by weight of sand in particle size categories in four zones across Loe Bar

Particle size category	Beach zone	Crest zone	Mid zone	Hind zone
>8 mm	2.2	1.94	1	0.09
>4 mm	4.13	3.49	2.7	0.53
>2 mm	17.37	10.04	9.21	8.79
>1 mm	39.47	28.65	30.2	41.39
>500 μm	27.13	34.64	37.59	34.76
>250 μm	7.94	17.37	16.58	12.55
>125 μm	1.59	3.37	2.19	1.56
$<125~\mu m$	0.15	0.44	0.32	0.18

n = 20 in each zone

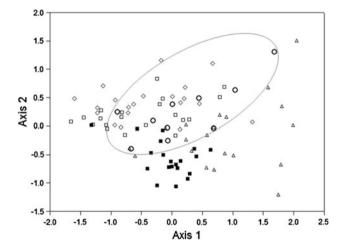


Fig. 1 Non-metric scaling plot of particle sizes taken at 80 sites across four biotope zones on Loe Bar and ten locations where emerging moths were found (*triangles* beach zone, *diamonds* crest zone, *white squares* mid-zone, *black squares* hind zone, *large circles and ellipse* emerging moth locations). Alienation 5.2% and Kruskal stress 4.9%

significant differences between the four beach zones for median beach particle size (Kruskal–Wallis test: H = 16.33, P = 0.001), especially between the beach zone and mid- and hind-zones (multiple tests, P < 0.001).

All emerging moths were found in the crest zone. Although median particle sizes of beach zones differed

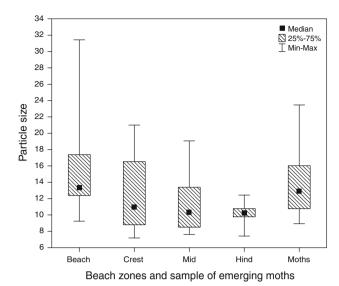


Fig. 2 Box plot of particle size (mm) for four beach zones and samples where emerging moths were located

significantly (K–W ANOVA H(4, 90) = 18.020, P = 0.001; multiple comparison tests indicate that the Beach zone differs significantly from Mid and Hind zones (H = 3.23 and 3.73, P = 0.01 and 0.002)) no significant difference was found in median particle size between beach samples where emerging moths were found and samples from distinct beach zones (multiple tests, H = 0.83 to 2.22, P > 0.26 < 1.00). However, the sites where moths were found had larger particles than were found in the hind and mid zones and smaller beach material than that found in the beach zone (Fig. 2); a comparison of particle sizes indicated that emerging moths occupied areas where the largest proportion (c. 60%) of particles was between +500 μ m and 2 mm.

Discussion

A classic observation in phytophage ecology is the mismatch between insect and host plant distribution; the insect does not occur everywhere the plant is found or in the same concentrations where the plant occurs. In the study of the Sandhill Rustic on *E. juncea*, there are large areas on Loe Bar where the plant occurs and the moth is absent. As in many previous studies (e.g. Thomas et al. 2011), host quality is suspected to be the key factor. Distinct differences are apparent in plant status where the moth is found and where it does not occur. In particular, where the moth occurs, there is significantly greater cover of the host plant and a greater number of stems and rhizomes. But in this study it has been possible to go further and link up the host plant associations to substrate conditions (% bare ground) and levels of disturbance. The latter is distinguished by bar

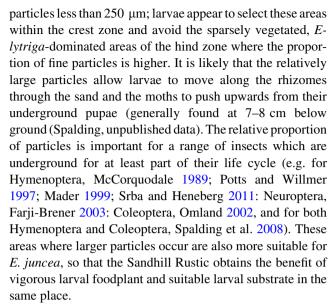


topography (beach zonation), vegetation community (plant associations) and beach particle composition. Disturbance on the site depends on wave action and wind. These are geomorphic processes which have a graded influence on bar topography, beach material, and therefore on plant colonization and competition, with the greatest impact in the tidal zone (beach zone). It is clear that the moth depends on host plant conditions held in a fine balance between disturbance and vegetation succession, but it may also be dependent on a particular balance of beach particle size.

