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ORIGINAL PAPER

Host-plant patch qualities and presence of a likely competitor species affect the distribution and abundance of a rare British moth, *Cucullia lychnitis*

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Abstract Understanding the environmental factors that affect the distribution and abundance of rare and threatened species can help identify priority sites for conservation action such as habitat management. The moth *Cucullia lychnitis* is identified in UK legislation as a priority species for conservation. Its conspicuous larvae feed on a patchily distributed host plant *Verbascum nigrum*, but are entirely absent from some host plant patches within the species' range. Environmental variability among patches was investigated to understand factors affecting (i) patch occupancy by *C. lychnitis* and (ii) abundance of *C. lychnitis*, where present. Occupancy of individual *V. nigrum* plants within occupied patches was also investigated. The likelihood of patch occupancy increased with patch size, and decreased with patch isolation. Abundance of *C. lychnitis* was negatively correlated with patch isolation and with abundance of the weevil *Cionus nigritarsis*, which exploits the same host plant and may be a competitor. Within occupied patches, larvae of *C. lychnitis* were significantly more likely to be found on taller plants with more flower spikes; such plants are typical of established rather than newly-created patches. These results may help to guide efforts to conserve *C. lychnitis*, highlighting the importance of habitat connectivity and indicating potential management actions to promote features positively associated with larval incidence and abundance.

Keywords Conservation · Interspecific competition · Lepidoptera · Metapopulations · Road verges · Spatial ecology

Introduction

Reversing declines in biodiversity will often require conservation action targeted at species that are in decline. In the United Kingdom (UK), for example, legislation identifies 2,888 species considered to be "of principal importance for the purpose of conserving biodiversity" which are priorities for conservation [Natural Environment and Rural Communities (NERC) Act 2006]. Among a number of Lepidoptera species on this list is the Striped Lychnis *Cucullia lychnitis* Rambur (Lepidoptera: Noctuidae; listed under its former name *Shargacucullia lychnitis*). This species occurs across much of Europe, but in the UK is restricted to two centres of population in central southern England, one in Oxfordshire, Berkshire and Buckinghamshire, and one slightly further south in Hampshire and West Sussex (Fig. 1). This restricted range is reported to represent a considerable contraction of the species' historic range, with the species historically recorded as far afield as Gloucestershire in the west of England and Essex in the east (Heath and Emmet 1983). Its declining range size accounts for its selection as a Priority Species in the NERC Act (2006), and *C. lychnitis* appears to have continued to decline since being listed (Rosenthal 2011).

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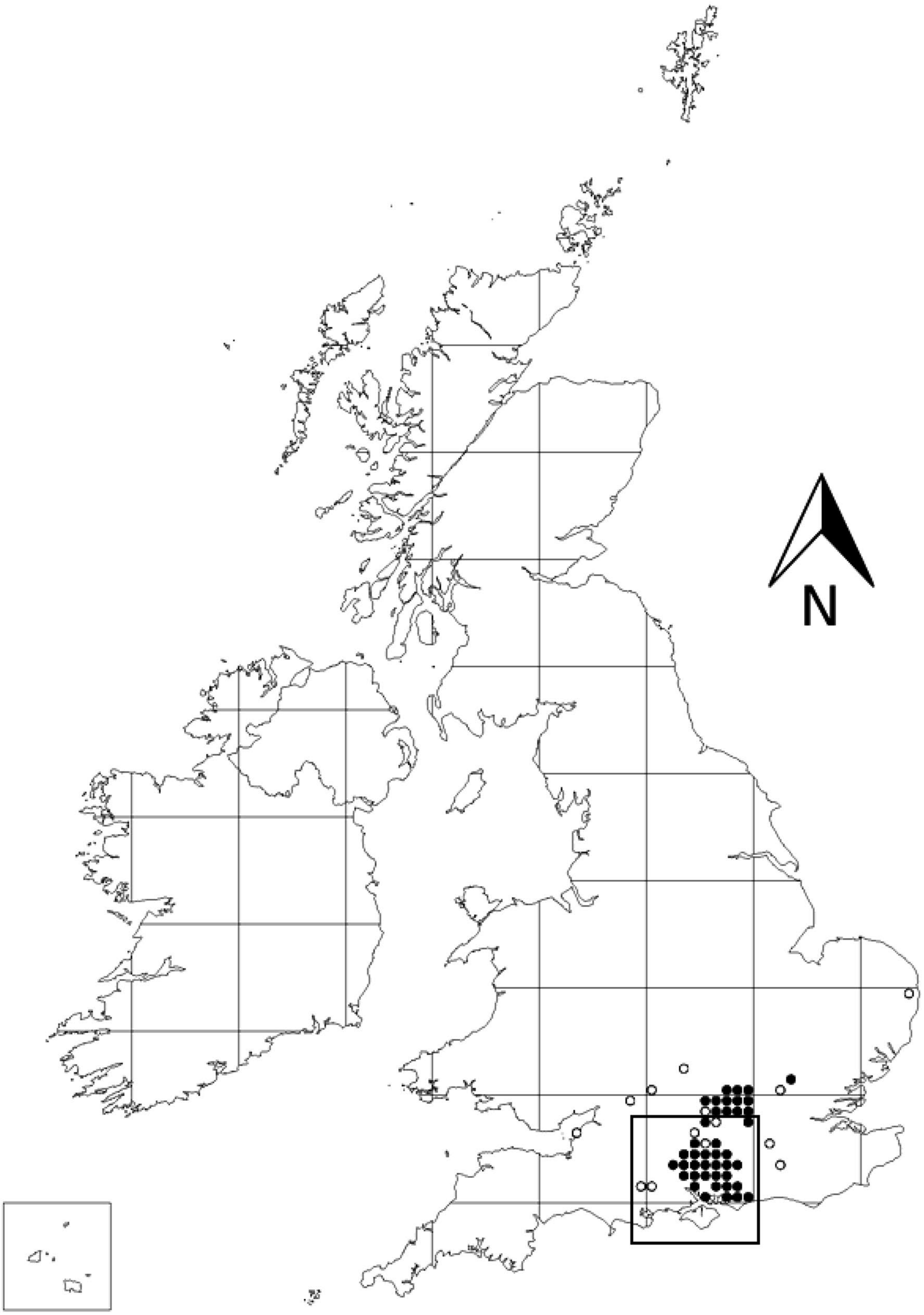
73.057 Striped Lychnis (Cucullia lychnitis)



