

This is a repository copy of *Decline of a rare moth at its last known English site : causes and lessons for conservation*.

White Rose Research Online URL for this paper:
<https://eprints.whiterose.ac.uk/104242/>

Version: Accepted Version

Article:

Baker, David, Barrett, Sinead, Beale, Colin M. orcid.org/0000-0002-2960-5666 et al. (9 more authors) (2016) Decline of a rare moth at its last known English site : causes and lessons for conservation. PLoS ONE. e0157423. ISSN 1932-6203

<https://doi.org/10.1371/journal.pone.0157423>

Reuse

This article is distributed under the terms of the Creative Commons Attribution (CC BY) licence. This licence allows you to distribute, remix, tweak, and build upon the work, even commercially, as long as you credit the authors for the original work. More information and the full terms of the licence here:

<https://creativecommons.org/licenses/>

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

PLOS ONE

Decline of a rare moth at its last known English site: causes and lessons for conservation.

--Manuscript Draft--

Manuscript Number:	PONE-D-15-54651R1
Article Type:	Research Article
Full Title:	Decline of a rare moth at its last known English site: causes and lessons for conservation.
Short Title:	Decline of a rare moth
Corresponding Author:	Peter J Mayhew University of York York, North Yorkshire UNITED KINGDOM
Keywords:	conservation; grazing management; habitat management; heathland; insect population; Lepidoptera; population monitoring; rare species
Abstract:	<p>The conditions required by rare species are often only approximately known. Monitoring such species over time can help refine management of their protected areas. We report population trends of a rare moth, the Dark Bordered Beauty <i>Epione vespertaria</i> (Linnaeus, 1767) (Lepidoptera: Geometridae) at its last known English site on a protected lowland heath, and those of its host-plant, <i>Salix repens</i> (L.) (Malpighiales: Salicaceae). Between 2007 and 2014, adult moth density reduced by an average of 30-35% annually over the monitored area, and its range over the monitored area contracted in concert. By comparing data from before this decline (2005) with data taken in 2013, we show that the density of host-plants over the monitored area reduced three-fold overall, and ten-fold in the areas of highest host-plant density. In addition, plants were significantly smaller in 2013. In 2005, moth larvae tended to be found on plants that were significantly larger than average at the time. By 2013, far fewer plants were of an equivalent size. This suggests that the rapid decline of the moth population coincides with, and is likely driven by, changes in the host-plant population. Why the host-plant population has changed remains less certain, but fire, frost damage and grazing damage have probably contributed. It is likely that a reduction in grazing pressure in parts of the site would aid host-plant recovery, although grazing remains an important site management activity. Our work confirms the value of constant monitoring of rare or priority insect species, of the risks posed to species with few populations even when their populations are large, of the potential conflict between bespoke management for species and generic management of habitats, and hence the value of refining our knowledge of rare species' requirements so that their needs can be incorporated into the management of protected areas.</p>
Order of Authors:	David Baker Sinead Barrett Colin M Beale Terry J Crawford Sam Ellis Tallulah Gullett Peter J Mayhew Mark S Parsons Penny Relf Paul Robertson Julian Small Dave Wainwright
Opposed Reviewers:	

Response to Reviewers:

Reviewer #2: This is an interesting paper that describes the decline of a rare species in a managed and protected habitat and it draws on this case history to provide a thoughtful discussion of several issues regarding the management of threatened species that are likely to be of wide interest to conservation biologists.

The manuscript is clearly written, and the discussions of the data are generally appropriate and cautious. However I believe that there are two sections in which the authors need to provide a more rigorous and comprehensive interpretation or analysis of their data.

Firstly, with respect to the regression analysis described in lines 307-316 and Fig. 5. For this analysis, four points (ca. 20% of the data) were labelled as "outliers" without adequate explanation and removed from the analysis. This seems (given the lack of explanation) to have been done on a purely ad-hoc basis, perhaps because these four points did not fall along the otherwise pleasingly linear relationship described by the fitted regression. More justification of this analysis is needed - why didn't the authors fit a non-linear regression, for example. WHY were these points considered as "outliers", rather than them simply being evidence that a linear relationship was not a good description of the data?

Response: We redid the linear regression testing for outliers, and indeed none of the datapoints are statistical outliers. However, the pattern of residuals strongly suggested non-linearity, so we conducted a polynomial regression in R, and the lowest AIC score (by >2 units from a simpler model) came from a cubic model which gave a good pattern of residuals, no outliers or influential datapoints, and an r-squared over double that of the linear model. We have thus reported and graphed this in the methods and results, and modified Figure 5 to accommodate it.

Secondly, the authors suggest that the decline in this moth species may largely be due to changes in the abundance and size/shape of its host plant *Salix repens* (and this is perhaps the main point of this paper). With respect to the latter variable, they test the difference in a principal component score (PC1) between 2005 patches with larvae and 2005 random patches (lines 341 and 342, A in Fig. 7) and find a significant difference. However when a subset of the 2005 (? - says 2005 on line 355, and 2013 on line 359) data was used ("to rule out the potential for biases in host-plant quality comparisons", C in Fig. 7) this pairwise comparison was not reported but the medians of these two groups appear to be very similar. It is therefore misleading to claim "This was the same finding as for the original full dataset" because only the significance of the difference between the three groups "2005 with larvae", "2005 random" and "2013" was reported, and the most pertinent comparison to test whether the moths prefer large plants (that between "2005 with larvae" and "2005 random" plants) was not reported for the restricted data set. It would seem that the similarity of the medians of these groups weakens the authors' claim that changes in the availability of large host-plant patches are linked to the moth's decline, and this comparison should be presented and more fully discussed.

Response: The reference to 2013 was a typo: it should have been 2005 and has been changed. The sentence about the "same finding" refers to the overall Kruskal-Wallis result and the comparison immediately beforehand, which refers to the difference between the 2005 random plants and 2013 plants. This is the same as for the whole dataset, so the sentence should stand. We have now tested the pairwise comparison between the 2005 random plants and 2005 plants with larvae in the restricted dataset and reported it, and it is indeed non-significant. We see your point that this might appear to weaken the overall claim that it is changes in the availability of large plants that is linked to the moth decline. However, the restricted dataset was performed to more fairly compare the 2005 (random) and 2013 plants, because the 2013 plants came from only that area, and was conducted in order to see if plant size declined overall between 2005 and 2013. The pairwise comparisons bear this out, insofar as the data go (the sample size of random plants is only 5). If we wished to test whether moth larvae are found on larger plants than random across the whole common in 2005, the larger dataset is clearly preferable from a sample size perspective and a sample fairness perspective.

As to why the comparison between 2005 random and 2005 plants with larvae is apparently different in the restricted dataset and the larger dataset: the probable

	<p>reason is that over the transect as a whole, plants were genuinely rather large in 2005 (see the box plots), but remember that this route was chosen after 2005 deliberately to cover areas where the moth was most common. We have added a clarifying sentence to the results to make this point. However, the restricted data are not very well suited for testing this question rigorously (small sample size in 2005 random plants) so we do not think that much emphasis should be placed on this "finding".</p> <p>Other minor points follow:- lines 50-51 - reword?</p> <p>Response: Yes, we see the point and have reworded.</p> <p>lines 127-129 - move Acknowledgements</p> <p>Response: actually we were specifically required to put this statement here by the editorial team at submission to comply with the journal rules on permissions.</p> <p>line 144 - unclear what a 'transect section' is.</p> <p>Response: The legend is now elaborated to explain what this is.</p> <p>line 240 - change to 'produce estimates of densities'</p> <p>Response: change made</p> <p>Fig.3 - would be nice to see some indication of error associated with the regression lines.</p> <p>Response: Figure 3 did not previously show the regression lines, but these are reported in the text. We have now changed the figure to show one of the regression lines and confidence bands for each subfigure (it's too messy if you show them all), and have added confidence estimates of the regression slopes to the text.</p> <p>line 291 - 'estimate' rather than 'calculate'?</p> <p>Response: change made</p> <p>line 359 'reduce' rather than 'rule out' ? esp. see above!</p> <p>Response: change made</p> <p>line 456. "and consequently <i>E. vespertaria</i>" - your interpretation, not an established fact, otherwise we wouldn't need this paper!</p> <p>Response: we have deleted the final clause of the sentence.</p>
Additional Information:	
Question	Response
<p>Financial Disclosure</p> <p>Please describe all sources of funding that have supported your work. A complete funding statement should do the following:</p> <p>Include grant numbers and the URLs of any funder's website. Use the full name, not acronyms, of funding institutions, and use initials to identify authors who received the funding.</p> <p>Describe the role of any sponsors or</p>	<p>This work was supported by : A Natural England grant (https://www.gov.uk/government/organisations/natural-england), S41 – Action for Moths, current ref. ECM108 to MSP.</p> <p>A Royal Society for the Protection of Birds Biodiversity Grant to MSP.</p> <p>A First TransPennine Express and Forestry Commission Green Grant (http://www.tpexpress.co.uk/mediafile/1480/4001-transpennine-network-green-grants-proof-2.pdf) to DW.</p> <p>The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript</p>

<p>funders in the study design, data collection and analysis, decision to publish, or preparation of the manuscript. If they had no role in any of the above, include this sentence at the end of your statement: "<i>The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.</i>"</p> <p>If the study was unfunded, provide a statement that clearly indicates this, for example: "<i>The author(s) received no specific funding for this work.</i>"</p> <p>* typeset</p>	
<p>Competing Interests</p> <p>You are responsible for recognizing and disclosing on behalf of all authors any competing interest that could be perceived to bias their work, acknowledging all financial support and any other relevant financial or non-financial competing interests.</p> <p>Do any authors of this manuscript have competing interests (as described in the PLOS Policy on Declaration and Evaluation of Competing Interests)?</p> <p>If yes, please provide details about any and all competing interests in the box below. Your response should begin with this statement: <i>I have read the journal's policy and the authors of this manuscript have the following competing interests:</i></p> <p>If no authors have any competing interests to declare, please enter this statement in the box: "<i>The authors have declared that no competing interests exist.</i>"</p> <p>* typeset</p>	<p>The authors have declared that no competing interests exist.</p>
<p>Ethics Statement</p> <p>You must provide an ethics statement if your study involved human participants, specimens or tissue samples, or</p>	<p>We are grateful to the Yorkshire Wildlife Trust and UK Ministry of Defence for permission to work on their land, and the Yorkshire Wildlife Trust for participation in survey work.</p>

vertebrate animals, embryos or tissues. All information entered here should **also be included in the Methods section** of your manuscript. Please write "N/A" if your study does not require an ethics statement.

Human Subject Research (involved human participants and/or tissue)

All research involving human participants must have been approved by the authors' Institutional Review Board (IRB) or an equivalent committee, and all clinical investigation must have been conducted according to the principles expressed in the [Declaration of Helsinki](#). Informed consent, written or oral, should also have been obtained from the participants. If no consent was given, the reason must be explained (e.g. the data were analyzed anonymously) and reported. The form of consent (written/oral), or reason for lack of consent, should be indicated in the Methods section of your manuscript.

Please enter the name of the IRB or Ethics Committee that approved this study in the space below. Include the approval number and/or a statement indicating approval of this research.

Animal Research (involved vertebrate animals, embryos or tissues)

All animal work must have been conducted according to relevant national and international guidelines. If your study involved non-human primates, you must provide details regarding animal welfare and steps taken to ameliorate suffering; this is in accordance with the recommendations of the Weatherall report, "[The use of non-human primates in research](#)." The relevant guidelines followed and the committee that approved the study should be identified in the ethics statement.

If anesthesia, euthanasia or any kind of animal sacrifice is part of the study, please include briefly in your statement which substances and/or methods were applied.

Please enter the name of your Institutional Animal Care and Use Committee (IACUC) or other relevant ethics board, and indicate whether they approved this research or granted a formal waiver of ethical approval. Also include an approval number if one was obtained.

Field Permit

Please indicate the name of the institution or the relevant body that granted permission.

Data Availability

PLOS journals require authors to make all data underlying the findings described in their manuscript fully available, without restriction and from the time of publication, with only rare exceptions to address legal and ethical concerns (see the [PLOS Data Policy](#) and [FAQ](#) for further details). When submitting a manuscript, authors must provide a Data Availability Statement that describes where the data underlying their manuscript can be found.

Your answers to the following constitute your statement about data availability and will be included with the article in the event of publication. **Please note that simply stating 'data available on request from the author' is not acceptable. If, however, your data are only available upon request from the author(s), you must answer "No" to the first question below, and explain your exceptional situation in the text box provided.**

Do the authors confirm that all data underlying the findings described in their manuscript are fully available without restriction?

Please describe where your data may be found, writing in full sentences. **Your answers should be entered into the box below and will be published in the form you provide them, if your manuscript is accepted.** If you are copying our sample text below, please ensure you replace any instances of XXX with the appropriate details.

If your data are all contained within the paper and/or Supporting Information files, please state this in your answer below.

Yes - all data are fully available without restriction

All relevant data are within the paper and its Supporting Information files.

For example, "All relevant data are within the paper and its Supporting Information files."

If your data are held or will be held in a public repository, include URLs, accession numbers or DOIs. For example, "All XXX files are available from the XXX database (accession number(s) XXX, XXX)." If this information will only be available after acceptance, please indicate this by ticking the box below.

If neither of these applies but you are able to provide details of access elsewhere, with or without limitations, please do so in the box below. For example:

"Data are available from the XXX Institutional Data Access / Ethics Committee for researchers who meet the criteria for access to confidential data."

"Data are from the XXX study whose authors may be contacted at XXX."

* typeset

Additional data availability information:

THE UNIVERSITY *of York*

DEPARTMENT OF BIOLOGY
Heslington, York YO10 5DD U K

Tel: 01904 328644
e-mail peter.mayhew@york.ac.uk

23rd May 2016

Dear Editor,

On behalf of my co-authors I am writing to submit our revised manuscript for publication in PLOS ONE as a research article entitled “Decline of a rare moth at its last known English site: causes and lessons for conservation”. Our responses to the referee’s suggestions are also enclosed.

Yours faithfully,



Dr Peter Mayhew.

Decline of a rare moth at its last known English site: causes and lessons for conservation.

David Baker^{1,2}, Sinead Barrett³, Colin M. Beale³, Terry J. Crawford^{1,3}, Sam Ellis⁴, Tallulah Gullett³, Peter J. Mayhew^{3*}, Mark S. Parsons⁴, Penny Relf^{1,2}, Paul Robertson³, Julian Small⁵ and Dave Wainwright⁴.

¹Yorkshire Naturalists' Union Lepidoptera Group, Yorkshire Naturalists' Union, York, UK

²Butterfly Conservation, Yorkshire Branch, York, UK.

³Department of Biology, University of York, York, UK

⁴Butterfly Conservation, East Lulworth, Wareham, Dorset, UK

⁵Natural England, York, UK

*Correspondence author

peter.mayhew@york.ac.uk

Abstract

The conditions required by rare species are often only approximately known. Monitoring such species over time can help refine management of their protected areas. We report population trends of a rare moth, the Dark Bordered Beauty *Epione vespertaria* (Linnaeus, 1767) (Lepidoptera: Geometridae) at its last known English site on a protected lowland heath, and those of its host-plant, *Salix repens* (L.) (Malpighiales: Salicaceae). Between 2007 and 2014, adult moth density reduced by an average of 30-35% annually over the monitored area, and its range over the monitored area contracted in concert. By comparing data from before this decline (2005) with data taken in 2013, we show that the density of host-plants over the monitored area reduced three-fold overall, and ten-fold in the areas of highest host-plant density. In addition, plants were significantly smaller in 2013. In 2005, moth larvae tended to be found on plants that were significantly larger than average at the time. By 2013, far fewer plants were of an equivalent size. This suggests that the rapid decline of the moth population coincides with, and is likely driven by, changes in the host-plant population. Why the host-plant population has changed remains less certain, but fire, frost damage and grazing damage have probably contributed. It is likely that a reduction in grazing pressure in parts of the site would aid host-plant recovery, although grazing remains an important site management activity. Our work confirms the value of constant monitoring of rare or priority insect species, of the risks posed to species with few populations even when their populations are large, of the potential conflict between bespoke management for species and generic management of habitats, and hence the value of refining our knowledge of rare species' requirements so that their needs can be incorporated into the management of protected areas.

27

28

Introduction

29

30

31

32

33

34

35

36

37

38

The 1992 Convention on Biological Diversity articulated a legal obligation for signatory countries to conserve their biodiversity [1], following widespread recognition of ongoing and increasing threats to biodiversity globally (summarized in [2–3]), and mindful of the strong link between biodiversity and human well-being. In response to the requirements of the convention, the UK, alongside other signatory countries, developed a National Biodiversity Action Plan (BAP), in which priority species and habitats were identified [4]. The listing of priority species and habitats was retained in the Natural Environment and Rural Communities (NERC) Act 2006, which superseded the national BAP. The priority species lists drew heavily on IUCN Red List criteria as applied in the UK species Red Lists (e.g. [5–7]).

39

40

41

42

43

44

45

46

47

48

49

Of the many challenges raised by attempting to meet the obligations of the 1992 convention, one of the greatest is to gather adequate knowledge of the habitat requirements of priority species, because of the sheer volume of such species (the last national BAP listed 1,149 in the UK) [4]. Knowledge of these requirements assists appropriate management of key sites. Because priority habitats tend to be managed to maintain communities of typical plant species, but not necessarily other species, optimal management for priority species and habitats may conflict. Here we report findings from population monitoring of a priority Lepidoptera species on a priority habitat that is managed for its conservation interest. Our results illustrate the value of ongoing monitoring of rare species, even at sites managed for conservation, and of potential conflict between generic habitat management and the needs of particular priority species.

50

51

52

53

54

55

56

57

58

59

60

Lowland heathland habitats are valued for their biodiversity and landscape, for recreation, and for agriculture [8]. They are a UK priority habitat [9] and are also designated as an Annex I habitat under the European Habitats Directive. The UK contains 20% of the total global area of this habitat [10]. However, just 16% of the total area of UK lowland heathlands existing in 1800 still remained in 2002 [10] due to changes in land use [11]. Lowland heathlands support populations of rare species, including specialist plants, birds, reptiles, and invertebrates, including Lepidoptera [12–17]. In the UK, lowland heathlands are a semi-natural habitat maintained by interference with the process of succession, via burning, grazing or cutting [18–21]. However, lowland heathlands are also the protected habitat category in the worst condition in the UK, with only 18% of heathland Sites of Special Scientific Interest (SSSIs) and Special

61 Areas of Conservation (SACs) in favourable condition, due to sub-optimal management
62 [22]. Different heathland species often have very different micro-habitat requirements
63 [23], and optimal management generally attempts to maintain a mosaic of different
64 successional stages that are suitable for a wide range of species.

65 Four substantial remnants of lowland heathland remain in the Vale of York in the
66 UK, all on former common lands — Allerthorpe, Skipwith, South Cliffe, and Strensall
67 Commons — all of which are SSSIs. Skipwith Common is also a National Nature
68 Reserve and SAC, whilst Strensall Common is an SAC. Parts of Allerthorpe Common
69 and Strensall Common are managed as nature reserves by the Yorkshire Wildlife Trust
70 (YWT). Strensall Common, the focus of this study, occupies 570 ha about 10km north of
71 York. Forty-five ha of the north-eastern part comprise the Yorkshire Wildlife Trust
72 reserve. Most of the rest of the land is owned by the UK Ministry of Defence and used
73 for military training, whilst about 10 ha of the eastern portion is managed by the UK
74 Forestry Commission. About 70% of the land is a mosaic of wet and dry heathland, with
75 most of the remainder being deciduous and ‘carr’ woodland. The heathland is the reason
76 for the SAC designation under Annex 1 of the EC Habitats Directive. The site has been
77 ranked as the third most important Lepidoptera site in Yorkshire [24]. Current
78 management includes sheep grazing from spring to autumn by a tenant farmer and
79 periodic scrub and tree removal by cutting to maintain a mosaic of different stages of
80 succession.