The crucial factor for the Sandhill Rustic would appear to be the vigour of the host plant. Near the sea, Elytrigia juncea grows in areas of sparsely vegetated ground often with H. peploides and E. maritimum. This finding confirms the observation in Rodwell et al. (2000). Further from the sea, in the hind zone, its abundance reduces where groundcover, mat-forming plants occur; F. rubra in particular can probably out-compete E. juncea (Pemadasa and Lovell 1974). Clumps are joined by rhizomes underground in the crest zone, but in the hind zone these rhizomes have disappeared and the above ground clumping is an historic record of previous underground connectivity, the individual Elytrigia clumps having become isolated. These rhizomes are likely to have died through water and nutrient starvation (Watkinson et al. 1979). In addition, the number of *Elytrigia* stems diminishes as the clumps become less vigorous; the Elytrigia plants in the hind zone had fewer stems and appeared to be in the senile degenerative phase.

Analysis of the component particles that form the surface layer of Loe Bar indicate that this material can be broadly divided into two components, the shingle or coarse fraction (>2 mm) and the matrix or fine fraction (<2 mm), typical of this class of beach (Scott 1963; King 1972; Packham and Willis 1997). A greater proportion of the largest particles occur at the seaward edge, where wave-sorting leaves the coarser pebbles and carries the finer particles down with the back-wash (Steers 1954); no vegetation survives here owing to regular sorting by waves (Fuller 1987). The proportion of sand (1 mm-250 µm) increases with distance from the sea and there is a decrease in variation between particle size samples. E. juncea survives well in the crest zone where there is still regular disturbance but grows less well away from the sea where there is much reduced disturbance. Here, the greater stability and finer particles allow other plants to grow. The presence of plants such as F. rubra and S. uniflora may be evidence of the development of a high proportion of fine particles below 2 mm in diameter (Fuller 1987) and increased competition from open ground colonisers such as P. lanceolata, Leontodon autumnalis and A. millefolium growing here may act to reduce Elytrigia vigour (Preston et al. 2002).

Sandhill Rustics appear to prefer areas where a large proportion of particles are over 2 mm, with few finer



Near the sea, E. juncea plants have abundant rhizomes which provide underground connectivity and Sandhill Rustic larvae can occasionally be found feeding on these interconnecting rhizomes (Young, personal observation); it is likely that they move along these rhizomes from one plant to another. Without such connectivity, larvae would be unable to find other Elytrigia plants as these are scattered across the beach; it is likely that larvae would die unless the host clumps are vigorous enough to support them to pupation. The moth lays eggs in clusters and larvae are often found close together in the early stages (Spalding, unpublished data). Egg-clustering is predicted to require either large host plants or dense patches of host plants (García-Barros and Fartmann 2009); apparently isolated Elytrigia plants near the sea are in fact subgroups of very large plants connected underground. The plants in the hind zone have less underground connectivity and fewer stems and are therefore less able to support larvae to pupation.

Emerging Sandhill Rustics were found in sparsely vegetated areas where E. juncea occurs. The reasons that Sandhill Rustics avoid areas where other plants occur are not clear. Moths may prefer open ground where *Elytrigia* is easily located and vigorous. The presence of other plants may act to reduce the vigour of E. juncea and where thicker vegetation occurs in the hind zone, the substrate may be more tightly bound such that subterranean movement by larvae is restricted. There may be a number of other possible explanations, which could be the subject of further investigation. These areas may affect temperature, and thus growth and development, competition (rhizomes of other plants, especially *H. peploides*, may intertwine with the network of *E.* juncea rhizomes) and plant vigour, predation levels, or perhaps even penetration of the substrate and vegetation for pupation and eclosion.



Conservation implications

The findings of the study point to some clear management proposals for the moth and its host plant. Management should aim to create areas of bare ground with coarse, wellmixed shingle, extensive patches of vigorous E. juncea with good underground connectivity and few other matforming or competing plants. Such areas demand occasional disturbance and so may only be attainable just to the rear of the main beach zone, where the disturbance regime deters the establishment of other plant species. Disturbance by people may be considered beneficial in this situation. Consideration could also be given to identifying alternative sites based on the optimal criteria for hostplant and bare ground and carrying out a controlled introduction. Identification of alternative sites with suitable Elytrigia plants and particle size, or modification of other sites to accommodate the Sandhill Rustic moth, combined with a translocation, would help to increase the probability of this UK BAP Priority species persisting. Long term persistence on a single site is not guaranteed.