◂**Fig. 1** Distribution of *Cucullia lychnitis* in the UK. *Black circles* represent 10 km grid squares with records of *C. lychnitis* (including both larvae and adults) from 2000 onwards, *white circles* represent additional grid squares with records of *C. lychnitis* from before 2000. *Box* indicates the area displayed in Fig. 2. Data were provided from the National Moth Recording Scheme, courtesy of Butterfly Conservation. Map produced by MapMate™ using Digital Map Data© HarperCollins-Bartholomew 2013

Adult *C. lychnitis* are nocturnal, and are active between May and early August, laying eggs throughout this period. Eggs are laid primarily on the leaves of Dark Mullein *Verbascum nigrum* L. (Scrophulariaceae), with occasional records from other *Verbascum* species and *Scrophularia* species (Heath and Emmet 1983). Larvae feed on the flowers and developing seedheads of the host plant before pupating on or just under the soil surface. *V. nigrum* also has a restricted range within the UK; it is a ruderal species (Fenner 1978), readily colonising disturbed soils and short turf, preferring calcareous soils and frequenting road verges, hedge banks and grassy places (Preston et al. 2002). Thus, mown road verges (if appropriately managed) are potentially an important habitat for this species and so for *C. lychnitis*. *V. nigrum* is biennial, but can persist for several years, and occurs in distinct patches varying in size from single plants to several hundreds. The NERC Act (2006) identifies host-plant availability as the key target for conserving *C. lychnitis*; however, within the range of *C. lychnitis*, larvae of the moth can be found readily in some patches of *V. nigrum* but are absent from others (Heath and Emmet 1983).

An important first step to conserve a species is an understanding of the biotic and abiotic variables that influence its distribution and abundance (Thomas et al. 2010). For *C. lychnitis* such information will be informative about the factors shaping the species' current distribution and potential future changes in distribution, as well as helping to inform habitat management strategies. Studies investigating the incidence and abundance of butterfly species within fragmented landscapes are frequent (Thomas et al. 1992; Hanski et al. 1994; Hill et al. 1996), but fewer such studies have focused on moths. Three specific questions were addressed: (1) Which ecological variables influence the occupancy of *V. nigrum* patches by larvae of *C. lychnitis*? (2) Which variables influence the abundance of *C. lychnitis* larvae within occupied patches? (3) Which variables influence the use of individual *V. nigrum* plants within occupied patches?

Materials and methods

Locating and identifying patches

Data were obtained detailing presence/absence of *V. nigrum* at tetrad resolution (2 km × 2 km squares) from the Botanical Society of the British Isles (BSBI) Maps Scheme, covering an area that included and surrounded the range of the southern English population of *C. lychnitis*. Tetrads in this area with *V. nigrum* present were further divided into two categories, those with and without records of *C. lychnitis* larvae during two extensive recent surveys (Hoare and Thomas 2006; Rosenthal 2011). Tetrads to be searched were randomly selected from each category in equal numbers. Tetrads were searched over a 6-week survey period from mid-July to early September 2012, timed to encompass the entire duration of the larval season.

Flower spikes of *V. nigrum* are tall (typically around 1 m), bright yellow and highly conspicuous. This, along with the plant's association with road verges, meant it was possible to locate the plant by systematically searching all road verges within a selected tetrad. A small number of occupied patches were known from previous surveys to exist away from roadsides; however, searching the entire accessible area of each tetrad would have been prohibitively labour-intensive and might have limited the total number of tetrads that could searched over the course of the survey. As the vast majority of known patches were road verges, and as these have been shown to be preferred to other habitats by *C. lychnitis* (Hall 2010), it was decided that limiting searching effort to road verges would be a suitable, and readily repeatable, method.