81 The Lepidoptera comprise one of the most species-rich orders of insects and are a
82 major component of terrestrial biodiversity [25]. In the UK, many species have seen
83 large population and range declines in the last few decades [26–27] and lepidopterans are
84 thought to be sensitive indicators of environmental change because many of them have
85 very specialized habitat requirements and have shown rapid range, phenological and
86 population responses to a range of factors [28–32]. In addition, their popularity with
87 amateur naturalists, along with the existence of organized monitoring schemes, means
88 that data on distribution and abundance trends are relatively rich, and they are ideal
89 flagship taxa with which to galvanize conservation effort [33].

90 In England, the Dark Bordered Beauty moth, *Epione vespertaria* (Geometridae:
91 Ennominae) (Fig 1) is currently confined to one site, Strensall Common, where it has
92 been known and collected since the 19th Century [34]. Until recently it was also found at
93 Newham Bog in Northumberland, where it is now considered extinct [35]. There are also
94 three known sites in Scotland, where the populations have a somewhat different ecology,

95 feeding on Aspen, *Populus tremula* [36], as opposed to Creeping Willow *Salix repens* in
96 England. *E. vespertaria* is listed as ‘Rare’ in the UK Red Data Book [6] and is listed as a
97 priority species because of the low number of populations, some of small size, and loss
98 of some populations due to suboptimal management [37].
99

100 **Fig 1. *Epione vespertaria*** (A) male and (B) female photographed at Strensall Common.
101

102 *E. vespertaria* is univoltine, with adults flying in July and early August [38]. At
103 Strensall Common, males can be seen flying over the vegetation searching for females
104 after sunrise, and take flight at other times of the day if disturbed, whilst females remain
105 hidden in vegetation during the day and are less easily detected. Both sexes are attracted
106 to light at night. The eggs are laid on host-plant stems, and stay on the host-plant over
107 winter, hatching in late spring the next year, developing through rapid larval and pupal
108 stages.

109 At Strensall Common, the SAC management plan calls for maintenance of a
110 typical plant species complement for this habitat, and focuses on control of scrub
111 invasion as a major threat, but includes no management action specific to *E. vespertaria*
112 [39]. Until recently, the population was thought to be healthy: just prior to the current
113 work, Robertson et al. [38] estimated the population of adults to be 500-1000 individuals
114 spread widely over the Common. As a result, the City of York Local Biodiversity Action
115 Plan does not include a Species Action Plan (SAP) for *E. vespertaria*, because it was not
116 considered threatened at the site, provided that current management was maintained [40].
117 The National SAP called for ten viable populations of the moth to be established by 2010
118 [37]. This aim was not met. However, other actions have been successfully implemented:
119 for example a regular monitoring transect was implemented at Strensall Common, in
120 2007, following work to identify the most important areas of the Common for the moth
121 [38]. In this paper we summarize some of the findings of this monitoring work and
122 subsequent work to establish underlying causes of the population changes. Our results
123 have implications for the management of *E. vespertaria*, and more generally for rare
124 species in protected areas.
125

126
127
128
129
130
131
132
133
134
135
136
137
138
139
140
141
142
143
144
145
146
147
148
149
150
151
152
153
154
155
156
157
158

Materials and Methods

We are grateful to the Yorkshire Wildlife Trust and UK Ministry of Defence for permission to work on their land, and the Yorkshire Wildlife Trust for participation in survey work.

Salix repens density in 2005

This study was conducted on the northern part of Strensall Common (OS grid cells SE6560 and 6561) where there is unrestricted public access (the area to the south is used for military training and access is restricted) (Fig 2). In 2005, to determine the most important locations of the Common for *E. vespertaria*, density estimates of *S. repens* patches were made for the whole of the northern part of the Common [38]. Rhizomatous growth in *S. repens* precludes easy identification of individual plants. Instead, discrete growth patches were identified [38]. Fifty 200m transects were walked from 3rd June to 17th June 2005 with east-to-west orientations, and with starting locations chosen by random number generation. The number of host plant patches within 2.5m either side of the route was counted every 50m, giving estimates of density in 200 spatial cells.

Fig 2. The northern part of Strensall Common, and surroundings. Grid references are British Grid Coordinates (the ‘4’ prefix refers to position in square ‘SE’ in the OS Grid), and the *E. vespertaria* transect route is marked, with transect sections (parts of the walk in which adults are recorded separately to get fine scale spatial distribution data) numbered. Transect sections 9–11 are separate from the other sections near the junction of Lords Moor Lane and the railway.

Salix repens morphology in 2005

Plant morphological measures (Table 1) were taken in 2005 to establish host-plant preferences of *E. vespertaria*. Larvae are hard to find, therefore to identify adequate samples of patches hosting larvae, a two-phase adaptive sampling technique was used. Patches were sampled from a selection of 44 randomly chosen locations across the northern part of the Common stratified by patch density from the above transect data. All these were thoroughly searched to assess the presence/absence of *E. vespertaria* larvae, and larvae were located in only four of these patches found in three distinct locations (corresponding to sections 3, 8, and 9-11 on the population monitoring transect described below and in Fig 2). In a second phase of searching, to increase the sample size of

159 patches hosting larvae, three 10ha plots were chosen for more systematic searches at the
 160 above three locations. At the centre of each of these plots was a patch on which initial
 161 searches had revealed larval presence. A spiral transect, 5m wide, was walked around
 162 this patch and all *S. repens* patches encountered were searched. The transect was
 163 terminated when more than an hour had elapsed without finding a larva. Sampling for
 164 larval presence was performed from 22nd – 30th June 2005. This raised the number of
 165 patches recorded hosting larvae to 32. To provide a balanced dataset, 32 patches were
 166 randomly sampled from the original 40 patches without larvae. Selected patches with and
 167 without larvae were then tagged and measured as in Table 1.

168 **Table 1. Measurements of *Salix repens* patch morphology**
 169
 170

Variable	Description	Value	Data Type	Method Details
Max Height	Height of tallest stem within a patch.	To an accuracy of 0.5cm	Continuous	Tape measure
Mean Height	Average height from max height and six other stem heights (where possible) – 3 taller stems and 3 shorter stems.	To an accuracy of 0.5cm	Continuous	Tape measure
Max Width	Greatest distance across a patch.	To an accuracy of 0.5cm	Continuous	Tape measure
Mean Leaf Length	Average length of leaves calculated from six individual leaf length measurements.	Measurements accurate to 1mm, mean calculated to 2 d.p.	Continuous	Tape measure – measure the 4 th leaf from the apex if possible. If unable to use 4 th leaf, the 5 th leaf was used.
Mean Leaf Density	The average number of leaves along a 10cm length of stem calculated from 3 separate counts from randomly chosen stems.	1 - ∞	Continuous	Tape measure, visual survey – measure a 10cm stretch of stem from the midpoint between apical leaves and first subsequent leaves. If less than 10cm, 5cm or 2cm lengths of stem were used and multiplied up to a standard 10cm length.
Number of Stems	The number of stems present within a patch.	1 - ∞	Integer	Visual survey
Patch Area	Index of planar area covered by patch, as a function of maximum patch width, W_{max} . The index is an estimate based on the assumption of a circular patch morphology.	1– ∞ cm ²	Continuous	$A=\pi(W_{max}/2)^2$
Patch Volume	Index of volume occupied by foliage, as a function of patch radius. Radius estimated as a combined function of maximum patch width, W_{max} , and maximum patch height, Z_{max} .	1– ∞ cm ²	Continuous	$V=2/3\pi[((W_{max}/2)+Z_{max})/2]^3$

171

172

173

174

***Epione vespertaria* population monitoring**

175

176

177

178

179

180

181

182

183

184

185

186

187

188

189

190

191

192

193

In 2007 a transect walk, modified from the UK Butterfly Monitoring Scheme (UKBMS) guidelines, was established to cover areas of high moth and host-plant density identified by Robertson et al. [38], but also taking in other areas of the northern part of the Common (Fig 2, SI Appendix). The route was walked at least twice weekly during the adult flight season, from the end of June until moths were no longer apparent, normally at the end of July or early August. All identifiable adult macrolepidoptera seen within 2.5m of the walker were recorded. To facilitate flushing of resting moths, walkers deviated up to 10m from the main route to include patches of *S. repens*, and the walk was conducted between 7 and 10am. Where possible, favourable weather conditions were preferred (warm, sunny, low wind-speed), and temperature and wind-speed were recorded. The walk was 2km long and was divided into 11 sections of between 100m and 275m, with boundaries based on major directional changes and landmarks (Fig 2). Sections 4, 5, and 6 were first added to the transect in 2008 following observations of moths in that vicinity. Sections 9–11 (Fig 2), on the YWT reserve, were included partly because this was where *E. vespertaria* was commonly regarded by the public as easy to find. However, following extinction of the moth in sections 9–11 many walks were terminated at section 8, although several walks each year continued to cover these sections to ensure that the moth was still absent (SI Dataset).

194

***Salix repens* morphology and density in 2013**

195

196

197

198

199

200

201

202

203

204

205

206

The location of *S. repens* patches on the monitoring transect was recorded with a hand-held GPS unit providing readings to the nearest 1m, including patches within 5m of the transect route, between 6th August and 3rd October 2013. Patches were defined as a stem or collection of stems isolated from other stems by at least 30cm. A subsample of the recorded patches was selected for measurement of host-plant morphology, stratified by patch density. In transect sections with fewer than ten patches, all patches were measured; in transect sections with between ten and 20 patches, ten patches were randomly selected and measured; and 20 for those sections with 20 or more (total measured =159). Size and other structural variables were quantified (Table 1). Plant morphology was also quantified at three other locations on the Common at which concentrations of adult moths had been observed in 2013. Two of these sites (named “Kidney Pond” and “Wild Goose Carr” on Ordnance Survey maps, grid refs SE 653597

207 and SE 655595) lie to the south of the studied area in the area restricted for military
208 training (20 patches for each location). The other site lies 15 metres east of the junction
209 between transect sections 2 and 3 (four patches).

210

211 **Data analysis**

212 To test whether adult *E. vespertaria* density had reduced over time, four summary
213 statistics were first compiled from the transect data for each year: (1) the peak count
214 overall for years 2008–2014; (2) the peak count, but omitting sections 4–6, for 2007–
215 2014; (3) the sum, from sections 1 to 11, of the mean count for each section between first
216 and last moth observation dates each year, for years 2008–2014; and (4) the same as (3)
217 but omitting sections 4–6, for years 2007–2014. The natural logarithm of these values
218 was then calculated. Ideally, to test for trends in density over time, one would apply time
219 series statistics to these data to take account of autocorrelation, but the short series
220 preclude this, and analyses were thus limited to simple parametric tests. Linear
221 regressions of all the \ln -transformed summary statistics against year were performed.
222 Although this assumes a lack of autocorrelation in the data, meaning that probabilities are
223 probably inflated, the regression slopes remain informative about the rate of density
224 change.

225 To account for differences in sampling methodology and the limited extent of
226 shared sampling area, comparison of the density of *S. repens* patches along the
227 monitoring transect in 2013 and 2005 required spatial interpolations, which were used to
228 estimate density values in 2005 at unsampled sites from the density data collected on the
229 50 transects that year. Four methods of spatial interpolation were performed for the 2005
230 data in QGIS at a cell size of 25x25m – inverse distance weighting (IDW) on
231 untransformed and \log_{10} -transformed data, and thin plate spline (TPS) on untransformed
232 and \log_{10} -transformed data.

233 The performance of spatial interpolations may be affected by various factors,
234 such as data normality and sample clustering [41]. Therefore, cross-validation was
235 performed to establish which interpolation method yielded the lowest mean-squared-
236 error (MSE). Ten-fold cross-validation was performed by sequentially leaving out a
237 randomly selected 10% of the data, performing the spatial interpolation on the remaining
238 90%, and calculating how close the interpolated density values at the missing 10% points
239 were to the actual density values. This was repeated 10 times for each spatial
240 interpolation method to allow calculation of a MSE for each interpolation method.

241 Kernel density interpolation was performed in R for the 2013 point data to produce
242 estimates of densities of the foodplant throughout the monitoring transect ha⁻¹. The
243 resolution of the 2005 data (100m transects with point measurements every 25m) provide
244 the scale limit for this analysis: we extracted the interpolated density for all 25 x 25 m
245 cells that had more than 50% overlap with the 2013 data (a total of 64 cells). Because the
246 finest scale resolution is the most uncertain estimate of density for 2013, we repeated the
247 extraction after first aggregating to 50 m resolution (resulting in 21 overlapping cells,
248 data reported in results), but the findings are very similar to an analysis at 25m
249 resolution. R packages used for the comparison were rgdal [42], maptools [43], spatstat
250 [44] and raster [45].

251 To explore the relationship between patch density in 2013 and interpolated patch
252 density in 2005, linear regression was performed. Since this produced a pattern of
253 residuals suggesting non-linearity, polynomial regression was performed in R, fitting
254 models of increasing numbers of power terms until the model AIC score no longer
255 reduced. The chosen best model was the simplest model within two AIC units of the
256 model with the lowest AIC score.

257 To explore the variation in plant morphology between the plant patches measured
258 in 2013, patches hosting larvae in 2005, and randomly chosen patches without larvae in
259 2005, Principal Component Analysis (PCA) was performed in R using the packages
260 devtools [46], car [47] and ggbiplot [48]. Standardised values (number of standard
261 deviations away from the mean value) were used to facilitate comparison of variables
262 with different units. A non-parametric one-way ANOVA (Kruskal-Wallis) was
263 performed to compare host-plant characteristics between ‘2013’ patches, ‘2005’ random
264 patches without larvae, and ‘2005’ patches with larvae. To test whether any changes in
265 morphology are restricted to the area of transect sections 1-8, the plants measured in
266 sections 9–11 in 2013 were compared separately with the six randomly chosen plants
267 measured there in 2005.

268

269

Results

270

Adult moth density changes

271

Linear regressions of all the *ln*-transformed summary statistics against year indicate

272

strong declines in adult moth density, which are approximately linear on a log scale,

273

indicating that a relatively constant proportion of the population has been lost annually

274

over the monitoring period (Fig 3). The regression slopes indicate that this proportion is

275

30-35% annually (Peak count: $y = 506.5 - 0.45x$, $95\%CI(b) = -0.633, -0.265$, $r^2 = 0.89$,

276

$F_{(1,5)} = 39.6$, $p = 0.001$; peak count omitting sections 4-6: $y = 892.4 - 0.44x$, $95\%CI(b) =$

277

$-0.558, -0.327$, $r^2 = 0.94$, $F_{(1,6)} = 88.0$, $p < 0.001$; sum of mean counts per section: $y =$

278

$760.5 - 0.38x$, $95\%CI(b) = -0.579, -0.174$, $r^2 = 0.82$, $F_{(1,5)} = 23.0$, $p = 0.005$; sum of

279

mean counts per section omitting sections 4-6: $y = 723.2 - 0.36x$, $95\%CI(b) = -0.498, -$

280

0.219 , $r^2 = 0.87$, $F_{(1,6)} = 39.9$, $p = 0.001$). Although there is no clear non-linearity to the

281

decline (Fig 3), there is also no strong decline in the initial three survey years. If the

282

decline is considered to begin in 2010 (and possibly to level-off in 2012) then the rate of

283

decline would be higher than estimated above. In addition to reductions in density over

284

time, there were reductions in the moth range measured by the number of transect

285

sections in which adults were observed (sections = $1730.3 - 0.86 \cdot \text{year}$, $r^2 = 0.69$, $F_{(1,5)} =$

286

11.25 , $p = 0.02$). In 2008, adults were seen over all 11 sections (see SI Dataset). That

287

was the last year in which adults were recorded from section 1. Furthermore, with the

288

exception of a single individual in 2010, no adults were recorded after 2008 in sections

289

9–11. The moth then disappeared from section 2 in 2012. No moths were seen in

290

sections 5 and 6 in 2014, and in every year the mean count per walk has been highest in

291

section 3. This is consistent with retraction in range over the monitored area towards a

292

core area.

293

294

Fig 3. Adult *E. vespertaria* density (natural logarithms) through time from transect

295

surveys. (A) peak counts and (B) sum of the mean counts for each transect section. Open

296

symbols are data for all sections combined, whilst closed symbols omit transect sections

297

4–6 which were first walked in 2008. Solid lines are the linear regressions through the

298

closed symbols, and the curves are the narrow-band (slope) 95% confidence limits on

299

those regressions.

300

301

Host-plant density changes

302 The untransformed TPS interpolation yielded the lowest MSE (Table 2), and was
 303 therefore used to estimate host-plant density (Fig 4). A linear regression of predicted
 304 host-plant density against actual host-plant density from the cross validations showed
 305 that there was a significant relationship between the two ($F_{(1,198)} = 270.5, p < 0.001$),
 306 and that there was a tendency to overestimate low densities and underestimate high
 307 densities in the predicted values compared to actual values (predicted = $62.9 +$
 308 $0.67 \cdot \text{observed}$, $r^2 = 0.577$). The host-plant was patchily distributed in 2005, with high-
 309 density patches located close to parts of the route subsequently chosen for the transect,
 310 and low-density areas across the eastern part of the site (Fig 4). A small number of
 311 negative values arose from the TPS caused by its smoothing effect during interpolation,
 312 and these were set to zero.

313

314 **Table 2. Mean Squared Error (MSE) of the four interpolation methods**

Interpolation method	MSE (per ha)
Inverse distance weighting on untransformed data	201
Inverse distance weighting on log-transformed data	271
Thin plate spline on untransformed data	195
Thin plate spline on log-transformed data	290

315

316 **Fig 4. Interpolated foodplant density (ha^{-1}) across the northern part of the Common**
 317 **in 2005.** The transect (sections with numbered labels) and the four areas of greatest
 318 density change between 2005 and 2013 are shown (green points, see Fig 5). UK Grid
 319 locations are given at 0.5km intervals.

320 Densities from 2013 measured along the monitoring transect were compared with the
 321 interpolated values for the same locations from 2005 (Fig 5). The relationship was
 322 significantly non-linear, with the AIC score for a cubic model (147.98) being lower than
 323 that of a linear model (169.46), a quadratic model (153.98) and a quadrinomial model
 324 (148.95). For locations with <100 patches per hectare in 2005, there was very little
 325 change in density. For locations with 200-600 patches per hectare in 2005, there was a
 326 density reduction of two-to-three fold by 2013. For the four locations with highest
 327 density in 2005, there was a density reduction of 9-fold to 14-fold by 2013. The most

328 dramatic of these was in section 3 of the transect (Figs 4 and 5) – a reduction from 1436
 329 ha⁻¹ in 2005 to 107 ha⁻¹ in 2013. Three out of four of these areas – the two most southerly
 330 and one most northerly in Fig 4 – were located in areas of highest plant density in 2005
 331 [38]. These “hot-spots” were no longer distinguishable as such in 2013.

332 **Fig 5. *Salix repens* patch density (ha⁻¹) on the transect in 2005 and 2013.** The solid
 333 black line is the cubic polynomial: $y = 99.19 + 158.19x - 177.01x^2 + 87.41x^3$, $r^2 = 0.795$.
 334 The dashed lines show the broad-band (prediction) 95% confidence limits.

335 **Host-plant morphology changes**

336 Eight morphology variables were used in the PCA (Table 1). PC1 accounted for 62.4%
 337 of the variation and PC2 accounted for 13.5% of the variation, thereby collectively
 338 explaining 75.9% of the variation in the data (Fig 6). PC1 was negatively correlated with
 339 overall size indicators such as plant width, height, stem number, area and volume (Table
 340 3). PC2 was negatively correlated with stem number, leaf density and area and positively
 341 correlated with plant height (Table 3), thereby differentiating between tall thin plants and
 342 short wide ones.