Acknowledgments The senior author would like to acknowledge the support of the National Trust, who own the site, permissions from Natural England and help in the field from Catriona Neil. We acknowledge the suggestions of unknown referees, whose contributions substantially improved this paper.

References

- Barbour DA, Young MR (1993) Ecology and conservation of the Kentish Glory moth (*Endromis versicolora* L.) in eastern Scotland. Entomologist 112:25–33
- Choong MF (1996) What makes a leaf tough and how this affects the patterns of *Castanopsis fissa* leaf consumption by caterpillars. Funct Ecol 10:668–674
- Dempster JP (1971) Some observations on a population of the Small Copper butterfly *Lycaena phlaeas* (Linnaeus) (Lep.: Lycaenidae). Ent Gaz 22:199–204
- Dempster JP, Pollard E (1981) Fluctuations in resource availability and insect populations. Oecologia 50:412–416
- Dennis RLH (1985) Choice of egg-laying sites in the Green-veined White butterfly (*Artogeia napi* (L.)) (Lep., Pieridae). Bull Amat Ent Soc 44:199–219
- Dennis RLH (2010) A resource-based habitat view for conservation: butterflies in the British Landscape. Wiley-Blackwell, Chichester
- Dennis RLH, Shreeve TG (1988) Hostplant-habitat structure and the evolution of butterfly mate-location behaviour. Zool J Linn Soc 94:301–318
- Dennis RLH, Sparks TH (2005) Landscape resources for the territorial nymphalid butterfly Inachis io: micro-site landform selection and behavioural responses to environmental conditions. J Insect Behav 18:725–742
- Dennis RLH, Shreeve TG, Van Dyck H (2003) Towards a resourcebased concept for habitat: a butterfly biology viewpoint. Oikos 102:417–426
- Emmet AM (1991) Chart showing the life history and habitats of the British Lepidoptera. In: Emmet AM, Heath J (eds) The moths

- and butterflies of Great Britain and Ireland, vol 10. Harley Books, Colchester
- Emmet AM, Langmaid JR (2002) The moths and butterflies of Great Britain and Ireland, vol 4(2). Harley Books, Colchester
- Farji-Brener AG (2003) Microhabitat selection by antlion larvae, *Myrmeleon crudelis*. Effect of soil particle size on pit-trap design and prey capture. J Insect Behav 16:783–796
- Feeny P (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:565–581
- Fowles AP, Bailey MP, Hale AD (2004) Trends in the recovery of a rosy marsh moth *Coenophila subrosea* (Lepidoptera, Noctuidae) population in response to fire and conservation management on a lowland mire. J Insect Conserv 8:149–158
- Fuller RM (1987) Vegetation establishment on shingle beaches. J Ecol 75:1077–1089
- García-Barros E, Fartmann T (2009) Butterfly oviposition sites: sites, behaviour and modes. In: Settele J, Shreeve TG, Konvička M, Van Dyck H (eds) Ecology of butterflies in Europe. Cambridge University Press, Cambridge, pp 29–42
- Gimingham CH (1964) Maritime and sub-maritime communities. In: Burnett HH (ed) The vegetation of Scotland. Oliver and Boyd, Edinburgh
- Harris D, Davy AJ (1986) Strandline colonization by *Elytrigia juncea* in relation to sand mobility and rabbit grazing. J Ecol 74: 1045–1056
- Harris D, Davy AJ (1987) Seedling growth in *Elytrigia juncea* after episodes of burial with sand. Ann Bot 60:587–593
- Haukioja E (1980) On the role of plant defences in the fluctuation of herbivore populations. Oikos 35:202–213
- JNCC (2011) Habitat action plan coastal vegetated shingle. (Originally published in 1999 in the UK Biodiversity Group Tranche 2 Action Plans—vol V: maritime species and habitats). JNCC, Peterborough
- Kershaw KA (1957) The use of cover and frequency in the detection of pattern in plant communities. Ecology 38:291–299
- Kershaw KA (1973) Quantitative and dynamic plant ecology. Edward Arnold, London
- Key R (2000) Bare ground and the conservation of invertebrates. Br Wildl 11:183–191
- King CAM (1972) Beaches and coasts. Arnold, London
- Lawton JH, Schroder D (1977) Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. Nature 265:137–140
- Mader D (1999) Geologische und biologische Entomoökologie der rezenten Seidenbiene Colletes. Entomoökologie der Nestbauten und Nistsubstrate der Seidenbiene Colletes daviesanus und anderer rezenter solitärer Wildbienen und Wespen in Buntsandstein, Rotliegend, Keuper, Lias, Dogger, Tertiär und Quartär. Band 1, Logabook, Koln
- McCorquodale DB (1989) Soil softness, nest initiation and nest sharing in the wasp, *Cerceris antipodes* (Hymenoptera: Sphecidae). Ecol Entom 14:191–196
- Omland KS (2002) Larval habitat and reintroduction site selection for *Cicindela puritana* in Connecticut. Northeast Nat 9:433–450
- Packham JR, Willis AJ (1997) Ecology of dunes, salt marsh and shingle. Chapman and Hall, London
- Pemadasa MA, Lovell PH (1974) Interference in populations of some dune annuals. J Ecol 62:855–872
- Potts SG, Willmer P (1997) Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. Ecol Entom 22:319–328
- Preston CE, Pearman DA, Dines TD (eds) (2002) New Atlas of the British and Irish Flora. Oxford University Press, Oxford
- Rodwell JS, Pigott CD, Ratcliffe DA, Malloch AJC, Birks HJB, Proctor MCF, Shimwell DW, Huntley JP, Radford E,