Anywhere that *V. nigrum* was located was considered a patch. Patch boundaries were defined by the criterion that no further *V. nigrum* could be found during a 1-min search on foot in every possible direction; the ease with which *V. nigrum* flower spikes can be spotted allowed a distance of several tens of metres to be searched within a minute. Such distances have been accepted as sufficient to distinguish patches in previous studies of lepidopterans using patch isolation as an explanatory variable (Hanski et al. 1994). In all but a very few cases, patches were separated by considerably greater distances than the threshold minimum, and no patches were separated by less than 100 m. Once a patch was identified, a range of variables were recorded, as described below.

Number of *Cucullia lychnitis* larvae

All flower spikes at each patch were comprehensively searched, and the total number of *C. lychnitis* larvae within the patch counted. Larvae were only readily located at third instar or later, primarily due to size, and indeed younger larvae were only ever located after larvae at third instar or older had already been observed at a patch. In addition, it was expected that larval abundance within a patch might vary over the course of the larval season (including frequency of more easily-located older larvae), and that it would not be possible to survey all patches simultaneously (nor would this be a perfect control for any phenological variation between patches). Therefore, it was decided that all patches would be revisited at least once over the course of the 6-week survey period, and the greatest number of larvae found at any one visit to each patch used in analyses looking at abundance of larvae. In addition, the number of flower spikes with larvae on them was recorded, although in most cases this differed little from the total number of larvae as it was rare to observe more than one larva on a flower spike.

Verbascum nigrum abundance and density

Patch size was estimated as the total abundance of *V. nigrum* flower spikes present, in accordance with previous surveys of *C. lychnitis* (Hoare and Thomas 2006; Rosenthal 2011). Most plants have a single flower spike, although some older plants may have several; however, due to the difficulty of separating plants (especially in long or dense swards), the number of individual flower spikes is accepted as a reasonable approximation for host plant abundance, and so every flower spike was counted even where it was clear that they belonged to the same plant. As a second measure of patch size, host plant density within a patch was estimated using a DAFOR scale (Fowler et al. 2013). Each patch was to be categorised into one of five categories by average density of *V. nigrum* across the full patch area (for category definitions, see Online Resource 1.1). However, no road verge patches were located fitting the 'Dominant' or 'Abundant' categories, meaning that *V. nigrum* in all patches was classified as being 'Frequent', 'Occasional' or 'Rare'.

Location and patch isolation

A GPS unit was used to record the six-figure grid reference (accurate to 100 m) of the approximate centre of each patch (Winfree et al. 2005). This was then used to plot the precise location of patches into Google Earth. Isolation from all patches of *V. nigrum*, as well as just those occupied by *C. lychnitis*, was considered. Four location-specific measures of patch isolation were examined. Firstly, the number of tetrads immediately surrounding a patch without *V. nigrum* records in the BSBI data was taken as a broad-brush measure of isolation; this provided each patch with a tetrad isolation score from 0 (not isolated) to 8 (very isolated). Secondly and thirdly, two variations on nearest neighbour (NN) methods were used; the absolute distance (in km) between patch grid references, calculated using the Ruler function of Google Earth, and the smoothed NN distance, calculated as the average distance in kilometres to each patch's three NNs. Using a mean distance to several neighbours reduced the tendency for paired but otherwise isolated patches to be recorded as having low isolation. Finally, the absolute distance in kilometres from each patch to the nearest patch occupied by *C. lychnitis* larvae was measured, again using Google Earth. As only a sample of tetrads was surveyed, rather than the entire landscape, these measures may be affected by neighbours of some patches being missed. However, the geographically random sampling procedure should ensure that analyses were unbiased.

Sward height

A standard drop disc (as described in Stewart et al. 2001: 30 cm in diameter and weighing 200 g, to be dropped from a height of 1 m) was used to measure sward height. Sward height was measured in five arbitrarily selected locations within 2 m of *V. nigrum* plants at each patch, and a mean value taken for the patch.

Wind shelter and insolation

Wind shelter at each patch was categorised by an estimate of the proportion of the patch periphery protected by obstacles to wind, which included hedges, woodlands, buildings or similar. For category definitions, see Online Resource 1.2. Slope was measured using a clinometer and a pair of 2 m ranging poles at 10 m distance, and aspect using a standard magnetic compass. However, the vast majority of patches had a slope value close to zero (and thus no discernible aspect); therefore, these variables were not analysed further.

Cionus nigritarsis abundance

Cionus nigritarsis Reitter (Coleoptera: Curculionidae) also feeds on *V. nigrum* at the larval stage (Morris 2002; Sõber et al. 2010). Larvae of *C. nigritarsis* can typically be located on *V. nigrum* at an earlier date than *C. lychnitis* larvae, and therefore likely emerge and begin feeding slightly earlier, potentially impacting larval survival through interspecific competition. Abundance of *C. nigritarsis* was estimated using an adaptation of the DAFOR scale (Fowler et al. 2013). The category boundaries used were altered to be suitable to estimate the abundance of the weevil rather than of a plant, and a sixth available category ('None') was added for patches where no larvae of *C. nigritarsis* were observed (for category definitions, see Online Resource 1.3).