343
 344 **Fig 6. Biplot of the first two Principle Components for *Salix repens* patch**
 345 **morphology.** Closed circles are patches containing *E. vespertaria* larvae from 2005,
 346 open circles are random patches from 2005, and open triangles are patches along the
 347 monitoring transect from 2013.

348
 349 **Table 3. The correlation of variables to Principal Components^a.**

Variable	PC1	PC2
Maximum width	-0.3969	-0.2575
Maximum height	-0.3673	0.3975
Mean height	-0.3692	0.4134
Stem number	-0.3745	-0.4099
Leaf length	-0.3240	0.3166
Leaf density	0.1623	-0.3808
Area	-0.3892	-0.4233
Volume	-0.3849	-0.1107

350 ^aThe higher the absolute value of the coefficient, the more important the variable is to the
 351 PC.

352 A significant difference in PC1 between ‘2005’ patches with larvae, ‘2005’
353 random patches and ‘2013’ patches was found (Kruskal-Wallis: $\chi^2 = 112.22$; d.f. = 2; $p <$
354 0.001) (Fig 7A). The largest host-plant patches (denoted by PC1) occurred in ‘2005’
355 plants with larvae. Random patches in 2005 were smaller (Mann-Whitney: $W = 859$, $n_1 =$
356 32 , $n_2 = 32$, $p < 0.001$), and smaller still were ‘2013’ patches (Mann-Whitney: $W = 851$,
357 $n_1 = 32$, $n_2 = 202$, $p < 0.001$). A significant difference in PC2 between ‘2005’ plants with
358 larvae, ‘2005’ random plants and ‘2013’ plants was also found (Kruskal-Wallis: $\chi^2 =$
359 24.4 ; d.f. = 2; $p < 0.001$) (Fig 7B). Although ‘2005’ plants with larvae had significantly
360 ‘taller-thinner’ shape than ‘2005’ random plants (Mann-Whitney: $W = 740$, $n_1 = 32$, $n_2 =$
361 32 , $p < 0.001$), there was no significant difference in PC2 between random 2005 and
362 2013 plants (Mann-Whitney: $W = 3628$, $n_1 = 32$, $n_2 = 202$, $p = 0.29$). This suggests that
363 although plants were significantly smaller in 2013 than 2005, there was no significant
364 difference in food-plant shape between the two years.

365

366 **Fig 7. Box plots comparing Principle Component values of *Salix repens* patch**
367 **morphology in ‘2005’ patches containing *E. vespertaria* larvae, ‘2005’ random**
368 **patches without larvae, and ‘2013’ patches. (A) PC1, all data, (B) PC2, all data, and**
369 **(C) PC1 for the subset of ‘2005’ plants sampled on the transect route. Plots show the**
370 **median, interquartile range, outliers ($>1.5 \times$ IQR), and the range for non-outliers**
371 **(whiskers).**

372

373 A subset of the data was investigated in order to reduce the potential for biases in
374 host-plant quality comparisons. Using 2005 patches located only in the monitoring
375 transect, differences in PC1 values were compared between the three groups (Fig 7C). A
376 significant difference between ‘2005’ patches with larvae in the transect, ‘2005’ random
377 patches in the transect and ‘2013’ patches was found (Kruskal-Wallis: $\chi^2 = 54.47$; d.f. =
378 2; $p < 0.001$), with significantly larger sizes in random 2005 patches than in 2013 patches
379 (Mann-Whitney: $W = 200$, $n_1 = 5$, $n_2 = 202$, $p = 0.02$). This was the same finding as for
380 the original full dataset. However, there was no difference between ‘2005’ patches with
381 larvae and ‘2005’ random patches (Mann-Whitney: $W = 64$, $n_1 = 29$, $n_2 = 5$, $p = 0.706$),
382 indicating that plants on the current transect route in 2005 were generally large and
383 suitable for larvae. Note however that the sample size for ‘2005’ random patches on the
384 transect is only 5. A Mann-Whitney U-test showed that the randomly chosen plants
385 measured close to transect sections 9-11 in 2005 had significantly smaller values of PC1

386 than the plants measured there in 2013 ($W = 869$, $n_1 = 6$, $n_2 = 36$, $p < 0.001$). This
387 suggests that the size changes are not restricted to one part of the site.

388 The frequency distributions of *S. repens* mean patch heights (Fig 8) shows the
389 extent of size reduction by 2013. The largest size classes from 2005 appear to be absent
390 in 2013. In 2005 6.3% of random patches were larger than the median height of patches
391 on which larvae were found, and 53% were larger than the fifth percentile of patch
392 heights. By 2013, on the monitoring transect, only 1% were larger than the median patch
393 height on which larvae were found in 2005, and just 14% were larger than the fifth
394 percentile. Recall that the monitoring transect route was chosen to encompass the best
395 habitat over the north of the Common for *E. vespertaria*.

396
397 **Fig 8. The height of *Salix repens* patches (mean of maximum height and six**
398 **other stems).** (A) patches with *E. vespertaria* larvae in 2005, (B) random patches in
399 2005 and (C) patches in 2013 on the monitoring transect.

400

401 Discussion

402 Here we have shown that, following commencement of a monitoring programme as part
403 of the UK Species Action Plan for *E. vespertaria*, adult numbers at Strensall Common,
404 its last known English site, declined on average by 30-35% annually from 2007 to 2014,
405 coincident also with a contraction in range towards a core location within the monitored
406 area. These strong declines indicate a reduction in the suitable environmental conditions
407 for the species during the same period. Data also suggest changes in the population of
408 host-plants during this time, with strong declines in *S. repens* patch density as well as
409 reductions in overall patch size. This suggests that effects of environmental changes on
410 the moth are being mediated through the host plant. Previous work on Lepidoptera
411 populations has also shown that the presence of the preferred subset of larval food
412 sources ('host-plant quality') is the most important factor determining population
413 trajectories within individual sites [49].

414 Strensall Common is a site with statutory protection under Annex I of the EU
415 Habitats Directive, and the site is managed to conserve the heathland by sheep grazing
416 and tree/shrub removal to maintain a mosaic of different stages of succession. Previous
417 work at the Common has shown that the presence of *E. vespertaria* larvae is predicted by
418 the presence of tall plant patches at high density close to trees [38]. Consistent with this,
419 Butterfly Conservation characterized the species' English habitat as lightly wooded

420 heathland [50]. Ostensibly then, the management strategy on the Common seems well-
421 suited to maintain the conditions required by the moth. However, Robertson et al. [38]
422 also found that larvae and adults were concentrated in a small number of ‘hot-spots’
423 where the most favourable habitat was found. This potentially made the population
424 vulnerable to subtle widespread environmental changes or to very drastic but local ones.

425 A drastic local change occurred between August 2009 and April 2010, when the
426 hot-spot in section 3 of the transect was destroyed by a fire (Fig 9) [51–53]. Some *S.*
427 *repens* is now regenerating in this area but the plants remain low-growing (e.g. Fig 10B),
428 and as indicated by Fig 5, fewer in number. Fig 3 indicates that 2009-10 coincided with a
429 greater reduction in *E. vespertaria* population density than had occurred previously.
430 However, two factors indicate that this is not the sole reason for the decline of the moth
431 on the Common. First, one of the other hot-spots, on the Yorkshire Wildlife Trust reserve
432 covered by sections 9-11, well separated from section 3, also showed a decline to
433 extinction even before the fire. Second, the overall decline continued well after 2010.

434

435 **Fig 9. Views of a location near transect section 3, OS Grid ref SE 65225 60975.** (A)

436 Looking south-west in 2005, with (1) large *S. repens* bushes (2) small and (3) large
437 *Betula pendula* (Silver Birch) trees, and (4) the path along which the transect runs. The
438 ruler is 1m high. (B) The same location at the same time of year looking north-east in
439 2013. The ground vegetation is considerably shorter with (1) the remains of dead shrubs
440 (2) regrowth of grasses. This area was burned between the 2009 and 2010 transect
441 surveys. (A) Reproduced from [38] with permission.

442

443 **Fig 10. *Salix repens* patches.** (A) a tall patch (>1m high) from 2005 (B) a prostrate
444 patch with low creeping growth from 2015 (~5cm high) (C) an upright shoot from 2015
445 (~40cm high), with foliage removed by grazing, showing attached sheep wool in the top
446 right of the photo. (A) Reproduced from [38] with permission.

447

448 One possible factor contributing towards a decline, both before and after 2010, is
449 grazing. Grazing damage has recently been evident on most *S. repens* patches covered by
450 the transect, from the loss of the growing tips of stems, the presence of sheep wool on the
451 plants, and the cropping of neighbouring plants of other species (Fig 10C). Although
452 there has been no official change in the grazing management strategy coincident with the
453 decline, it appears likely that local changes in grazing pressure have occurred. In 2007

454 there was a change in grazier, and since then sheep on the northern part of the Common
455 appear to have been concentrated close to transect sections 1-8, especially when
456 supplemental fodder is left out (near sections 7 and 8). In addition, sheep have been
457 observed on the Common outside the established grazing period, indicating that not all
458 sheep were removed for the whole winter [54]. Even in areas unaffected by fire, these
459 changes may have been sufficient to reduce the size and density of host-plant patches.
460 However, the declines in plant patch size seen around transect sections 9-11 indicate that
461 proximity to supplemental fodder may not be the sole cause of the changes seen.

462 Another possible contributor to the post-2009 declines is frost damage to plants.
463 The winter of 2009-2010 was locally the coldest since 1987 [55]. The following winter
464 was also severe, with the coldest start to the year (2011) for 100 years [56]. February
465 2012 was severe with an ice storm on 8th, and severe frosts in April [57], whilst January
466 to March 2013 were cold, with an ice storm on 25th Jan, and the second-coldest March on
467 record [58]. *Ad hoc* observations suggest that many of the larger plants experienced die-
468 back of exposed stems during this period [53]. However, the processes causing die-back
469 and size reduction at the site are not well-understood; observations of a clump of large *S.*
470 *repens* bushes just east of transect section 2 in summer of 2014 indicated blackening of
471 leaves and stem die-back, clearly not caused by frost or fire, while grazing damage was
472 evident. It is possible that grazing contributes to die-back and infection of plants by
473 weakening them. Overall it appears that there are multiple, perhaps interacting, causes of
474 the decline in *S. repens*.

475 There are several possible reasons why the observed changes to host-plants might
476 cause a decline in moth density. First, they might decrease the oviposition rate of female
477 *E. vespertaria*. Females might experience a reduction in oviposition cues from smaller,
478 low-density plants. Other species of Lepidoptera are known to avoid ovipositing on
479 damaged plants and to select preferentially large, robust or vigorously growing plants
480 (e.g. [59-61], although the preferred characteristics of each host-plant varies widely
481 across Lepidoptera species [49]. Death or removal of stems, such as through grazing,
482 may also cause direct mortality of juvenile life history stages, especially eggs. *E.*
483 *vespertaria* eggs are laid on host-plant stems and remain there from August through to
484 late spring [38]. They are therefore vulnerable to removal or damage for extensive
485 periods of time. The Dingy Skipper *Erynnis tages* (L.) is another Lepidoptera species of
486 conservation concern in the UK that is vulnerable to grazing pressure during the egg
487 stage because females oviposit on the tips of large host-plants [60] which are likely to be

488 removed by grazing animals. Grazing is also typically used to improve the overall
489 condition of the grassland sites that it favours, and conservation recommendations now
490 advise lack of grazing during this critical life history stage. However, the egg stage of *E.*
491 *vespertaria* is vulnerable for a much longer period than that of *E. tages*.

492 Although we have shown declines in the moth population and changes to the
493 foodplant on the northern part of the Common, the monitoring transect does not cover
494 areas to the south of the study area where access is restricted due to military training. In
495 2013, surveys found adult moths present at two discrete locations in this area, and
496 smaller numbers were seen at both in 2014, although searches in other areas where it was
497 formerly present have failed to locate it, suggesting a general decline over the Common.
498 The disappearance of the moth from sections 9-11 of the monitoring transect along with
499 changes in host plants there suggests that the environmental changes affecting the moth
500 are not entirely localized. Sheep grazing is also present within this restricted area.
501 Targeted conservation work in this area is difficult, making the conservation of the
502 population on the northern part of the Common all the more important.

503 Although the plant-patch size measurements were made in different months in
504 2005 and 2013, the later measurement dates in 2013 would be expected to produce a
505 height bias in the opposite direction to that found in the absence of a decline, given the
506 additional time for annual growth prior to leaf fall. Photographic evidence (e.g. Fig 9)
507 and testimony of transect walkers is consistent with the statistical height trends found
508 across years [53]. Consistency of measurement is more difficult when assessing the
509 density of patches and their width, especially since different observers made the
510 measurements in different years, and interpolation techniques were used to compare
511 density. In practice, distinguishing *S. repens* patches consistently is not easy, as there are
512 many marginal cases (where one observer might distinguish only one patch, but others
513 identify multiple patches). Small *S. repens* patches may be missed in amongst other
514 vegetation. Nonetheless, several factors argue that the major statistical trends are valid.
515 First, the differences are very large and there was appreciable intersection of the areas
516 sampled, particularly in the high-density hotspots where the overall direction of the
517 changes is likely to be robust (e.g. Fig 9). Second, they are consistent with the anecdotal
518 observations of transect walkers, where transect sections once well populated by patches
519 are now nearly devoid of them [53]. Third, some likely biases would probably operate in
520 the opposite direction to the major findings; for example, small low growing patches are
521 less likely to have been missed in 2013 when they were the typical form of the plant,

522 suggesting that density at this time is unlikely to have been underestimated, whilst the
523 density estimates in 2005 tended to underestimate high densities (see Results).

524 Immediate conservation action on Strensall Common must focus on the recovery
525 of large, high density patches of *S. repens* in areas still occupied by *E. vespertaria*, and
526 then extending a network of such patches across the Common to create a more robust
527 population. To this end, on 22nd April 2015, nine small (2.4 x 2.4m) grazing exclosures
528 containing established but mainly low-growing *S. repens* patches, were erected along the
529 transect route. Some of these exclosures have been enhanced by planting pot-grown *S.*
530 *repens* using cuttings or seed taken from Strensall Common. It is hoped that these will
531 create patches of large plants which may help stem the decline of the moth in the
532 monitored area. Measurements of the *S. repens* inside and immediately outside the
533 exclosures will test the hypothesis that a reduction in grazing pressure can increase the
534 size of *S. repens* patches, establishing a basis for a more general change in management
535 on the Common. This might take the form of changes in the local distribution of sheep on
536 the Common, perhaps by more active shepherding of animals into areas of less
537 importance to *E. vespertaria*. Cattle or pony grazing may be an alternative that could
538 benefit *S. repens* through dissipating grazing more widely across other plant species and
539 by providing disturbance that can encourage *S. repens* establishment [62–64]. Further
540 into the future, it is essential that more populations of the moth be established, as
541 recommended on the SAP. There would have been more scope to carry this out before
542 the current decline at Strensall occurred, as the population at Strensall is now too small to
543 justify removal of individuals, and could be genetically impoverished, whereas the
544 numbers necessary to establish new populations were readily available up until 2009
545 (although other relevant factors, such as the identification of suitable introduction sites,
546 were not in place at that time). In the meantime, the risk of extinction of the population at
547 Strensall Common now translates into a risk of extinction in England as a whole.

548 More generally, our work reinforces some important lessons for conservationists.
549 First, given the sheer number of species and limited resources for conservation, the
550 majority of species can never receive direct, targeted management. The survival of rare
551 but relatively poorly-understood species must therefore rely on the maintenance of
552 suitable habitats, but the particular requirements of different species make it likely that
553 generic management strategies for habitats will not benefit all species [65]. This may
554 have been the case with *E. vespertaria* at Strensall Common, which could probably have
555 benefited from reduced grazing pressure in recent years, despite the need to maintain

556 grazing of the site more generally. Had *E. vespertaria* not been monitored, as is the case
557 for many taxonomic groups, ignorance of its decline would preclude any targeted action
558 to aid recovery, making extinction more likely. Indeed, there is a history of rare species
559 disappearing from protected areas due to inappropriate management [66]. The solution to
560 this problem is not simple, but probably rests in securing greater knowledge of the
561 requirements of a large number of species, and an increase in the robustness of the
562 protected area network [67]. In the case of *E. vespertaria*, volunteer and student effort
563 has greatly underpinned much of the data we present here.

564 Second, our study warns against complacency when species are restricted to small
565 numbers of sites, even if their populations at such sites appear healthy. In the case of *E.*
566 *vespertaria*, the national SAP recommended an increase in the number of sites, but this
567 was not subsequently implemented, even with relatively good knowledge of the species’
568 requirements as described by Robertson et al. [38]. In fact a local SAP was deemed
569 unnecessary. However, it can be argued that a period when populations of localized rare
570 species are healthy presents the greatest opportunity to increase the number of
571 populations, providing other necessary factors are also in place [68].

572 Third, our study illustrates the value of monitoring programmes for rare species.
573 Resources do not always make this practical (e.g. for species not easily counted, or for
574 which there is little volunteer enthusiasm), but the information gained can allow time for
575 remedial action to be taken and also provide data or observations helpful to reversing
576 declines and implementing revised management.

577 In summary, we have shown that the decline of the rare moth *E. vespertaria* at its
578 last English site is likely linked to changes in host plant density and size. We hope in
579 future to report on the effects of restorative action to reduce grazing in areas critical for
580 *E. vespertaria* and increase the size of host-plants. Ultimately we hope to implement
581 management actions that will once again make the Dark Bordered Beauty a common
582 sight at Strensall, and secure its long-term future in England.

583

584 **Acknowledgements**

585 We are grateful to the Yorkshire Wildlife Trust and UK Ministry of Defence for
586 permission to work on their land, and the Yorkshire Wildlife Trust for participation in
587 survey work.

588

589

591

592

593

References

594

1. United Nations. Convention on Biological Diversity. Montreal: Secretariat of the Convention on Biological Diversity; 1992.

595

596

2. Dirzo R, Raven PH. Global state of biodiversity and loss. *Annu Rev Env Resour.* 2003; 28: 137-167.

597

598

3. Millennium Ecosystem Assessment. *Ecosystems and Human Well-being: Synthesis.* Washington: World Resources Institute, Island Press; 2005.

599

600

4. Biodiversity Reporting and Information Group. Report on the Species and Habitat Review: Report by the Biodiversity Reporting and Information Group. Peterborough: Joint Nature Conservation Committee; 2007.

601

602

603

5. Perring FH, Farrell L (editors). *British Red Data Books: 1 Vascular Plants.* 2nd ed. Lincoln: Royal Society for Nature Conservation; 1983.

604

605

6. Shirt D (editor). *British Red Data Books: 2 Insects.* Peterborough: Nature Conservancy Council; 1987.

606

607

7. Bratton JH (editor). *British Red Data Books: 3 Invertebrates other than Insects.* Peterborough: Nature Conservancy Council; 1991.

608

609

8. English Nature. *Grazing management of lowland heathlands.* Peterborough: English Nature; 2005.

610

611

9. UK Biodiversity Steering Group. *Biodiversity: The UK Steering Group Report. Vol 2. Action Plans.* London: HMSO; 1995.

612

613

10. English Nature. *Lowland heathland: a cultural and endangered landscape.* Peterborough: English Nature; 2002.

614

615

11. Pywell RF, Meek WR, Webb NR, Putwain PD, Bullock JM. Long-term heathland restoration on former grassland: the results of a 17-year experiment. *Biol Conserv.* 2011; 144: 1602-1609.