- Wiggington MJ, Wilkins P (2000) British plant communities, vol 5. Cambridge University Press, Cambridge
- Scott GAM (1963) The ecology of shingle beach plants. J Ecol 51:517-527
- Skinner B (2009) Colour identification guide to moths of the British Isles, 3rd edn. Apollo Books, Stenstrup
- Spalding A (1997) The use of the butterfly transect method for the study of the nocturnal moth *Luperina nickerlii leechi* Goater (Lepidoptera: Noctuidae) and its possible application to other species. Biol Conserv 80:147–152
- Spalding A (2002) In the field: searching for Sandhill Rustic. Atropos 17:50–52
- Spalding A, Parsons M (2004) Light trap transects—a field method for ascertaining the habitat preferences of night-flying Lepidoptera, using *Mythima turca* (Linnaeus 1761) (Lepidoptera: Noctuidae) as an example. J Insect Conserv 8:185–190
- Spalding A, Young M (2011) The persistence of the Sandhill Rustic moth *Luperina nickerlii* ssp. *leechi* (Lepidoptera: Noctuidae) at an isolated site in Cornwall, UK. Br J Ent Nat Hist 24:75–85
- Spalding A, Collins GA, Haes ECM (2008) Factors affecting the presence of insects on a small un-vegetated bank at an abandoned mining site in west Cornwall. Br J Ent Nat Hist 21:205–214

- Srba M, Heneberg P (2011) Nesting habitat segregation between closely related terricolous sphecid species (Hymenoptera:Spheciformes): key role of soil physical characteristics. J Insect Conserv. doi:10.1007/s10841-011-9441-4
- Steers JA (1954) The sea coast. The New Naturalist. Collins, London Stevenson PC, Blaney WM, Simmonds MJS, Wightman JA (1993) The identification and characterization of resistance in wild species of *Arachis* to *Spodoptera litura* (Lepidoptera: Noctuidae). Bull Entom Res 83:421–429
- Strong DR Jr, Levin DA (1979) Species richness of plant parasites and growth form of their hosts. Am Nat 114:1–22
- Sutton P (1999) The Scaly Cricket in Britain—a complete history from discovery to citizenship. Br Wildl 10:145–151
- Sykes MT, Wilson JB (1990) Dark tolerance in plants of dunes. Funct Ecol 4:799–805
- Thomas JA, Simcox DJ, Hovestadt T (2011) Evidence based conservation of butterflies. J Insect Conserv 15:241–258
- Watkinson AR, Huiskes AHL, Noble JC (1979) The demography of sand dune species with contrasting life cycles. In: Jeffries RL, Davy AJ (eds) Ecological processes in the coastal environment. Blackwell Scientific, Oxford