Within-patch variables

At the majority of patches where *C. lychnitis* larvae were present, the number of flower spikes and height of the tallest flower spike was recorded for each plant, along with whether larvae were present on each plant. Flower spike height was measured using two 1 m rulers, held end-to-end where flower spikes were taller than 1 m. Multiple flower spikes on a single plant could usually be identified, as flower spikes branched above ground level in the sward. These measurements were not taken at patches with only one or two larvae and a large number of *V. nigrum* plants, as it was considered that patterns deduced from such low densities of *C. lychnitis* might not be reliable. Several patches were revisited on multiple occasions, and larvae were at no time observed to move between plants, although it is possible that this could occur.

Statistical analyses

Generalized linear models (GLMs) were constructed to test for differences in *C. lychnitis* abundance and patch- and plant-level occupancy attributable to the ecological variables described above. Significance of effects within models was tested using likelihood ratio tests.

For each patch-level dependent variable (patch occupancy by *C. lychnitis*, abundance of *C. lychnitis*, and density of *C. nigritarsis*), we first selected variables for patch size and isolation for use in subsequent models by constructing models separately for each recorded measure for each variable. The variables used in the models with the lowest Akaike information criterion (AIC) values were selected for subsequent analysis in each case. A global model was then constructed with the two selected variables alongside mean sward height, *C. nigritarsis* density (except when this was analysed as a dependent variable) and wind shelter. Finally, this was narrowed down to the final model by removing variables in a stepwise fashion according to AIC values until no variable could be removed to reduce the AIC value further. For the plant-level occupancy analysis, plant height and number of flower spikes were included as fixed effects and patch as a random effect in a generalized linear mixed-effects model (GLMM). Significance of variables in all final models was tested using a likelihood ratio test. In cases where outliers were suspected to have influenced the results, the steps above were repeated with potential outliers removed; if this did not change the outcome, the original model (with potential outliers included) was used.

Data were analysed and figures plotted using R version 3.3.2 (R Core Team 2016). GLMs and GLMMs were constructed using the lme4 package (Bates et al. 2015). Figures were plotted using the packages ggplot2 (Wickham 2009) and ggmap (Kahle and Wickham 2013). R scripts used in analysis and plotting of figures are included in RMarkdown format in Online Resource 2.

Results

A total of 47 patches were identified with *V. nigrum* present (Fig. 2); larvae of *C. lychnitis* were located at 12 of these (26%). A minimum of 84 *C. lychnitis* larvae were identified across those 12 patches; the maximum located in a single visit to 1 patch was 20, and 4 patches had only 1 larva at each visit. A total of 203 individual *V. nigrum* plants were measured across seven occupied sites.

Patch-level occupancy was significantly affected by both patch size, measured as *V. nigrum* abundance (Table 1; $\chi^2 = 22.76$, $P < 0.001$), and patch isolation, measured as mean NN distance (Table 1; $\chi^2 = 11.15$, $P < 0.001$). Larvae of *C. lychnitis* were most likely to occupy patches that were close to other patches and had higher abundances of *V. nigrum* (Fig. 3).

Abundance of *C. lychnitis* larvae at patches where they were present was significantly affected by both *C. nigritarsis* larval density (Table 1; $\chi^2 = 47.11$, $P < 0.001$), and patch isolation, measured as mean NN distance (Table 1; $\chi^2 = 4.97$, $P = 0.026$). Larvae of *C. lychnitis* were most abundant in patches with low densities of *C. nigritarsis* (Fig. 4) and that were more isolated from other patches (Fig. 5). Neither the direction nor the significance of these effects was changed by the removal of an apparent outlier (the patch with simultaneously the highest abundance of *C. lychnitis* and the greatest isolation) from the dataset (Table 1).

Plant-level occupancy was significantly affected by both plant height (Table 1; $\chi^2 = 7.05$, $P = 0.008$) and number of flower spikes (Table 1; $\chi^2 = 54.76$, $P < 0.001$). Larvae of *C. lychnitis* were most likely to occupy plants that were tall and had many flower spikes (Fig. 6), indicating a preference for plants in their second year or older.

Density of *C. nigritarsis* larvae between patches was significantly affected by both patch size, measured as *V. nigrum* abundance (Table 1; $\chi^2 = 15.49$, $P < 0.001$), and patch isolation, measured as mean NN distance (Table 1; $\chi^2 = 4.56$, $P = 0.033$). Larvae of *C. nigritarsis* were at higher density in patches that were close to other patches and had high abundances of *V. nigrum*.