616

617

618

12. Ying-Chi L, James R, Dolman PM. Conservation of heathland ground beetles (Coleoptera, Carabidae): the value of lowland coniferous plantations. *Biodivers Conserv.* 2007; 16: 1337-1358.

619

620

- 621 13. Clements, R. The Hobby in Britain: A new population estimate. *British Birds*. 2001;
622 94: 402-408.
- 623 14. van den Berg LJL, Bullock JM, Clarke RT, Langston RHW, Rose RJ. Territory
624 15. selection by the Dartford warbler (*Sylvia undata*) in Dorset, England: the role of
625 vegetation type, habitat fragmentation and population size. *Biol Conserv*. 2001; 101:
626 217-228.
- 627 16. English Nature. Reptiles: guidelines for developers. Peterborough: English Nature;
628 2004.
- 629 17. Stokes KE, Allchin AE, Bullock JM, Watkinson AR. Population responses of *Ulex*
630 shrubs to fire in a lowland heath community. *J Veg Sci*. 2004; 15: 505-514.
- 631 18. Schirmel J, Fartmann T. Coastal heathland succession influences butterfly
632 community composition and threatens endangered butterfly species. *J Insect Conserv*.
633 2014; 18: 111-120.
- 634 19. Bakker JP, de Bie S, Dallinga JH, Tjaden P, de Vries Y. Sheep-grazing as a
635 management tool for heathland conservation and regeneration in the Netherlands. *J*
636 *Appl Ecol*. 1983; 20: 541-560.
- 637 20. Webb N. Heathlands. *New Naturalist* 72. London: Collins; 1986.
- 638 21. Newton AC, Stewart GB, Myers G, Diaz A, Lake S, Bullock JM, Pullin AS. Impacts
639 of grazing on lowland heathland in north-west Europe. *Biol Conserv*. 2009; 142: 935-
640 947.
- 641 22. Williams JM (editor). Common Standards Monitoring for Designated Sites: First Six
642 Year Report. Peterborough: Joint Nature Conservation Committee; 2006.
- 643 23. Thomas JA, Rose RJ, Clarke RT, Thomas CD, Webb NR. Intraspecific variation in
644 habitat availability among ectothermic animals near their climatic limits and at their
645 centres of range. *Funct Ecol*. 1999; 13: 55-64.
- 646 24. Rutherford CI. The Lepidoptera of Yorkshire: A commentary. *Naturalist*. 1971; 918:
647 93-104.
- 648 25. Resh VH, Cardé RT (editors). *Encyclopedia of Insects*. 2nd edn. San Diego:
649 Academic Press; 2009.

- 650 **26.** Fox R, Brereton TM, Asher J, Botham MS, Middlebrook I, Roy DB, Warren MS.
651 The state of the UK's butterflies 2011. Wareham, Dorset: Butterfly Conservation and
652 the Centre for Ecology & Hydrology; 2011.
- 653 **27.** Fox R, Parsons MS, Chapman JW, Woiwod IP, Warren MS, Brooks DR. The State of
654 Britain's Larger Moths 2013. Wareham, Dorset: Butterfly Conservation and
655 Rothamsted Research; 2013.
- 656 **28.** Roy DB, Sparks TH. Phenology of British butterflies and climate change. *Glob*
657 *Chang Biol.* 2000; 6: 407-416.
- 658 **29.** Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, et al. Rapid responses
659 of British butterflies to opposing forces of climate and habitat change. *Nature*, 2001;
660 **414**: 65-69.
- 661 **30.** Sparks TH, Huber K, Dennis RLH. Complex phenological responses to climate
662 warming trends? Lessons from history. *Eur J Entomol.* 2006; 103: 379-386.
- 663 **31.** Fox R. The decline of moths in Great Britain: a review of possible causes. *Insect*
664 *Conserv Divers.* 2013; 6: 5-19.
- 665 **32.** Fox R, Oliver TH, Harrower C, Parsons MS, Thomas CD, Roy DB. Long-term
666 changes to the frequency of occurrence of British moths are consistent with opposing
667 and synergistic effects of climate and land-use changes. *J Appl Ecol.* 2014; 51: 949-
668 957.
- 669 **33.** New TR. *Lepidoptera and Conservation.* Oxford: Wiley-Blackwell; 2013.
- 670 **34.** Frost HM, Beaumont HE, Crawford TJ, Fryer G, Yeates CSM (editors). *Porritt's*
671 *Lists: A Reprint of George T Porritt's Yorkshire Butterfly & Moth Records First*
672 *Published in 1883-86, 1904, 1907, & 1922 - Revised into Modern Order with*
673 *Detailed Comments and Background.* Butterfly Conservation Yorkshire, Yorkshire
674 *Naturalists' Union; 2011.*
- 675 **35.** Tams TJ. Northumberland Lepidoptera review 2013. *The Vasculum.* 2014; 99: 33-48.
- 676 **36.** Parrott J, MacKenzie N (editors). *Aspen in Scotland: biodiversity and management.*
677 *Boat of Garten: Highland Aspen Group; 2009.*
- 678 **37.** UK Biodiversity Group. *Tranche 2 Action Plans: Invertebrates.* Peterborough:
679 *English Nature; 1999.*

- 680 **38.** Robertson P, Ellis S, Small J. The Dark Bordered Beauty *Epione vespertaria* (L.)
681 moth in northern England. Butterfly Conservation Report No S06-02. Wareham,
682 Dorset: Butterfly Conservation; 2006.
- 683 **39.** Natural England. Site Improvement Plan: Strensall Common (SIP273), 2014.
684 Available: <http://publications.naturalengland.org.uk/publication/6435201697710080>
- 685 **40.** City of York Council. City of York Biodiversity Action Plan (May 2013). York: City
686 of York Council; 2013.
- 687 **41.** Li J, Heap AD. A review of comparative studies of spatial interpolation methods in
688 environmental sciences: performance and impact factors. *Ecol Inform.* 2011; 6: 228-
689 241.
- 690 **42.** Bivand R, Keitt T, Rowlingson B. rgdal: Bindings for the Geospatial Data
691 Abstraction Library. R package version 0.9-1. 2014. Available: [http://CRAN.R-](http://CRAN.R-project.org/package=rgdal)
692 [project.org/package=rgdal](http://CRAN.R-project.org/package=rgdal)
- 693 **43.** Bivand R, Lewin-Koh N. maptools: Tools for Reading and Handling Spatial Objects.
694 R package version 0.8-30. 2014. Available: [http://CRAN.R-](http://CRAN.R-project.org/package=maptools)
695 [project.org/package=maptools](http://CRAN.R-project.org/package=maptools)
- 696 **44.** Baddeley A, Turner R. spatstat: an R package for analyzing spatial point patterns. *J*
697 *Stat Softw.* 2005; 12: 1-42.
- 698 **45.** Hijmans RJ. raster: Geographic Data Analysis and Modelling. R package version 2.3-
699 24. 2015. Available: <http://CRAN.R-project.org/package=raster>
- 700 **46.** Wickham H, Chang W. devtools: Tools to Make Developing R Packages Easier. R
701 package version 1.7.0. 2015. Available: [http://CRAN.R-](http://CRAN.R-project.org/package=devtools)
702 [project.org/package=devtools](http://CRAN.R-project.org/package=devtools)
- 703 **47.** Fox J, Weisberg S. An R Companion to Applied Regression. 2nd ed. Thousand Oaks,
704 CA: Sage; 2011.
- 705 **48.** Vu VQ. ggbiplot: A ggplot2 based biplot. R package version 0.55. 2011. Available:
706 <http://github.com/vqv/ggbiplot>
- 707 **49.** Thomas JA, Simcox DJ, Hovestadt T. Evidence based conservation of butterflies. *J*
708 *Insect Conserv.* 2011; 15, 241-258.

- 709 **50.** Wigglesworth T, Parsons M, Warren M. Dark Bordered beauty *Epione vespertaria*
710 Factsheet. Wareham, Dorset: Butterfly Conservation. Available: <http://butterfly->
711 conservation.org/files/dark_bordered_beauty-psf.pdf
- 712 **51.** Baker D. Yorkshire's Dark Bordered Beauty. *Naturalist*. 2012; 137: 11-15.
- 713 **52.** Baker D. The Dark Bordered Beauty: background. *Argus*. 2012; 65: 6-12.
- 714 **53.** Crawford, TJ. Monitoring the Dark Bordered Beauty at Strensall 2007-2012. *Argus*.
715 2012; 65: 12-15.
- 716 **54.** Graham B. Preliminary exploration on quantifying winter grazing to aid conservation
717 of the *Epione vespertaria*. MSc Thesis, The University of York, UK. 2014.
- 718 **55.** Frost HM (editor). Yorkshire Butterflies and Moths 2010. *Argus*. 2011; 63.
- 719 **56.** Frost HM (editor). Yorkshire Butterflies and Moths 2011. *Argus*. 2012; 66.
- 720 **57.** Frost HM (editor). Yorkshire Butterflies and Moths 2012. *Argus*. 2013; 69.
- 721 **58.** Frost HM (editor). Yorkshire Butterflies and Moths 2013. *Argus*. 2014; 72.
- 722 **59.** Ravenscroft NOM. The ecology of the Chequered Skipper Butterfly *Carterocephalus*
723 *palaemon* in Scotland. I. Microhabitat. *J Appl Ecol*. 1994; 31: 613-622.
- 724 **60.** Gutiérrez D, Thomas CD, León-Cortés JL. Dispersal, distribution, patch network and
725 metapopulation dynamics of the dingy skipper butterfly (*Erynnis tages*). *Oecologia*.
726 1999; 121: 506-517.
- 727 **61.** Betzholtz P-E, Ehrig A, Lindeborg M, Dinnétz P. Food plant density, patch isolation
728 and vegetation height determine occurrence in a Swedish metapopulation of the
729 marsh fritillary *Euphydryas aurinia* (Rottemburg, 1775) (Lepidoptera, Nymphalidae).
730 *J Insect Conserv*. 2007; 11: 343-350.
- 731 **62.** Grant SA, Torvell L, Common TG, Sim EM, Small JL. Controlled grazing studies on
732 *Molinia* grassland: effects of different seasonal patterns and levels of defoliation on
733 *Molinia* growth and responses of swards to controlled grazing by cattle. *J Appl Ecol*.
734 1996; 33: 1267-1280.
- 735 **63.** Taylor K, Rowland AP, Jones HE. *Molinia caerulea* (L.) Moench. *J Ecol*. 2001; 89:
736 126-144.

- 737 **64.** Martin D, Fraser MD, Pakeman RJ, Moffat AM. Natural England Review of Upland
738 Evidence 2012: Impact of moorland grazing and stocking rates. Natural England
739 Evidence Review, Number 006. Sheffield: Natural England; 2013.
- 740 **65.** Webb JR, Drewitt AL, Measures GH. Managing for species: integrating the needs of
741 England's priority species into habitat management. Part 1 Report. Natural England
742 Research Reports, Number 024. Sheffield: Natural England; 2010.
- 743 **66.** Rothschild M, Marren P. Rothschild's Reserves: Time and Fragile Nature. Rehovot:
744 Balaban; 1997.
- 745 **67.** Lawton JH, Brotherton PNM, Brown VK, Elphick C, Fitter AH, Forshaw J, et al.
746 Making space for nature: a review of England's wildlife sites and ecological network.
747 Report to Defra. London: Defra; 2010.
- 748 **68.** Hochkirch A, Witzemberger KA, Teerling A, Niemeyer F. Translocation of an
749 endangered insect species, the field cricket (*Gryllus campestris* Linnaeus, 1758) in
750 northern Germany. *Biodivers Conserv.* 2007; 16: 3597–3607.

751

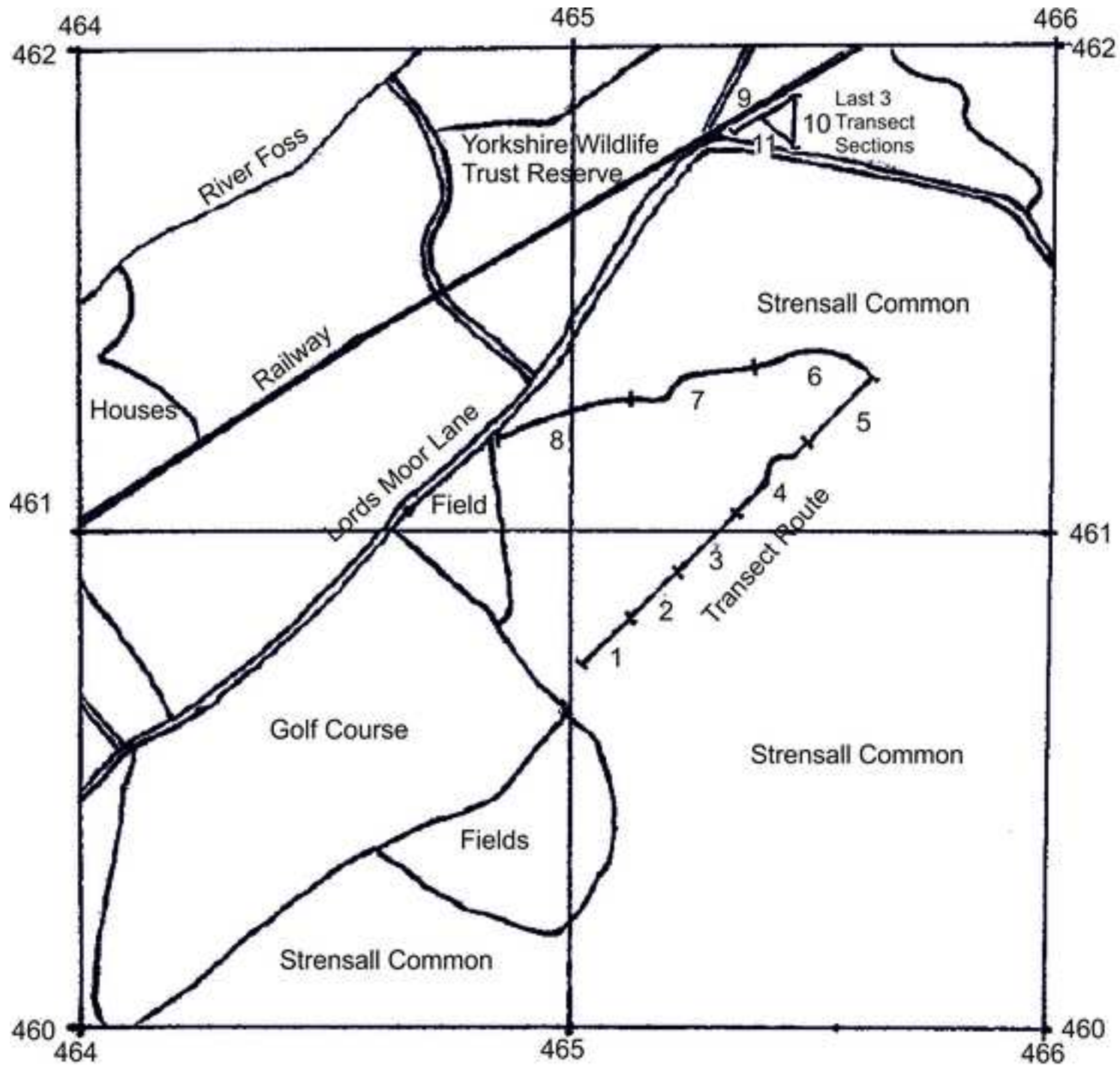
752

753 **Supporting Information**

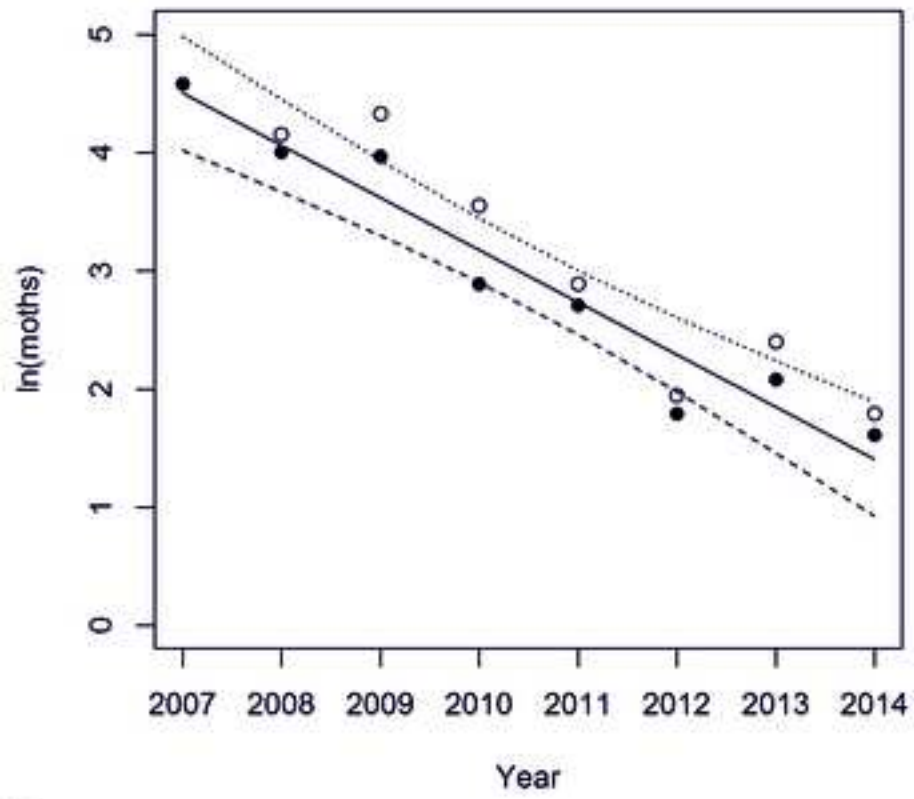
754 **SI Appendix: Transect route description written in 2008.**

755 **SI Dataset: Transect count data for adult *Epione vespertaria* 2007–2014; 2013 *Salix***
756 ***repens* patch location data along the transect route; 2013 *S. repens* patch**
757 **morphology data along the transect route; 2005 *S. repens* patch density data; 2005**
758 ***S. repens* patch morphology data.**