Discussion

Our results reveal that the success of *C. lychnitis* is affected by different abiotic and biotic variables at different scales. At a landscape scale, larvae of *C. lychnitis* were most likely to occupy patches with abundant *V. nigrum*, and patches that were close to several other patches, regardless of whether or not these patches were occupied by *C. lychnitis* (Fig. 3). This pattern reflects that found by Thomas et al. (1992) in four species of UK butterflies, but is less well

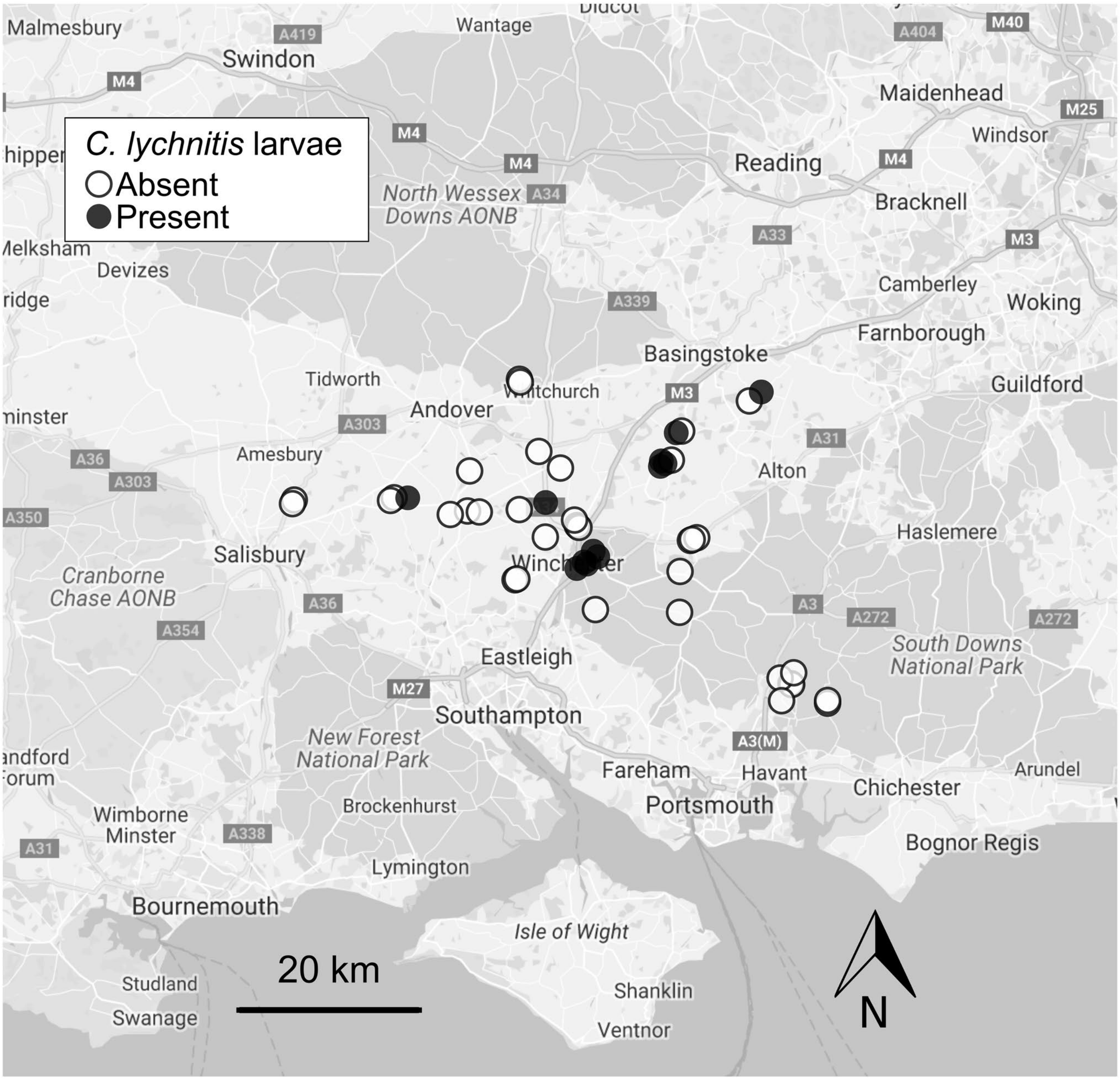


Fig. 2 Patches recorded in the study came from the southern UK population of *C. lychnitis*, centred around Winchester, Hampshire, UK. Surveyed patches occupied by larvae of *C. lychnitis* are shown as *black circles*, unoccupied patches as *white circles*. Map data© Google 2017

documented for moths (but see Ravenscroft and Young 1996; Menéndez and Thomas 2000). The importance of host plant abundance as a predictor of patch occupancy is consistent with previous studies emphasising the requirements of immature stages (Bourn and Thomas 2002). The results suggest that conservation approaches typically applied to butterflies may be appropriate more widely for Lepidoptera, including both diurnal and nocturnal species, living in fragmented landscapes.

The results are consistent with isolation-dependent recolonisation rates and area-dependent extinction rates, with both dispersal and demography influencing occupancy (Thomas and Kunin 1999). Some tetrads have records of the adult moth only (including a single record over 40 km from known larval colonies), and while it seems likely that many larval sites go unrecorded, this is suggestive of high mobility. High dispersal is important to metapopulation dynamics as it facilitates recolonisation of patches. Equally, extinction of local populations of *C. lychnitis* is more likely in smaller patches of *V. nigrum* where resources are limited, making them more vulnerable to environmental or demographic stochasticity.