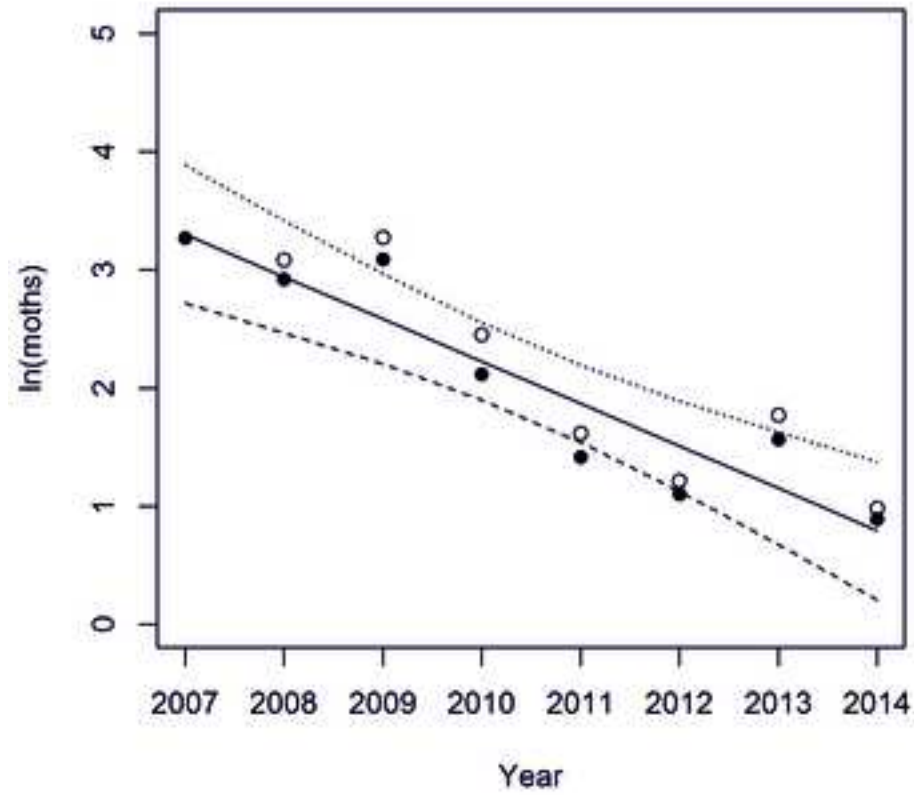


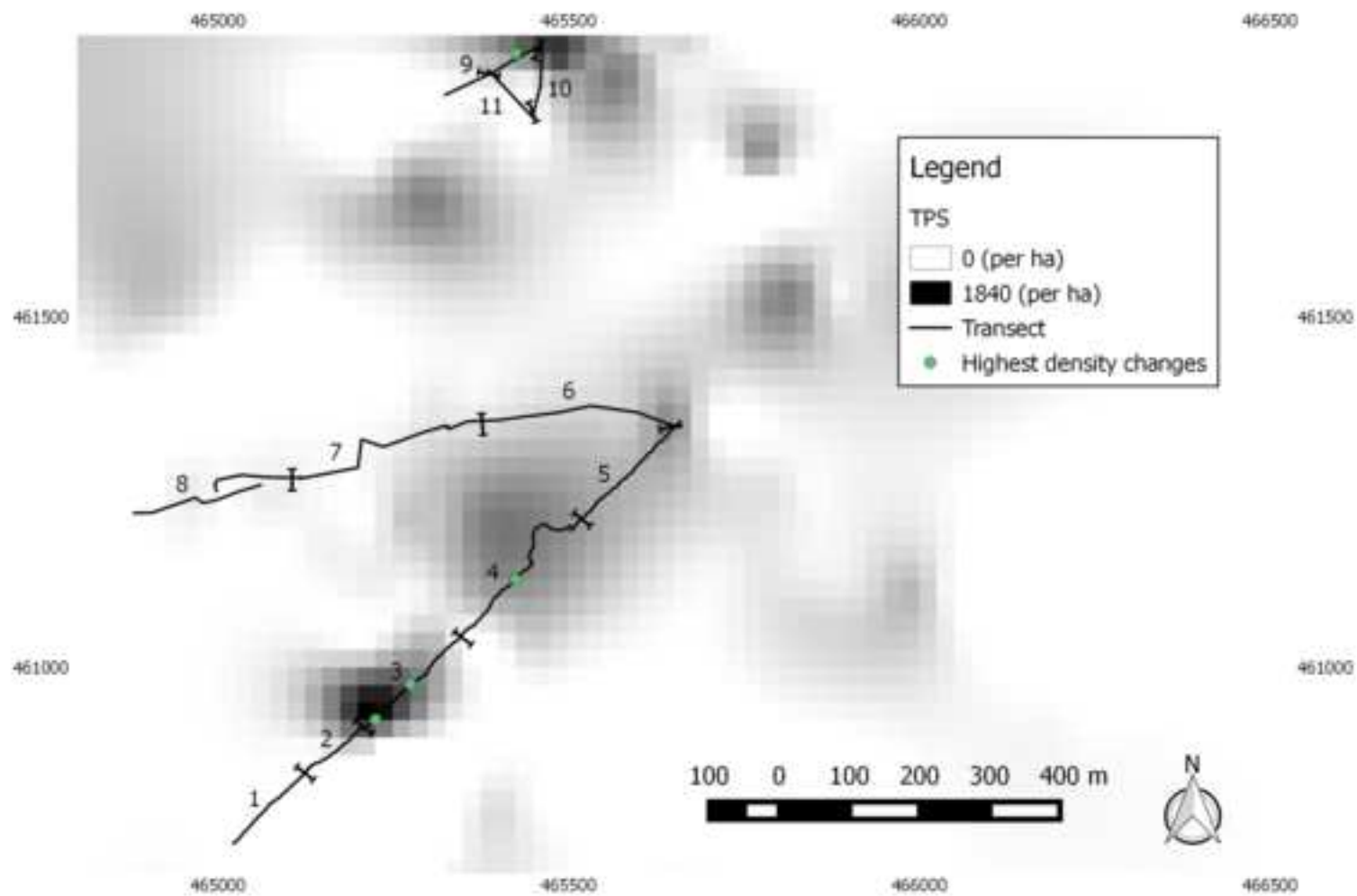


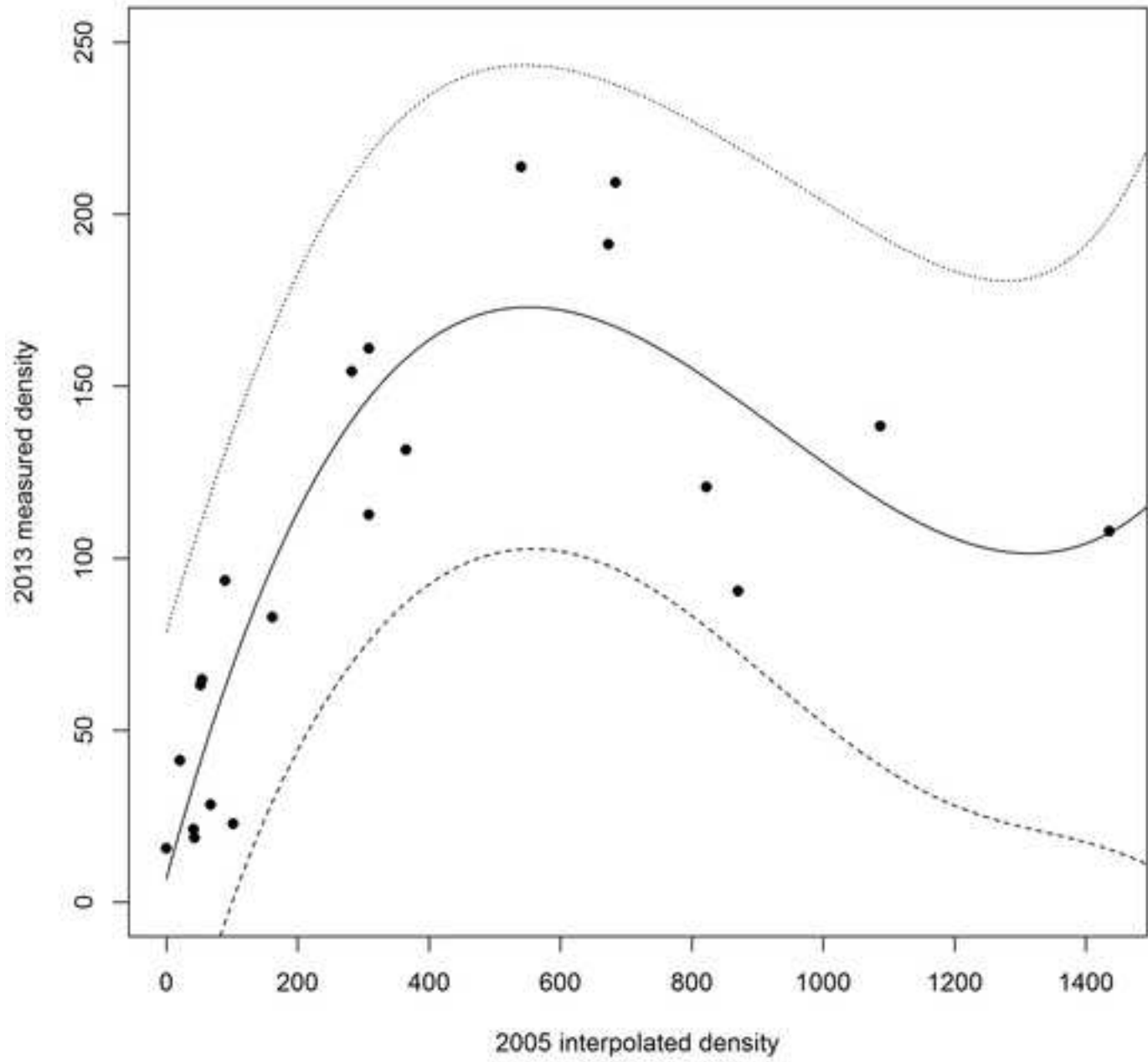
A

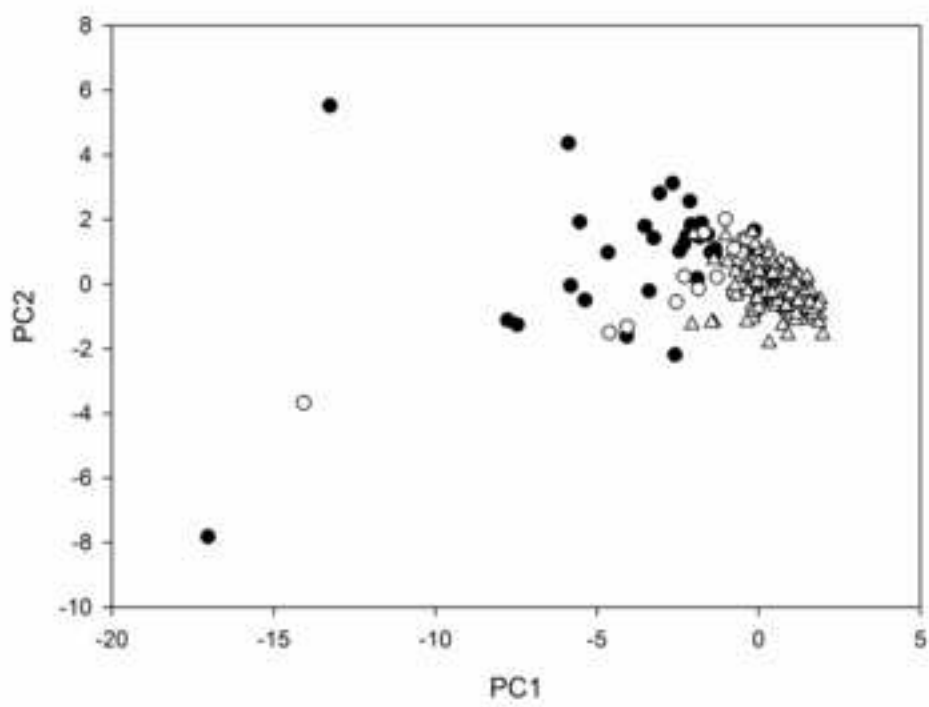


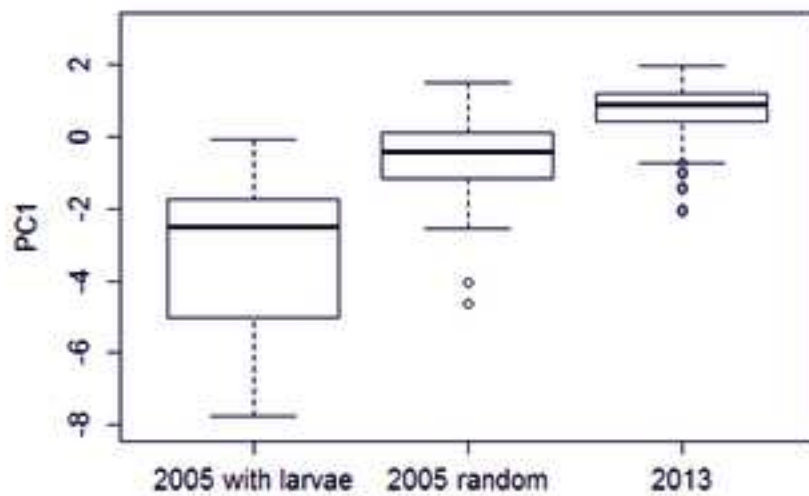
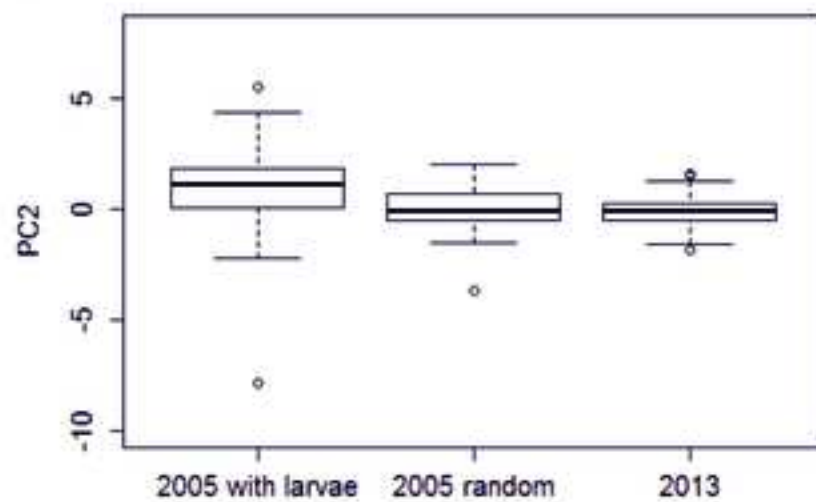
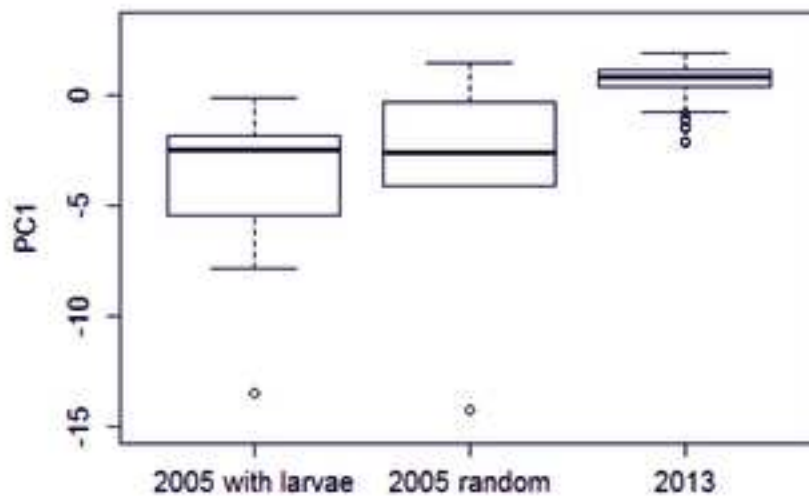
B

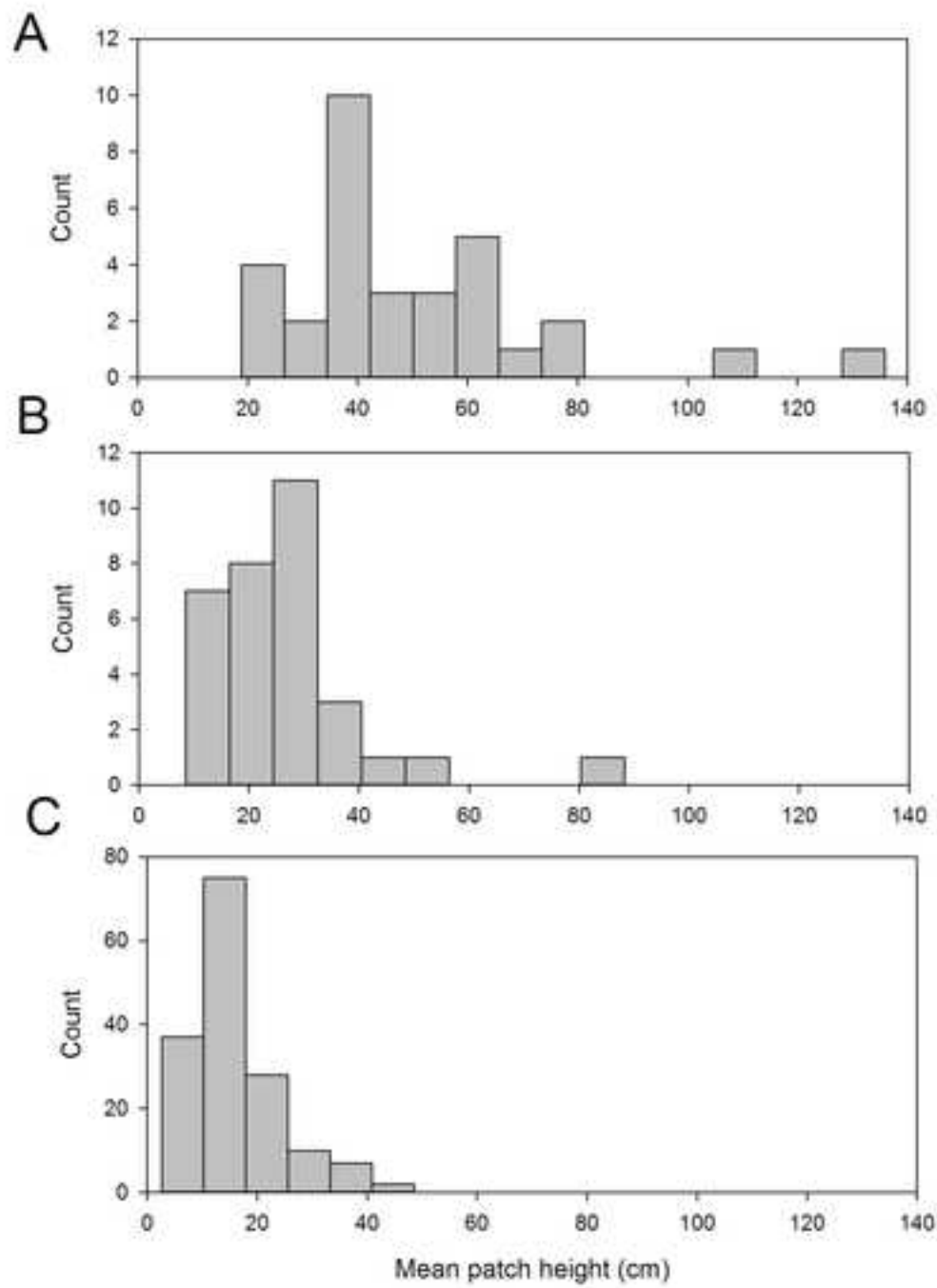




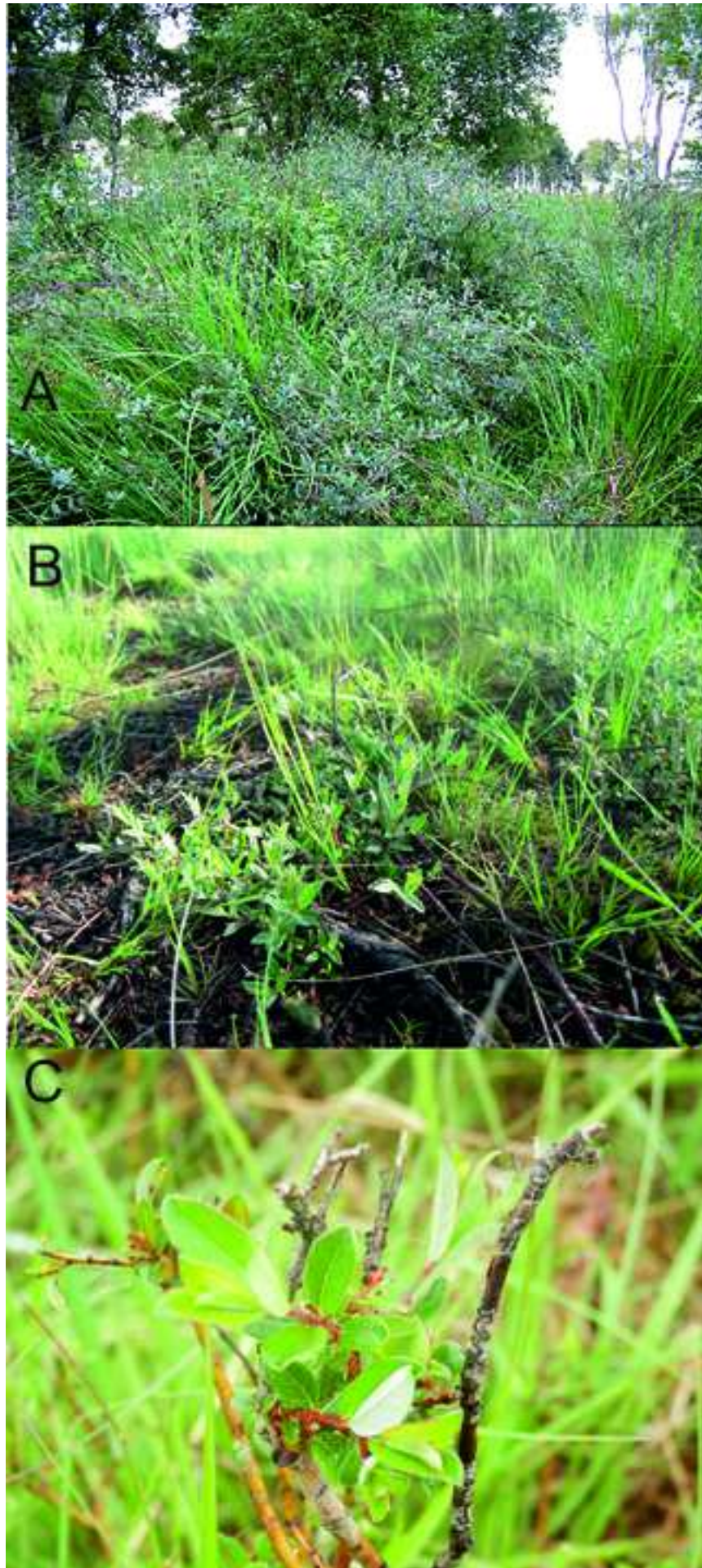




A**B****C**









Click here to access/download
Supporting Information
SI Appendix.pdf





Click here to access/download
Supporting Information
SI Dataset.xls



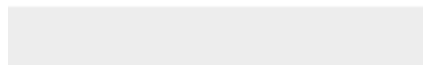


Click here to access/download
Supporting Information
Argus papers.pdf





Click here to access/download
Supporting Information
DBB report BC No. S06-02.pdf





Click here to access/download
Supporting Information
permissionletter.docx





Decline of a rare moth at its last known English site: causes and lessons for conservation.

David Baker^{1,2}, Sinead Barrett³, Colin M. Beale³, Terry J. Crawford^{1,3}, Sam Ellis⁴, Tallulah Gullett³, Peter J. Mayhew^{3*}, Mark S. Parsons⁴, Penny Relf^{1,2}, Paul Robertson³, Julian Small⁵ and Dave Wainwright⁴.

¹Yorkshire Naturalists' Union Lepidoptera Group, Yorkshire Naturalists' Union, York, UK

²Butterfly Conservation, Yorkshire Branch, York, UK.

³Department of Biology, University of York, York, UK

⁴Butterfly Conservation, East Lulworth, Wareham, Dorset, UK

⁵Natural England, York, UK

*Correspondence author

peter.mayhew@york.ac.uk

Abstract

The conditions required by rare species are often only approximately known. Monitoring such species over time can help refine management of their protected areas. We report population trends of a rare moth, the Dark Bordered Beauty *Epione vespertaria* (Linnaeus, 1767) (Lepidoptera: Geometridae) at its last known English site on a protected lowland heath, and those of its host-plant, *Salix repens* (L.) (Malpighiales: Salicaceae). Between 2007 and 2014, adult moth density reduced by an average of 30-35% annually over the monitored area, and its range over the monitored area contracted in concert. By comparing data from before this decline (2005) with data taken in 2013, we show that the density of host-plants over the monitored area reduced three-fold overall, and ten-fold in the areas of highest host-plant density. In addition, plants were significantly smaller in 2013. In 2005, moth larvae tended to be found on plants that were significantly larger than average at the time. By 2013, far fewer plants were of an equivalent size. This suggests that the rapid decline of the moth population coincides with, and is likely driven by, changes in the host-plant population. Why the host-plant population has changed remains less certain, but fire, frost damage and grazing damage have probably contributed. It is likely that a reduction in grazing pressure in parts of the site would aid host-plant recovery, although grazing remains an important site management activity. Our work confirms the value of constant monitoring of rare or priority insect species, of the risks posed to species with few populations even when their populations are large, of the potential conflict between bespoke management for species and generic management of habitats, and hence the value of refining our knowledge of rare species' requirements so that their needs can be incorporated into the management of protected areas.

Introduction

The 1992 Convention on Biological Diversity articulated a legal obligation for signatory countries to conserve their biodiversity [1], following widespread recognition of ongoing and increasing threats to biodiversity globally (summarized in [2–3]), and mindful of the strong link between biodiversity and human well-being. In response to the requirements of the convention, the UK, alongside other signatory countries, developed a National Biodiversity Action Plan (BAP), in which priority species and habitats were identified [4]. The listing of priority species and habitats was retained in the Natural Environment and Rural Communities (NERC) Act 2006, which superseded the ~~n~~National BAP. The priority species lists drew heavily on IUCN Red List criteria as applied in the UK species Red Lists (e.g. [5–7]).

Of the many challenges raised by attempting to meet the obligations of the 1992 convention, one of the greatest is to gather adequate knowledge of the habitat requirements of priority species, because of the sheer volume of such species (the last ~~n~~National BAP listed 1,149 in the UK) [4]. Knowledge of these requirements assists appropriate management of key sites. Because priority habitats tend to be managed to maintain communities of typical plant species, but not necessarily other species, optimal management for priority species and habitats may conflict. Here we report findings from population monitoring of a priority Lepidoptera species on a priority habitat that is managed for its conservation interest. Our results illustrate the value of ongoing monitoring of rare species, even at sites managed for conservation, and of potential conflict between generic habitat management and the needs of particular priority species.

~~Lowland heathland habitats are valued for their biodiversity and landscape, for recreation, and for agriculture [8] Lowland heathland habitats are of high conservation value, because of their biodiversity, for recreation, and for their landscape and agriculture [8].~~ They are a UK priority habitat [9] and are also designated as an Annex I habitat under the European Habitats Directive. The UK contains 20% of the total global area of this habitat [10]. However, just 16% of the total area of UK lowland heathlands existing in 1800 still remained in 2002 [10] due to changes in land use [11]. Lowland heathlands support populations of rare species, including specialist plants, birds, reptiles, and invertebrates, including Lepidoptera [12–17]. In the UK, lowland heathlands are a semi-natural habitat maintained by interference with the process of succession, via burning, grazing or cutting [18–21]. However, lowland heathlands are also the protected habitat

61 category in the worst condition in the UK, with only 18% of heathland Sites of Special
62 Scientific Interest (SSSIs) and Special Areas of Conservation (SACs) in favourable
63 condition, due to sub-optimal management [22]. Different heathland species often have
64 very different micro-habitat requirements [23], and optimal management generally
65 attempts to maintain a mosaic of different successional stages that are suitable for a wide
66 range of species.

67 Four substantial remnants of lowland heathland remain in the Vale of York in the
68 UK, all on former common lands — Allerthorpe, Skipwith, South Cliffe, and Strensall
69 Commons — all of which are SSSIs. Skipwith Common is also a National Nature
70 Reserve and SAC, whilst Strensall Common is an SAC. Parts of Allerthorpe Common
71 and Strensall Common are managed as nature reserves by the Yorkshire Wildlife Trust
72 (YWT). Strensall Common, the focus of this study, occupies 570 ha about 10km north of
73 York. Forty-five ha of the north-eastern part comprise the Yorkshire Wildlife Trust
74 reserve. Most of the rest of the land is owned by the UK Ministry of Defence and used
75 for military training, whilst about 10 ha of the eastern portion is managed by the UK
76 Forestry Commission. About 70% of the land is a mosaic of wet and dry heathland, with
77 most of the remainder being deciduous and ‘carr’ woodland. The heathland is the reason
78 for the SAC designation under Annex 1 of the EC Habitats Directive. The site has been
79 ranked as the third most important Lepidoptera site in Yorkshire [24]. Current
80 management includes sheep grazing from spring to autumn by a tenant farmer and
81 periodic scrub and tree removal by cutting to maintain a mosaic of different stages of
82 succession.

83 The Lepidoptera comprise one of the most species-rich orders of insects and are a
84 major component of terrestrial biodiversity [25]. In the UK, many species have seen
85 large population and range declines in the last few decades [26–27] and lepidopterans are
86 thought to be sensitive indicators of environmental change because many of them have
87 very specialized habitat requirements and have shown rapid range, phenological and
88 population responses to a range of factors [28–32]. In addition, their popularity with
89 amateur naturalists, along with the existence of organized monitoring schemes, means
90 that data on distribution and abundance trends are relatively rich, and they are ideal
91 flagship taxa with which to galvanize conservation effort [33].

92 In England, the Dark Bordered Beauty moth, *Epione vespertaria* (Geometridae:
93 Ennominae) (Fig 1) is currently confined to one site, Strensall Common, where it has
94 been known and collected since the 19th Century [34]. Until recently it was also found at

95 Newham Bog in Northumberland, where it is now considered extinct [35]. There are also
96 three known sites in Scotland, where the populations have a somewhat different ecology,
97 feeding on Aspen, *Populus tremula* [36], as opposed to Creeping Willow *Salix repens* in
98 England. *E. vespertaria* is listed as ‘Rare’ in the UK Red Data Book [6] and is listed as a
99 priority species because of the low number of populations, some of small size, and loss
100 of some populations due to suboptimal management [37].

101
102 **Fig 1. *Epione vespertaria*** (A) male and (B) female photographed at Strensall Common.

103
104 *E. vespertaria* is univoltine, with adults flying in July and early August [38]. At
105 Strensall Common, males can be seen flying over the vegetation searching for females
106 after sunrise, and take flight at other times of the day if disturbed, whilst females remain
107 hidden in vegetation during the day and are less easily detected. Both sexes are attracted
108 to light at night. The eggs are laid on host-plant stems, and stay on the host-plant over
109 winter, hatching in late spring the next year, developing through rapid larval and pupal
110 stages.

111 At Strensall Common, the SAC management plan calls for maintenance of a
112 typical plant species complement for this habitat, and focuses on control of scrub
113 invasion as a major threat, but includes no management action specific to *E. vespertaria*
114 [39]. Until recently, the population was thought to be healthy: just prior to the current
115 work, Robertson et al. [38] estimated the population of adults to be 500-1000 individuals
116 spread widely over the Common. As a result, the City of York Local Biodiversity Action
117 Plan does not include a Species Action Plan (SAP) for *E. vespertaria*, because it was not
118 considered threatened at the site, provided that current management was maintained [40].
119 The National SAP called for ten viable populations of the moth to be established by 2010
120 [37]. This aim was not met. However, other actions have been successfully implemented:
121 for example a regular monitoring transect was implemented at Strensall Common, in
122 2007, following work to identify the most important areas of the Common for the moth
123 [38]. In this paper we summarize some of the findings of this monitoring work and
124 subsequent work to establish underlying causes of the population changes. Our results
125 have implications for the management of *E. vespertaria*, and more generally for rare
126 species in protected areas.

Materials and Methods

We are grateful to the Yorkshire Wildlife Trust and UK Ministry of Defence for permission to work on their land, and the Yorkshire Wildlife Trust for participation in survey work.

Salix repens density in 2005

This study was conducted on the northern part of Strensall Common (OS grid cells SE6560 and 6561) where there is unrestricted public access (the area to the south is used for military training and access is restricted) (Fig 2). In 2005, to determine the most important locations of the Common for *E. vespertaria*, density estimates of *S. repens* patches were made for the whole of the northern part of the Common [38]. Rhizomatous growth in *S. repens* precludes easy identification of individual plants. Instead, discrete growth patches were identified [38]. Fifty 200m transects were walked from 3rd June to 17th June 2005 with east-to-west orientations, and with starting locations chosen by random number generation. The number of host plant patches within 2.5m either side of the route was counted every 50m, giving estimates of density in 200 spatial cells.

Fig 2. The northern part of Strensall Common, and surroundings. Grid references are British Grid Coordinates (the ‘4’ prefix refers to position in square ‘SE’ in the OS Grid), and the *E. vespertaria* transect route is marked, with transect sections [\(parts of the walk in which adults are recorded separately to get fine scale spatial distribution data\)](#) numbered. Transect sections 9–11 are separate from the other sections near the junction of Lords Moor Lane and the railway.

Salix repens morphology in 2005

Plant morphological measures (Table 1) were taken in 2005 to establish host-plant preferences of *E. vespertaria*. Larvae are hard to find, therefore to identify adequate samples of patches hosting larvae, a two-phase adaptive sampling technique was used. Patches were sampled from a selection of 44 randomly chosen locations across the northern part of the Common stratified by patch density from the above transect data. All these were thoroughly searched to assess the presence/absence of *E. vespertaria* larvae, and larvae were located in only four of these patches found in three distinct locations (corresponding to sections 3, 8, and 9-11 on the population monitoring transect described below and in Fig 2). In a second phase of searching, to increase the sample size of

161 patches hosting larvae, three 10ha plots were chosen for more systematic searches at the
 162 above three locations. At the centre of each of these plots was a patch on which initial
 163 searches had revealed larval presence. A spiral transect, 5m wide, was walked around
 164 this patch and all *S. repens* patches encountered were searched. The transect was
 165 terminated when more than an hour had elapsed without finding a larva. Sampling for
 166 larval presence was performed from 22nd – 30th June 2005. This raised the number of
 167 patches recorded hosting larvae to 32. To provide a balanced dataset, 32 patches were
 168 randomly sampled from the original 40 patches without larvae. Selected patches with and
 169 without larvae were then tagged and measured as in Table 1.

170 **Table 1. Measurements of *Salix repens* patch morphology**
 171
 172

Variable	Description	Value	Data Type	Method Details
Max Height	Height of tallest stem within a patch.	To an accuracy of 0.5cm	Continuous	Tape measure
Mean Height	Average height from max height and six other stem heights (where possible) – 3 taller stems and 3 shorter stems.	To an accuracy of 0.5cm	Continuous	Tape measure
Max Width	Greatest distance across a patch.	To an accuracy of 0.5cm	Continuous	Tape measure
Mean Leaf Length	Average length of leaves calculated from six individual leaf length measurements.	Measurements accurate to 1mm, mean calculated to 2 d.p.	Continuous	Tape measure – measure the 4 th leaf from the apex if possible. If unable to use 4 th leaf, the 5 th leaf was used.
Mean Leaf Density	The average number of leaves along a 10cm length of stem calculated from 3 separate counts from randomly chosen stems.	1 - ∞	Continuous	Tape measure, visual survey – measure a 10cm stretch of stem from the midpoint between apical leaves and first subsequent leaves. If less than 10cm, 5cm or 2cm lengths of stem were used and multiplied up to a standard 10cm length. Visual survey
Number of Stems	The number of stems present within a patch.	1 - ∞	Integer	Visual survey
Patch Area	Index of planar area covered by patch, as a function of maximum patch width, W_{max} . The index is an estimate based on the assumption of a circular patch morphology.	1 - ∞ cm ²	Continuous	$A=\pi(W_{max}/2)^2$
Patch Volume	Index of volume occupied by foliage, as a function of patch radius. Radius estimated as a combined function of maximum patch width, W_{max} , and maximum patch height, Z_{max} .	1 - ∞ cm ²	Continuous	$V=2/3\pi[((W_{max}/2)+Z_{max})/2]^3$

173

174

175

176

***Epione vespertaria* population monitoring**

177

178

179

180

181

182

183

184

185

186

187

188

189

190

191

192

193

194

195

In 2007 a transect walk, modified from the UK Butterfly Monitoring Scheme (UKBMS) guidelines, was established to cover areas of high moth and host-plant density identified by Robertson et al. [38], but also taking in other areas of the northern part of the Common (Fig 2, SI Appendix). The route was walked at least twice weekly during the adult flight season, from the end of June until moths were no longer apparent, normally at the end of July or early August. All identifiable adult macrolepidoptera seen within 2.5m of the walker were recorded. To facilitate flushing of resting moths, walkers deviated up to 10m from the main route to include patches of *S. repens*, and the walk was conducted between 7 and 10am. Where possible, favourable weather conditions were preferred (warm, sunny, low wind-speed), and temperature and wind-speed were recorded. The walk was 2km long and was divided into 11 sections of between 100m and 275m, with boundaries based on major directional changes and landmarks (Fig 2). Sections 4, 5, and 6 were first added to the transect in 2008 following observations of moths in that vicinity. Sections 9–11 (Fig 2), on the YWT reserve, were included partly because this was where *E. vespertaria* was commonly regarded by the public as easy to find. However, following extinction of the moth in sections 9–11 many walks were terminated at section 8, although several walks each year continued to cover these sections to ensure that the moth was still absent (SI Dataset).

196

***Salix repens* morphology and density in 2013**

197

198

199

200

201

202

203

204

205

206

207

208

The location of *S. repens* patches on the monitoring transect was recorded with a hand-held GPS unit providing readings to the nearest 1m, including patches within 5m of the transect route, between 6th August and 3rd October 2013. Patches were defined as a stem or collection of stems isolated from other stems by at least 30cm. A subsample of the recorded patches was selected for measurement of host-plant morphology, stratified by patch density. In transect sections with fewer than ten patches, all patches were measured; in transect sections with between ten and 20 patches, ten patches were randomly selected and measured; and 20 for those sections with 20 or more (total measured =159). Size and other structural variables were quantified (Table 1). Plant morphology was also quantified at three other locations on the Common at which concentrations of adult moths had been observed in 2013. Two of these sites (named “Kidney Pond” and “Wild Goose Carr” on Ordnance Survey maps, grid refs SE 653597

209 and SE 655595) lie to the south of the studied area in the area restricted for military
210 training (20 patches for each location). The other site lies 15 metres east of the junction
211 between transect sections 2 and 3 (four patches).
212

213 **Data analysis**

214 To test whether adult *E. vespertaria* density had reduced over time, four summary
215 statistics were first compiled from the transect data for each year: (1) the peak count
216 overall for years 2008–2014; (2) the peak count, but omitting sections 4–6, for 2007–
217 2014; (3) the sum, from sections 1 to 11, of the mean count for each section between first
218 and last moth observation dates each year, for years 2008–2014; and (4) the same as (3)
219 but omitting sections 4–6, for years 2007–2014. The natural logarithm of these values
220 was then calculated. Ideally, to test for trends in density over time, one would apply time
221 series statistics to these data to take account of autocorrelation, but the short series
222 preclude this, and analyses were thus limited to simple parametric tests. Linear
223 regressions of all the \ln -transformed summary statistics against year were performed.
224 Although this assumes a lack of autocorrelation in the data, meaning that probabilities are
225 probably inflated, the regression slopes remain informative about the rate of density
226 change.

227 To account for differences in sampling methodology and the limited extent of
228 shared sampling area, comparison of the density of *S. repens* patches along the
229 monitoring transect in 2013 and 2005 required spatial interpolations, which were used to
230 estimate density values in 2005 at unsampled sites from the density data collected on the
231 50 transects that year. Four methods of spatial interpolation were performed for the 2005
232 data in QGIS at a cell size of 25x25m – inverse distance weighting (IDW) on
233 untransformed and \log_{10} -transformed data, and thin plate spline (TPS) on untransformed
234 and \log_{10} -transformed data.