Table 1 Summary of analyses testing for variation in *Cucullia lychnitis* larval occupancy and abundance and *Cionus nigritarsis* density attributable to a range of ecological variables

Unit of replication	Dependent variables	Model structures	Independent variables	Effect size (standard error)	LRT χ^2	*P*
Patch (all)	Patch occupancy by *C. lychnitis* larvae	Binomial GLM	Isolation (mean NN distance)	−0.82 (0.31)	11.15	<0.001
			Patch size (no. flower spikes)	0.08 (0.02)	22.76	<0.001
Patch (occupied)	Abundance of *C. lychnitis* larvae at occupied patches	Poisson GLM	Isolation (mean NN distance)	0.17 (0.08)	4.97	0.026
			C. nigritarsis density	−1.71 (0.63)	47.11	<0.001
	As above (outlier removed)	Poisson GLM	Isolation (mean NN distance)	1.81 (0.93)	4.00	0.045
			C. nigritarsis density	−4.07 (1.49)	44.53	<0.001
Patch (all)	Density of *C. nigritarsis* larvae at patches	Ordinal GLM	Isolation (mean NN distance)	−0.28 (0.13)	4.56	0.033
			Patch size (no. flower spikes)	0.03 (0.01)	15.49	<0.001
Plant (patches with abundant *C. lychnitis*)	Occupancy of plants by *C. lychnitis* larvae	Binomial GLMM	Plant height	0.02 (0.01)	7.05	0.008
			No. flower spikes	0.68 (0.12)	54.76	<0.001

Independent variables shown are those retained in the final model for each dependent variable. Significance of variables was tested with a likelihood ratio test

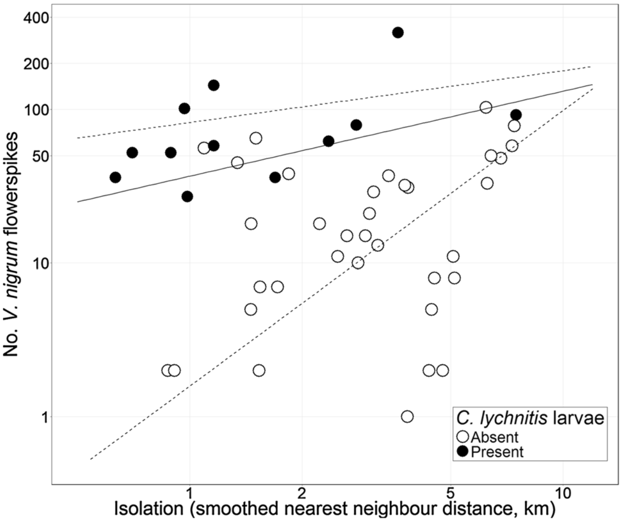


Fig. 3 The occupancy of patches by larvae of *C. lychnitis* is affected by patch size and isolation. *Points* show patches recorded in the study; *black circles* indicate larvae of *C. lychnitis* were present. Model-predicted probability of larval occupancy is >50% for patches above the *solid line* (*dashed lines* show 95% confidence interval)

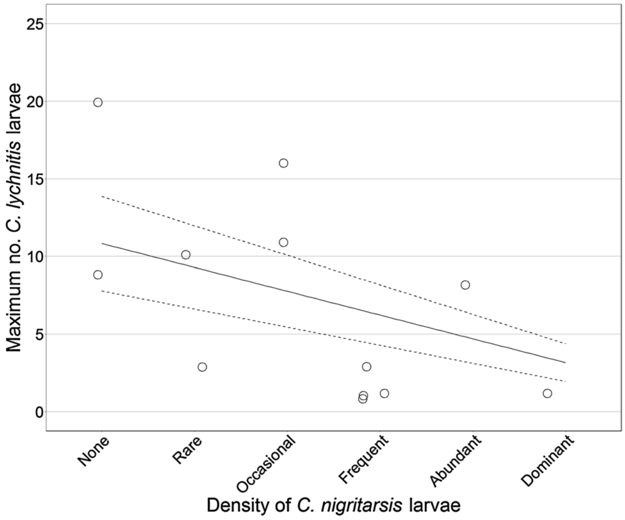


Fig. 4 The maximum abundance of *C. lychnitis* larvae at occupied patches is influenced by the density of larvae of competitor *C. nigritarsis*. *Points* show *C. lychnitis* larval abundance at occupied patches recorded in the study. A line-of-best-fit is plotted through model-predicted larval abundances at each level of *C. nigritarsis* density (*dashed lines* show standard error)

Comparing between occupied patches, abundance of *C. lychnitis* larvae was not related to abundance of *V. nigrum* but instead was affected by density of larvae of the weevil *C. nigritarsis*. Eggs of *C. nigritarsis* are laid directly on the flower buds of *V. nigrum* (Sõber et al. 2010), whereas *C. lychnitis* eggs are laid on the leaves (Heath and Emmet 1983). High densities of *C. nigritarsis* were observed throughout the study to cause severe feeding damage to *V. nigrum* flower spikes from around 14 days before the first larvae of *C. lychnitis* were recorded, reducing the food resource available to the moth larvae. As *C. lychnitis* larvae were not readily located until the third instar (due to small size and lack of conspicuousness), it is possible that the

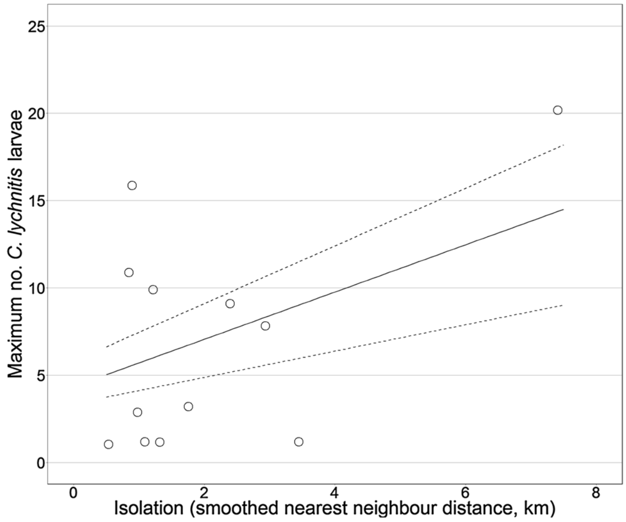


Fig. 5 The maximum abundance of *C. lychnitis* larvae at occupied sites is influenced by patch isolation. *Points* show *C. lychnitis* larval abundance at occupied patches recorded in the study. *Solid line* shows model-predicted larval abundance (*dashed lines* show standard error)

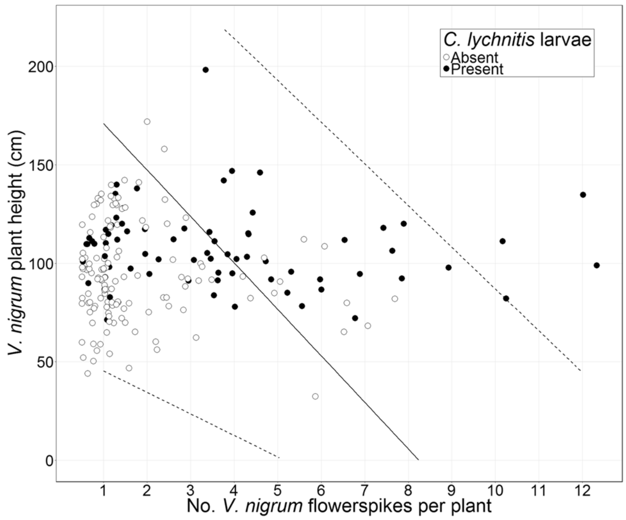


Fig. 6 The occupancy of individual *V. nigrum* plants by *C. lychnitis* within occupied patches is influenced by plant height and number of flower spikes. *Points* show plants recorded in the study; *black circles* indicate larvae of *C. lychnitis* were present. Model-predicted probability of larval occupancy is >50% for patches above the *solid line* (*dashed lines* show 95% confidence interval)

observed pattern can be attributed to variation in survival rates of *C. lychnitis* larvae during the early instars, caused by varying levels of interspecific competition for food with *C. nigritarsis* larvae.

Surprisingly, larvae of *C. lychnitis*, where found, were more abundant at more isolated patches. One possible explanation is a tendency for female *C. lychnitis* to lay more eggs on a plant if they have not recently located any others; this strategy has been recorded in other species of Lepidoptera (Mackay and Singer 1982). Alternatively, density of *C. nigritarsis* across patches was affected by the same variables as patch occupancy by *C. lychnitis*, patch size and isolation, potentially explaining this pattern. Larvae of *C. lychnitis* in less isolated patches may experience elevated competition from *C. nigritarsis* larvae, but further study is needed to establish whether competition from *C. nigritarsis* can influence *C. lychnitis* population dynamics. However, *V. nigrum* seed set and pollinator visitation rate both decrease with increased intensity of florivory by *C. nigritarsis* (Sõber et al. 2009). As *C. lychnitis* larvae primarily feed on developing seed heads (i.e., fertilized flowers), it is therefore probable that *C. nigritarsis* presence reduces the available food resource for *C. lychnitis*, providing a mechanism for such competitive exclusion.

Cionus nigritarsis is also rare in the UK, recorded in only 17 tetrads since 2000 (although it is unlikely to have received the same survey effort as *C. lychnitis* and may therefore be under-recorded) and, as a specialist on *V. nigrum* (Morris 2002), may also have been impacted by the decreasing range of *V. nigrum*. The abundance of *C. nigritarsis* increases with *V. nigrum* patch size (Sõber et al. 2009), but the dispersal abilities of *C. nigritarsis* adults and the influence of patch isolation on its abundance are unknown. The weevil is able to fly (Sõber et al. 2010), but if it is less mobile than *C. lychnitis* the moth would be more likely to locate and capitalise on isolated patches than the weevil. Such a difference in dispersal abilities could facilitate coexistence of these competing species if colonisation–competition trade-offs generate a spatial refuge in isolated patches (Tilman 1994). However, in our models, the effect of patch isolation was greater for *C. lychnitis* occupancy than for *C. nigritarsis* density, which does not support this hypothesis (Table 1). The existence of such a mechanism would warrant further investigation; if operating then there may be important implications for the conservation of isolated patches and for the consequences of further habitat destruction (Nee and May 1992).