235 The performance of spatial interpolations may be affected by various factors,
236 such as data normality and sample clustering [41]. Therefore, cross-validation was
237 performed to establish which interpolation method yielded the lowest mean-squared-
238 error (MSE). Ten-fold cross-validation was performed by sequentially leaving out a
239 randomly selected 10% of the data, performing the spatial interpolation on the remaining
240 90%, and calculating how close the interpolated density values at the missing 10% points
241 were to the actual density values. This was repeated 10 times for each spatial
242 interpolation method to allow calculation of a MSE for each interpolation method.

243 Kernel density interpolation was performed in R for the 2013 point data to produce
244 estimates of densitiesdensities of the foodplant throughout the monitoring transect ha⁻¹.
245 The resolution of the 2005 data (100m transects with point measurements every 25m)
246 provide the scale limit for this analysis: we extracted the interpolated density for all 25 x
247 25 m cells that had more than 50% overlap with the 2013 data (a total of 64 cells).
248 Because the finest scale resolution is the most uncertain estimate of density for 2013, we
249 repeated the extraction after first aggregating to 50 m resolution (resulting in 21
250 overlapping cells, data reported in results), but the findings are very similar to an analysis
251 at 25m resolution. R packages used for the comparison were rgdal [42], maptools [43],
252 spatstat [44] and raster [45].

253 To explore the relationship between patch density in 2013 and interpolated patch
254 density in 2005, linear regression was performed. Since this produced a pattern of
255 residuals suggesting non-linearity, polynomial regression was performed in R, fitting
256 models of increasing numbers of power terms until the model AIC score no longer
257 reduced. The chosen best model was the simplest model within two AIC units of the
258 model with the lowest AIC score.

259 To explore the variation in plant morphology between the plant patches measured
260 in 2013, patches hosting larvae in 2005, and randomly chosen patches without larvae in
261 2005, Principal Component Analysis (PCA) was performed in R using the packages
262 devtools [46], car [47] and ggbiplot [48]. Standardised values (number of standard
263 deviations away from the mean value) were used to facilitate comparison of variables
264 with different units. A non-parametric one-way ANOVA (Kruskal-Wallis) was
265 performed to compare host-plant characteristics between ‘2013’ patches, ‘2005’ random
266 patches without larvae, and ‘2005’ patches with larvae. To test whether any changes in
267 morphology are restricted to the area of transect sections 1-8, the plants measured in
268 sections 9–11 in 2013 were compared separately with the six randomly chosen plants
269 measured there in 2005.

Results

Adult moth density changes

Linear regressions of all the \ln -transformed summary statistics against year indicate strong declines in adult moth density, which are approximately linear on a log scale, indicating that a relatively constant proportion of the population has been lost annually over the monitoring period (Fig 3). The regression slopes indicate that this proportion is 30-35% annually (Peak count: $y = 506.5 - 0.45x$, $95\%CI(b) = -0.633, -0.265$, $r^2 = 0.89$, $F_{(1,5)} = 39.6$, $p = 0.001$; peak count omitting sections 4-6: $y = 892.4 - 0.44x$, $95\%CI(b) = -0.558, -0.327$, $r^2 = 0.94$, $F_{(1,6)} = 88.0$, $p < 0.001$; sum of mean counts per section: $y = 760.5 - 0.38x$, $95\%CI(b) = -0.579, -0.174$, $r^2 = 0.82$, $F_{(1,5)} = 23.0$, $p = 0.005$; sum of mean counts per section omitting sections 4-6: $y = 723.2 - 0.36x$, $95\%CI(b) = -0.498, -0.219$, $r^2 = 0.87$, $F_{(1,6)} = 39.9$, $p = 0.001$). Although there is no clear non-linearity to the decline (Fig 3), there is also no strong decline in the initial three survey years. If the decline is considered to begin in 2010 (and possibly to level-off in 2012) then the rate of decline would be higher than estimated above. In addition to reductions in density over time, there were reductions in the moth range measured by the number of transect sections in which adults were observed (sections = $1730.3 - 0.86 \times \text{year}$, $r^2 = 0.69$, $F_{(1,5)} = 11.25$, $p = 0.02$). In 2008, adults were seen over all 11 sections (see SI Dataset). That was the last year in which adults were recorded from section 1. Furthermore, with the exception of a single individual in 2010, no adults were recorded after 2008 in sections 9–11. The moth then disappeared from section 2 in 2012. No moths were seen in sections 5 and 6 in 2014, and in every year the mean count per walk has been highest in section 3. This is consistent with retraction in range over the monitored area towards a core area.

Fig 3. Adult *E. vespertaria* density (natural logarithms) through time from transect surveys. (A) peak counts and (B) sum of the mean counts for each transect section. Open symbols are data for all sections combined, whilst closed symbols omit transect sections 4–6 which were first walked in 2008. Solid lines are the linear regressions through the closed symbols, and the curves are the narrow-band (slope) 95% confidence limits on those regressions.

Formatted: Font: Italic

Host-plant density changes

The untransformed TPS interpolation yielded the lowest MSE (Table 2), and was therefore used to ~~calculate~~ estimate host-plant density (Fig 4). A regression of predicted host-plant density against actual host-plant density from the cross validations showed that there was a significant relationship between the two ($F_{(1,198)} = 270.5, p < 0.001$), and that there was a tendency to overestimate low densities and underestimate high densities in the predicted values compared to actual values (predicted = $62.9 + 0.67 \cdot \text{observed}$, $r^2 = 0.577$). The host-plant was patchily distributed in 2005, with high-density patches located close to parts of the route subsequently chosen for the transect, and low-density areas across the eastern part of the site (Fig 4). A small number of negative values arose from the TPS caused by its smoothing effect during interpolation, and these were set to zero.

Table 2. Mean Squared Error (MSE) of the four interpolation methods

Interpolation method	MSE (per ha)
Inverse distance weighting on untransformed data	201
Inverse distance weighting on log-transformed data	271
Thin plate spline on untransformed data	195
Thin plate spline on log-transformed data	290

Fig 4. Interpolated foodplant density (ha^{-1}) across the northern part of the Common in 2005. The transect (sections with numbered labels) and the four areas of greatest density change between 2005 and 2013 are shown (green points, see Fig 5). UK Grid locations are given at 0.5km intervals.

Densities from 2013 measured along the monitoring transect were compared with the interpolated values for the same locations from 2005 (Fig 5). The relationship was significantly non-linear, with the AIC score for a cubic model (147.98) being lower than that of a linear model (169.46), a quadratic model (153.98) and a quadrinomial model (148.95). For locations with <100 patches per hectare in 2005, there was very little change in density. For locations with 200-600 patches per hectare in 2005, there was a density reduction of two-to-three fold by 2013. For the four locations with highest

density in 2005, there was a density reduction of 9-fold to 14-fold by 2013. Excluding four outliers, there was a strong linear relationship between the density measures ($y = 32.1 + 0.29x$, $r^2 = 0.86$, $F_{(1,15)} = 91.7$, $p < 0.001$), suggesting that on average patch density had reduced three fold between 2005 and 2013. The outliers (Fig 5), showed a density reduction of 9 fold to 14 fold. The most dramatic of these was in section 3 of the transect (Figs 4 and 5) — a reduction from 1436 ha⁻¹ in 2005 to 107 ha⁻¹ in 2013. Three out of four of these areas – the two most southerly and one most northerly in Fig 4 – were located in areas of highest plant density in 2005 [38]. These “hot-spots” were no longer distinguishable as such in 2013.

Fig 5. *Salix repens* patch density (ha⁻¹) on the transect in 2005 and 2013.

The solid black line is the cubic polynomial: $y = 99.19 + 158.19x - 177.01x^2 + 87.41x^3$, $r^2 = 0.795$. The dashed lines show the broad-band (prediction) 95% confidence limits.

The solid black line is $y = x$, the dashed line is the linear regression excluding the four outliers on the right of the graph (green points in Fig 4), which represented the stronghold of the population in 2005, and have undergone the most severe density reductions.

Host-plant morphology changes

Eight morphology variables were used in the PCA (Table 1). PC1 accounted for 62.4% of the variation and PC2 accounted for 13.5% of the variation, thereby collectively explaining 75.9% of the variation in the data (Fig 6). PC1 was negatively correlated with overall size indicators such as plant width, height, stem number, area and volume (Table 3). PC2 was negatively correlated with stem number, leaf density and area and positively correlated with plant height (Table 3), thereby differentiating between tall thin plants and short wide ones.

Fig 6. Biplot of the first two Principle Components for *Salix repens* patch morphology. Closed circles are patches containing *E. vespertaria* larvae from 2005, open circles are random patches from 2005, and open triangles are patches along the monitoring transect from 2013.

Table 3. The correlation of variables to Principal Components^a.

Variable	PC1	PC2
Maximum width	-0.3969	-0.2575

Maximum height	-0.3673	0.3975
Mean height	-0.3692	0.4134
Stem number	-0.3745	-0.4099
Leaf length	-0.3240	0.3166
Leaf density	0.1623	-0.3808
Area	-0.3892	-0.4233
Volume	-0.3849	-0.1107

^aThe higher the absolute value of the coefficient, the more important the variable is to the PC.

A significant difference in PC1 between ‘2005’ patches with larvae, ‘2005’ random patches and ‘2013’ patches was found (Kruskal-Wallis: $\chi^2 = 112.22$; d.f. = 2; $p < 0.001$) (Fig 7A). The largest host-plant patches (denoted by PC1) occurred in ‘2005’ plants with larvae. Random patches in 2005 were smaller (Mann-Whitney: $W = 859$, $n_1 = 32$, $n_2 = 32$, $p < 0.001$), and smaller still were ‘2013’ patches (Mann-Whitney: $W = 851$, $n_1 = 32$, $n_2 = 202$, $p < 0.001$). A significant difference in PC2 between ‘2005’ plants with larvae, ‘2005’ random plants and ‘2013’ plants was also found (Kruskal-Wallis: $\chi^2 = 24.4$; d.f. = 2; $p < 0.001$) (Fig 7B). Although ‘2005’ plants with larvae had significantly ‘taller-thinner’ shape than ‘2005’ random plants (Mann-Whitney: $W = 740$, $n_1 = 32$, $n_2 = 32$, $p < 0.001$), there was no significant difference in PC2 between random 2005 and 2013 plants (Mann-Whitney: $W = 3628$, $n_1 = 32$, $n_2 = 202$, $p = 0.29$). This suggests that although plants were significantly smaller in 2013 than 2005, there was no significant difference in food-plant shape between the two years.

Fig 7. Box plots comparing Principle Component values of *Salix repens* patch morphology in ‘2005’ patches containing *E. vespertaria* larvae, ‘2005’ random patches without larvae, and ‘2013’ patches. (A) PC1, all data, (B) PC2, all data, and (C) PC1 for the subset of ‘2005’ plants sampled on the transect route. Plots show the median, interquartile range, outliers ($>1.5 \times \text{IQR}$), and the range for non-outliers (whiskers).

A subset of ~~200513~~ data was investigated in order to ~~rule out~~reduce the potential for biases in host-plant quality comparisons. Using patches located only in the monitoring transect, differences in PC1 values were compared between the three groups (Fig 7C). A significant difference between ‘2005’ patches with larvae in the transect, ‘2005’ random patches in the transect and ‘2013’ patches was found (Kruskal-Wallis: χ^2

388 = 54.47; d.f. = 2; $p < 0.001$), with significantly larger sizes in random 2005 patches than
389 in 2013 patches (Mann-Whitney: $W = 200$, $n_1 = 5$, $n_2 = 202$, $p = 0.02$). This was the same
390 finding as for the original full dataset. However, there was no difference between ‘2005’
391 patches with larvae and ‘2005’ random patches (Mann-Whitney: $W = 64$, $n_1 = 29$, $n_2 = 5$,
392 $p = 0.706$), indicating that plants on the current transect route in 2005 were generally
393 large and suitable for larvae. Note however that the sample size for ‘2005’ random
394 patches on the transect is only 5. A Mann-Whitney U-test showed that the randomly
395 chosen plants measured close to transect sections 9-11 in 2005 had significantly smaller
396 values of PC1 than the plants measured there in 2013 ($W = 869$, $n_1 = 6$, $n_2 = 36$, $p <$
397 0.001). This suggests that the size changes are not restricted to one part of the site.

398 The frequency distributions of *S. repens* mean patch heights (Fig 8) shows the
399 extent of size reduction by 2013. The largest size classes from 2005 appear to be absent
400 in 2013. In 2005 6.3% of random patches were larger than the median height of patches
401 on which larvae were found, and 53% were larger than the fifth percentile of patch
402 heights. By 2013, on the monitoring transect, only 1% were larger than the median patch
403 height on which larvae were found in 2005, and just 14% were larger than the fifth
404 percentile. Recall that the monitoring transect route was chosen to encompass the best
405 habitat over the north of the Common for *E. vespertaria*.

406
407 **Fig 8. The height of *Salix repens* patches (mean of maximum height and six**
408 **other stems).** (A) patches with *E. vespertaria* larvae in 2005, (B) random patches in
409 2005 and (C) patches in 2013 on the monitoring transect.

411 Discussion

412 Here we have shown that, following commencement of a monitoring programme as part
413 of the UK Species Action Plan for *E. vespertaria*, adult numbers at Strensall Common,
414 its last known English site, declined on average by 30-35% annually from 2007 to 2014,
415 coincident also with a contraction in range towards a core location within the monitored
416 area. These strong declines indicate a reduction in the suitable environmental conditions
417 for the species during the same period. Data also suggest changes in the population of
418 host-plants during this time, with strong declines in *S. repens* patch density as well as
419 reductions in overall patch size. This suggests that effects of environmental changes on
420 the moth are being mediated through the host plant. Previous work on Lepidoptera
421 populations has also shown that the presence of the preferred subset of larval food

422 sources ('host-plant quality') is the most important factor determining population
423 trajectories within individual sites [49].

424 Strensall Common is a site with statutory protection under Annex I of the EU
425 Habitats Directive, and the site is managed to conserve the heathland by sheep grazing
426 and tree/shrub removal to maintain a mosaic of different stages of succession. Previous
427 work at the Common has shown that the presence of *E. vespertaria* larvae is predicted by
428 the presence of tall plant patches at high density close to trees [38]. Consistent with this,
429 Butterfly Conservation characterized the species' English habitat as lightly wooded
430 heathland [50]. Ostensibly then, the management strategy on the Common seems well-
431 suited to maintain the conditions required by the moth. However, Robertson et al. [38]
432 also found that larvae and adults were concentrated in a small number of 'hot-spots'
433 where the most favourable habitat was found. This potentially made the population
434 vulnerable to subtle widespread environmental changes or to very drastic but local ones.

435 A drastic local change occurred between August 2009 and April 2010, when the
436 hot-spot in section 3 of the transect was destroyed by a fire (Fig 9) [51–53]. Some *S.*
437 *repens* is now regenerating in this area but the plants remain low-growing (e.g. Fig 10B),
438 and as indicated by Fig 5, fewer in number. Fig 3 indicates that 2009-10 coincided with a
439 greater reduction in *E. vespertaria* population density than had occurred previously.
440 However, two factors indicate that this is not the sole reason for the decline of the moth
441 on the Common. First, one of the other hot-spots, on the Yorkshire Wildlife Trust reserve
442 covered by sections 9-11, well separated from section 3, also showed a decline to
443 extinction even before the fire. Second, the overall decline continued well after 2010.

444
445 **Fig 9. Views of a location near transect section 3, OS Grid ref SE 65225 60975.** (A)
446 Looking south-west in 2005, with (1) large *S. repens* bushes (2) small and (3) large
447 *Betula pendula* (Silver Birch) trees, and (4) the path along which the transect runs. The
448 ruler is 1m high. (B) The same location at the same time of year looking north-east in
449 2013. The ground vegetation is considerably shorter with (1) the remains of dead shrubs
450 (2) regrowth of grasses. This area was burned between the 2009 and 2010 transect
451 surveys. (A) Reproduced from [38] with permission.

452
453 **Fig 10. *Salix repens* patches.** (A) a tall patch (>1m high) from 2005 (B) a prostrate
454 patch with low creeping growth from 2015 (~5cm high) (C) an upright shoot from 2015

455 (~40cm high), with foliage removed by grazing, showing attached sheep wool in the top
456 right of the photo. (A) Reproduced from [38] with permission.

457
458 One possible factor contributing towards a decline, both before and after 2010, is
459 grazing. Grazing damage has recently been evident on most *S. repens* patches covered by
460 the transect, from the loss of the growing tips of stems, the presence of sheep wool on the
461 plants, and the cropping of neighbouring plants of other species (Fig 10C). Although
462 there has been no official change in the grazing management strategy coincident with the
463 decline, it appears likely that local changes in grazing pressure have occurred. In 2007
464 there was a change in grazer, and since then sheep on the northern part of the Common
465 appear to have been concentrated close to transect sections 1-8, especially when
466 supplemental fodder is left out (near sections 7 and 8). In addition, sheep have been
467 observed on the Common outside the established grazing period, indicating that not all
468 sheep were removed for the whole winter [54]. Even in areas unaffected by fire, these
469 changes may have been sufficient to reduce the size and density of host-plant patches.
470 However, the declines in plant patch size seen around transect sections 9-11 indicate that
471 proximity to supplemental fodder may not be the sole cause of the changes seen.

472 Another possible contributor to the post-2009 declines is frost damage to plants.
473 The winter of 2009-2010 was locally the coldest since 1987 [55]. The following winter
474 was also severe, with the coldest start to the year (2011) for 100 years [56]. February
475 2012 was severe with an ice storm on 8th, and severe frosts in April [57], whilst January
476 to March 2013 were cold, with an ice storm on 25th Jan, and the second-coldest March on
477 record [58]. *Ad hoc* observations suggest that many of the larger plants experienced die-
478 back of exposed stems during this period [53]. However, the processes causing die-back
479 and size reduction at the site are not well-understood; observations of a clump of large *S.*
480 *repens* bushes just east of transect section 2 in summer of 2014 indicated blackening of
481 leaves and stem die-back, clearly not caused by frost or fire, while grazing damage was
482 evident. It is possible that grazing contributes to die-back and infection of plants by
483 weakening them. Overall it appears that there are multiple, perhaps interacting, causes of
484 the decline in *S. repens*, ~~and consequently *E. vespertaria*.~~

485 There are several possible reasons why the observed changes to host-plants might
486 cause a decline in moth density. First, they might decrease the oviposition rate of female
487 *E. vespertaria*. Females might experience a reduction in oviposition cues from smaller,
488 low-density plants. Other species of Lepidoptera are known to avoid ovipositing on

489 damaged plants and to select preferentially large, robust or vigorously growing plants
490 (e.g. [59-61], although the preferred characteristics of each host-plant varies widely
491 across Lepidoptera species [49]. Death or removal of stems, such as through grazing,
492 may also cause direct mortality of juvenile life history stages, especially eggs. *E.*
493 *vespertina* eggs are laid on host-plant stems and remain there from August through to
494 late spring [38]. They are therefore vulnerable to removal or damage for extensive
495 periods of time. The Dingy Skipper *Erynnis tages* (L.) is another Lepidoptera species of
496 conservation concern in the UK that is vulnerable to grazing pressure during the egg
497 stage because females oviposit on the tips of large host-plants [60] which are likely to be
498 removed by grazing animals. Grazing is also typically used to improve the overall
499 condition of the grassland sites that it favours, and conservation recommendations now
500 advise lack of grazing during this critical life history stage. However, the egg stage of *E.*
501 *vespertina* is vulnerable for a much longer period than that of *E. tages*.