Occupancy of individual *V. nigrum* plants by *C. lychnitis* within occupied patches was affected by both plant height and number of flower spikes, with larvae more likely to occupy taller plants with more flower spikes. As *C. lychnitis* larvae feed directly upon the flower spikes, both taller plants and those with more flower spikes provide a greater resource to larvae. Both of these variables should correlate with increasing plant age; in particular, multiple flower spikes are only expected to occur on plants in their second or subsequent flowering season. Therefore, patches that are present over a number of years may contain older, larger *V. nigrum* plants and thus provide greater larval resources for *C. lychnitis*. Plant age might also plausibly correlate with total leaf area, which would provide a mechanism for adult female *C. lychnitis* to select older, larger plants when laying eggs, before flower spikes have grown. On repeat visits to occupied patches, larvae were never observed to have moved between flower spikes, suggesting plant-level occupancy is determined at the egg-laying stage.

These findings suggest several actions that may aid the conservation of *C. lychnitis*. The relationship between patch occupancy and both abundance of *V. nigrum* and proximity to other patches indicates that conservation efforts should concentrate on large patches of *V. nigrum* located close to other patches. A number of patches located during the survey were very small, with 7 patches having 5 or fewer flower spikes of *V. nigrum* present; however, the smallest occupied patch had 27 flower spikes, although *C. lychnitis* larvae have been recorded at smaller patches and even single, isolated host plants in subsequent surveys (MSP, unpublished data). Thus, increasing the size (through planting or ground disturbance followed by seeding of *V. nigrum*) of small patches close to occupied patches may provide opportunities for dispersal and establishment of new local populations. However, the parallel preference of *C. nigritarsis* for larger, less isolated patches of *V. nigrum* indicates that a balance between large patch size and low weevil density may be of most benefit to *C. lychnitis*. Finally, the apparent preference within occupied patches for plants that have been flowering for more than 1 year highlights the potential importance of ensuring that existing patches persist, although it is not clear from this study whether patch persistence affects patch occupancy or larval abundance. As *V. nigrum* is a ruderal species, regular if infrequent disturbance of patches may be necessary to prevent ecological succession from proceeding; however, it is clearly important that such disturbance, especially in the form of road verge mowing, should not take place during the flowering period of *V. nigrum*, to ensure that larvae of *C. lychnitis* are able to complete development and pupate safely in the soil.

While clear patterns emerged from our data, a larger data set across a wider set of *C. lychnitis* populations would be valuable. Weather conditions were poor during the flight period of *C. lychnitis* prior to the survey work, with prolonged and heavy rainfall. This may explain why both the abundance of *C. lychnitis* larvae and the number of occupied patches were lower than had been documented in previous surveys of the same sites. To increase the area that could be searched, we limited the survey to accessible road verges, meaning that data for some occupied patches was not included. In combination, these factors mean that sample sizes for some aspects of the study were small; in particular, analyses of variables affecting variations in abundance of *C. lychnitis* larvae between patches were based on just 12 data points. Furthermore, *C. lychnitis* exists in two distinct populations in the UK, of which this study focussed exclusively on the southern, Hampshire population. We cannot assume that the same variables are important in influencing the incidence and abundance of *C. lychnitis* throughout its range.

A valuable area for future study would be the factors that determine presence and abundance of *V. nigrum* itself. This species has been previously shown to suffer reduced visitation by pollinators (primarily bumblebees) under infestation by *C. nigritarsis*, especially in large patches (Sõber et al. 2009, 2010), although a separate study found no evidence for pollination limitation (Dauber et al. 2010). Nevertheless, these studies address success of *V. nigrum* where it is already established, and so the reason why patches exist in some places but are absent from others is also unclear. It is likely that the ruderal nature of the species has some effect: seeds germinate more successfully and produce faster-growing shoots on bare soil than in even short swards, and may fail entirely in tall swards (Fenner 1978). A fuller understanding of the ecology of this plant would facilitate efforts to increase the size, and reduce the isolation, of *C. lychnitis* local populations.

Conclusions

This study has identified a number of ecological variables which appear to have an effect upon the Striped Lychnis moth *C. lychnitis*. These include both isolation and size of patches of the host plant *V. nigrum*, abundance of a potentially competitive species of weevil, *C. nigritarsis*, and possibly persistence of patches of *V. nigrum* for multiple consecutive breeding seasons. These findings should be of use in guiding policy for the conservation of *C. lychnitis*, while areas of uncertainty and priorities for future work have been identified.

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