502 Although we have shown declines in the moth population and changes to the
503 foodplant on the northern part of the Common, the monitoring transect does not cover
504 areas to the south of the study area where access is restricted due to military training. In
505 2013, surveys found adult moths present at two discrete locations in this area, and
506 smaller numbers were seen at both in 2014, although searches in other areas where it was
507 formerly present have failed to locate it, suggesting a general decline over the Common.
508 The disappearance of the moth from sections 9-11 of the monitoring transect along with
509 changes in host plants there suggests that the environmental changes affecting the moth
510 are not entirely localized. Sheep grazing is also present within this restricted area.
511 Targeted conservation work in this area is difficult, making the conservation of the
512 population on the northern part of the Common all the more important.

513 Although the plant-patch size measurements were made in different months in
514 2005 and 2013, the later measurement dates in 2013 would be expected to produce a
515 height bias in the opposite direction to that found in the absence of a decline, given the
516 additional time for annual growth prior to leaf fall. Photographic evidence (e.g. Fig 9)
517 and testimony of transect walkers is consistent with the statistical height trends found
518 across years [53]. Consistency of measurement is more difficult when assessing the
519 density of patches and their width, especially since different observers made the
520 measurements in different years, and interpolation techniques were used to compare
521 density. In practice, distinguishing *S. repens* patches consistently is not easy, as there are
522 many marginal cases (where one observer might distinguish only one patch, but others

523 identify multiple patches). Small *S. repens* patches may be missed in amongst other
524 vegetation. Nonetheless, several factors argue that the major statistical trends are valid.
525 First, the differences are very large and there was appreciable intersection of the areas
526 sampled, particularly in the high-density hotspots where the overall direction of the
527 changes is likely to be robust (e.g. Fig 9). Second, they are consistent with the anecdotal
528 observations of transect walkers, where transect sections once well populated by patches
529 are now nearly devoid of them [53]. Third, some likely biases would probably operate in
530 the opposite direction to the major findings; for example, small low growing patches are
531 less likely to have been missed in 2013 when they were the typical form of the plant,
532 suggesting that density at this time is unlikely to have been underestimated, whilst the
533 density estimates in 2005 tended to underestimate high densities (see Results).

534 Immediate conservation action on Strensall Common must focus on the recovery
535 of large, high density patches of *S. repens* in areas still occupied by *E. vespertaria*, and
536 then extending a network of such patches across the Common to create a more robust
537 population. To this end, on 22nd April 2015, nine small (2.4 x 2.4m) grazing exclosures
538 containing established but mainly low-growing *S. repens* patches, were erected along the
539 transect route. Some of these exclosures have been enhanced by planting pot-grown *S.*
540 *repens* using cuttings or seed taken from Strensall Common. It is hoped that these will
541 create patches of large plants which may help stem the decline of the moth in the
542 monitored area. Measurements of the *S. repens* inside and immediately outside the
543 exclosures will test the hypothesis that a reduction in grazing pressure can increase the
544 size of *S. repens* patches, establishing a basis for a more general change in management
545 on the Common. This might take the form of changes in the local distribution of sheep on
546 the Common, perhaps by more active shepherding of animals into areas of less
547 importance to *E. vespertaria*. Cattle or pony grazing may be an alternative that could
548 benefit *S. repens* through dissipating grazing more widely across other plant species and
549 by providing disturbance that can encourage *S. repens* establishment [62–64]. Further
550 into the future, it is essential that more populations of the moth be established, as
551 recommended on the SAP. There would have been more scope to carry this out before
552 the current decline at Strensall occurred, as the population at Strensall is now too small to
553 justify removal of individuals, and could be genetically impoverished, whereas the
554 numbers necessary to establish new populations were readily available up until 2009
555 (although other relevant factors, such as the identification of suitable introduction sites,

556 were not in place at that time). In the meantime, the risk of extinction of the population at
557 Strensall Common now translates into a risk of extinction in England as a whole.

558 More generally, our work reinforces some important lessons for conservationists.
559 First, given the sheer number of species and limited resources for conservation, the
560 majority of species can never receive direct, targeted management. The survival of rare
561 but relatively poorly-understood species must therefore rely on the maintenance of
562 suitable habitats, but the particular requirements of different species make it likely that
563 generic management strategies for habitats will not benefit all species [65]. This may
564 have been the case with *E. vespertaria* at Strensall Common, which could probably have
565 benefited from reduced grazing pressure in recent years, despite the need to maintain
566 grazing of the site more generally. Had *E. vespertaria* not been monitored, as is the case
567 for many taxonomic groups, ignorance of its decline would preclude any targeted action
568 to aid recovery, making extinction more likely. Indeed, there is a history of rare species
569 disappearing from protected areas due to inappropriate management [66]. The solution to
570 this problem is not simple, but probably rests in securing greater knowledge of the
571 requirements of a large number of species, and an increase in the robustness of the
572 protected area network [67]. In the case of *E. vespertaria*, volunteer and student effort
573 has greatly underpinned much of the data we present here.

574 Second, our study warns against complacency when species are restricted to small
575 numbers of sites, even if their populations at such sites appear healthy. In the case of *E.*
576 *vespertaria*, the national SAP recommended an increase in the number of sites, but this
577 was not subsequently implemented, even with relatively good knowledge of the species'
578 requirements as described by Robertson et al. [38]. In fact a local SAP was deemed
579 unnecessary. However, it can be argued that a period when populations of localized rare
580 species are healthy presents the greatest opportunity to increase the number of
581 populations, providing other necessary factors are also in place [68].

582 Third, our study illustrates the value of monitoring programmes for rare species.
583 Resources do not always make this practical (e.g. for species not easily counted, or for
584 which there is little volunteer enthusiasm), but the information gained can allow time for
585 remedial action to be taken and also provide data or observations helpful to reversing
586 declines and implementing revised management.

587 In summary, we have shown that the decline of the rare moth *E. vespertaria* at its
588 last English site is likely linked to changes in host plant density and size. We hope in
589 future to report on the effects of restorative action to reduce grazing in areas critical for

590 *E. verspertina* and increase the size of host-plants. Ultimately we hope to implement
591 management actions that will once again make the Dark Bordered Beauty a common
592 sight at Strensall, and secure its long-term future in England.
593

594 **Acknowledgements**

595 We are grateful to the Yorkshire Wildlife Trust and UK Ministry of Defence for
596 permission to work on their land, and the Yorkshire Wildlife Trust for participation in
597 survey work.
598
599
600

601
602
603
604
605
606
607
608
609
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
628
629
630

References

1. United Nations. Convention on Biological Diversity. Montreal: Secretariat of the Convention on Biological Diversity; 1992.
2. Dirzo R, Raven PH. Global state of biodiversity and loss. *Annu Rev Env Resour.* 2003; 28: 137-167.
3. Millennium Ecosystem Assessment. *Ecosystems and Human Well-being: Synthesis.* Washington: World Resources Institute, Island Press; 2005.
4. Biodiversity Reporting and Information Group. Report on the Species and Habitat Review: Report by the Biodiversity Reporting and Information Group. Peterborough: Joint Nature Conservation Committee; 2007.
5. Perring FH, Farrell L (editors). *British Red Data Books: 1 Vascular Plants.* 2nd ed. Lincoln: Royal Society for Nature Conservation; 1983.
6. Shirt D (editor). *British Red Data Books: 2 Insects.* Peterborough: Nature Conservancy Council; 1987.
7. Bratton JH (editor). *British Red Data Books: 3 Invertebrates other than Insects.* Peterborough: Nature Conservancy Council; 1991.
8. English Nature. *Grazing management of lowland heathlands.* Peterborough: English Nature; 2005.
9. UK Biodiversity Steering Group. *Biodiversity: The UK Steering Group Report. Vol 2. Action Plans.* London: HMSO; 1995.
10. English Nature. *Lowland heathland: a cultural and endangered landscape.* Peterborough: English Nature; 2002.
11. Pywell RF, Meek WR, Webb NR, Putwain PD, Bullock JM. Long-term heathland restoration on former grassland: the results of a 17-year experiment. *Biol Conserv.* 2011; 144: 1602-1609.
12. Ying-Chi L, James R, Dolman PM. Conservation of heathland ground beetles (Coleoptera, Carabidae): the value of lowland coniferous plantations. *Biodivers Conserv.* 2007; 16: 1337-1358.

- 631 13. Clements, R. The Hobby in Britain: A new population estimate. *British Birds*. 2001;
632 94: 402-408.
- 633 14. van den Berg LJJ, Bullock JM, Clarke RT, Langston RHW, Rose RJ. Territory
634 15. selection by the Dartford warbler (*Sylvia undata*) in Dorset, England: the role of
635 vegetation type, habitat fragmentation and population size. *Biol Conserv*. 2001; 101:
636 217-228.
- 637 16. English Nature. Reptiles: guidelines for developers. Peterborough: English Nature;
638 2004.
- 639 17. Stokes KE, Allchin AE, Bullock JM, Watkinson AR. Population responses of *Ulex*
640 shrubs to fire in a lowland heath community. *J Veg Sci*. 2004; 15: 505-514.
- 641 18. Schirmel J, Fartmann T. Coastal heathland succession influences butterfly
642 community composition and threatens endangered butterfly species. *J Insect Conserv*.
643 2014; 18: 111-120.
- 644 19. Bakker JP, de Bie S, Dallinga JH, Tjaden P, de Vries Y. Sheep-grazing as a
645 management tool for heathland conservation and regeneration in the Netherlands. *J*
646 *Appl Ecol*. 1983; 20: 541-560.
- 647 20. Webb N. Heathlands. *New Naturalist* 72. London: Collins; 1986.
- 648 21. Newton AC, Stewart GB, Myers G, Diaz A, Lake S, Bullock JM, Pullin AS. Impacts
649 of grazing on lowland heathland in north-west Europe. *Biol Conserv*. 2009; 142: 935-
650 947.
- 651 22. Williams JM (editor). *Common Standards Monitoring for Designated Sites: First Six*
652 *Year Report*. Peterborough: Joint Nature Conservation Committee; 2006.
- 653 23. Thomas JA, Rose RJ, Clarke RT, Thomas CD, Webb NR. Intraspecific variation in
654 habitat availability among ectothermic animals near their climatic limits and at their
655 centres of range. *Funct Ecol*. 1999; 13: 55-64.
- 656 24. Rutherford CI. The Lepidoptera of Yorkshire: A commentary. *Naturalist*. 1971; 918:
657 93-104.
- 658 25. Resh VH, Cardé RT (editors). *Encyclopedia of Insects*. 2nd edn. San Diego:
659 Academic Press; 2009.

- 660 **26.** Fox R, Brereton TM, Asher J, Botham MS, Middlebrook I, Roy DB, Warren MS.
661 The state of the UK's butterflies 2011. Wareham, Dorset: Butterfly Conservation and
662 the Centre for Ecology & Hydrology; 2011.
- 663 **27.** Fox R, Parsons MS, Chapman JW, Woiwod IP, Warren MS, Brooks DR. The State of
664 Britain's Larger Moths 2013. Wareham, Dorset: Butterfly Conservation and
665 Rothamsted Research; 2013.
- 666 **28.** Roy DB, Sparks TH. Phenology of British butterflies and climate change. *Glob*
667 *Chang Biol.* 2000; 6: 407-416.
- 668 **29.** Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, et al. Rapid responses
669 of British butterflies to opposing forces of climate and habitat change. *Nature*, 2001;
670 **414**: 65-69.
- 671 **30.** Sparks TH, Huber K, Dennis RLH. Complex phenological responses to climate
672 warming trends? Lessons from history. *Eur J Entomol.* 2006; 103: 379-386.
- 673 **31.** Fox R. The decline of moths in Great Britain: a review of possible causes. *Insect*
674 *Conserv Divers.* 2013; 6: 5-19.
- 675 **32.** Fox R, Oliver TH, Harrower C, Parsons MS, Thomas CD, Roy DB. Long-term
676 changes to the frequency of occurrence of British moths are consistent with opposing
677 and synergistic effects of climate and land-use changes. *J Appl Ecol.* 2014; 51: 949-
678 957.
- 679 **33.** New TR. *Lepidoptera and Conservation.* Oxford: Wiley-Blackwell; 2013.
- 680 **34.** Frost HM, Beaumont HE, Crawford TJ, Fryer G, Yeates CSM (editors). *Porritt's*
681 *Lists: A Reprint of George T Porritt's Yorkshire Butterfly & Moth Records First*
682 *Published in 1883-86, 1904, 1907, & 1922 - Revised into Modern Order with*
683 *Detailed Comments and Background.* Butterfly Conservation Yorkshire, Yorkshire
684 *Naturalists' Union;* 2011.
- 685 **35.** Tams TJ. Northumberland Lepidoptera review 2013. *The Vasculum.* 2014; 99: 33-48.
- 686 **36.** Parrott J, MacKenzie N (editors). *Aspen in Scotland: biodiversity and management.*
687 *Boat of Garten: Highland Aspen Group;* 2009.
- 688 **37.** UK Biodiversity Group. *Tranche 2 Action Plans: Invertebrates.* Peterborough:
689 *English Nature;* 1999.

- 690 38. Robertson P, Ellis S, Small J. The Dark Bordered Beauty *Epione vespertaria* (L.)
691 moth in northern England. Butterfly Conservation Report No S06-02. Wareham,
692 Dorset: Butterfly Conservation; 2006.
- 693 39. Natural England. Site Improvement Plan: Strensall Common (SIP273), 2014.
694 Available: <http://publications.naturalengland.org.uk/publication/6435201697710080>
- 695 40. City of York Council. City of York Biodiversity Action Plan (May 2013). York: City
696 of York Council; 2013.
- 697 41. Li J, Heap AD. A review of comparative studies of spatial interpolation methods in
698 environmental sciences: performance and impact factors. *Ecol Inform.* 2011; 6: 228-
699 241.
- 700 42. Bivand R, Keitt T, Rowlingson B. rgdal: Bindings for the Geospatial Data
701 Abstraction Library. R package version 0.9-1. 2014. Available: [http://CRAN.R-](http://CRAN.R-project.org/package=rgdal)
702 [project.org/package=rgdal](http://CRAN.R-project.org/package=rgdal)
- 703 43. Bivand R, Lewin-Koh N. maptools: Tools for Reading and Handling Spatial Objects.
704 R package version 0.8-30. 2014. Available: [http://CRAN.R-](http://CRAN.R-project.org/package=maptools)
705 [project.org/package=maptools](http://CRAN.R-project.org/package=maptools)
- 706 44. Baddeley A, Turner R. spatstat: an R package for analyzing spatial point patterns. *J*
707 *Stat Softw.* 2005; 12: 1-42.
- 708 45. Hijmans RJ. raster: Geographic Data Analysis and Modelling. R package version 2.3-
709 24. 2015. Available: <http://CRAN.R-project.org/package=raster>
- 710 46. Wickham H, Chang W. devtools: Tools to Make Developing R Packages Easier. R
711 package version 1.7.0. 2015. Available: [http://CRAN.R-](http://CRAN.R-project.org/package=devtools)
712 [project.org/package=devtools](http://CRAN.R-project.org/package=devtools)
- 713 47. Fox J, Weisberg S. An R Companion to Applied Regression. 2nd ed. Thousand Oaks,
714 CA: Sage; 2011.
- 715 48. Vu VQ. ggbiplot: A ggplot2 based biplot. R package version 0.55. 2011. Available:
716 <http://github.com/vqv/ggbiplot>
- 717 49. Thomas JA, Simcox DJ, Hovestadt T. Evidence based conservation of butterflies. *J*
718 *Insect Conserv.* 2011; 15, 241-258.

- 719 **50.** Wigglesworth T, Parsons M, Warren M. Dark Bordered beauty *Epione vespertaria*
720 Factsheet. Wareham, Dorset: Butterfly Conservation. Available: <http://butterfly->
721 [conservation.org/files/dark_bordered_beauty-psf.pdf](http://butterfly-conservation.org/files/dark_bordered_beauty-psf.pdf)
- 722 **51.** Baker D. Yorkshire's Dark Bordered Beauty. *Naturalist*. 2012; 137: 11-15.
- 723 **52.** Baker D. The Dark Bordered Beauty: background. *Argus*. 2012; 65: 6-12.
- 724 **53.** Crawford, TJ. Monitoring the Dark Bordered Beauty at Strensall 2007-2012. *Argus*.
725 2012; 65: 12-15.
- 726 **54.** Graham B. Preliminary exploration on quantifying winter grazing to aid conservation
727 of the *Epione vespertaria*. MSc Thesis, The University of York, UK. 2014.
- 728 **55.** Frost HM (editor). Yorkshire Butterflies and Moths 2010. *Argus*. 2011; 63.
- 729 **56.** Frost HM (editor). Yorkshire Butterflies and Moths 2011. *Argus*. 2012; 66.
- 730 **57.** Frost HM (editor). Yorkshire Butterflies and Moths 2012. *Argus*. 2013; 69.
- 731 **58.** Frost HM (editor). Yorkshire Butterflies and Moths 2013. *Argus*. 2014; 72.
- 732 **59.** Ravenscroft NOM. The ecology of the Chequered Skipper Butterfly *Carterocephalus*
733 *palaemon* in Scotland. I. Microhabitat. *J Appl Ecol*. 1994; 31: 613-622.
- 734 **60.** Gutierrez D, Thomas CD, León-Cortés JL. Dispersal, distribution, patch network and
735 metapopulation dynamics of the dingy skipper butterfly (*Erynnis tages*). *Oecologia*.
736 1999; 121: 506-517.
- 737 **61.** Betzholtz P-E, Ehrig A, Lindeborg M, Dinnétz P. Food plant density, patch isolation
738 and vegetation height determine occurrence in a Swedish metapopulation of the
739 marsh fritillary *Euphydryas aurinia* (Rottemburg, 1775) (Lepidoptera, Nymphalidae).
740 *J Insect Conserv*. 2007; 11: 343-350.
- 741 **62.** Grant SA, Torvell L, Common TG, Sim EM, Small JL. Controlled grazing studies on
742 *Molinia* grassland: effects of different seasonal patterns and levels of defoliation on
743 *Molinia* growth and responses of swards to controlled grazing by cattle. *J Appl Ecol*.
744 1996; 33: 1267-1280.
- 745 **63.** Taylor K, Rowland AP, Jones HE. *Molinia caerulea* (L.) Moench. *J Ecol*. 2001; 89:
746 126-144.

- 747 **64.** Martin D, Fraser MD, Pakeman RJ, Moffat AM. Natural England Review of Upland
748 Evidence 2012: Impact of moorland grazing and stocking rates. Natural England
749 Evidence Review, Number 006. Sheffield: Natural England; 2013.
- 750 **65.** Webb JR, Drewitt AL, Measures GH. Managing for species: integrating the needs of
751 England's priority species into habitat management. Part 1 Report. Natural England
752 Research Reports, Number 024. Sheffield: Natural England; 2010.
- 753 **66.** Rothschild M, Marren P. Rothschild's Reserves: Time and Fragile Nature. Rehovot:
754 Balaban; 1997.
- 755 **67.** Lawton JH, Brotherton PNM, Brown VK, Elphick C, Fitter AH, Forshaw J, et al.
756 Making space for nature: a review of England's wildlife sites and ecological network.
757 Report to Defra. London: Defra; 2010.
- 758 **68.** Hochkirch A, Witzemberger KA, Teerling A, Niemeyer F. Translocation of an
759 endangered insect species, the field cricket (*Gryllus campestris* Linnaeus, 1758) in
760 northern Germany. *Biodivers Conserv.* 2007; 16: 3597–3607.

761

762

763

Supporting Information

764

SI Appendix: Transect route description written in 2008.

765

SI Dataset: Transect count data for adult *Epione vespertaria* 2007–2014; 2013 *Salix*

766

***repens* patch location data along the transect route; 2013 *S. repens* patch**

767

morphology data along the transect route; 2005 *S. repens* patch density data; 2005

768

***S. repens* patch morphology data.**