

Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation

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Abstract. How best to manage forest patches, mitigate the consequences of forest fragmentation, and enable landscape permeability are key questions facing conservation scientists and managers. Many temperate forests have become increasingly fragmented, resulting in reduced interior forest habitat, increased edge habitats, and reduced connectivity. Using a citizen science landscape-scale mark–release–recapture study on 87 macro-moth species, we investigated how both life-history traits and landscape characteristics predicted macro-moth responses to forest fragmentation. Wingspan, wing shape, adult feeding, and larval feeding guild predicted macro-moth mobility, although the predictive power of wingspan and wing shape depended on the species' affinity to the forest. Solitary trees and small fragments functioned as “stepping stones,” especially when their landscape connectivity was increased, by being positioned within hedgerows or within a favorable matrix. Mobile forest specialists were most affected by forest fragmentation: despite their high intrinsic dispersal capability, these species were confined mostly to the largest of the forest patches due to their strong affinity for the forest habitat, and were also heavily dependent on forest connectivity in order to cross the agricultural matrix. Forest fragments need to be larger than five hectares and to have interior forest more than 100 m from the edge in order to sustain populations of forest specialists. Our study provides new insights into the movement patterns of a functionally important insect group, with implications for the landscape-scale management of forest patches within agricultural landscapes.

Key words: *agricultural matrix; citizen science; dispersal ability; habitat fragmentation; habitat specificity; landscape connectivity; Lepidoptera; mark–release–recapture; species mobility; temperate woodland.*

INTRODUCTION

Functional landscape connectivity refers to the ability of organisms to disperse among habitat resource patches (Baguette and Van Dyck 2007). Landscape connectivity theory is grounded within island biogeography and metapopulation dynamics, which explain species occurrence by probabilities of immigration to, and survival in, habitat patches (MacArthur and Wilson 1967, Hanski 1999). Modeling these processes has taken on increasing practical importance in biological conservation, as habitats become fragmented and isolated, and populations are forced to move in response to climate change (Devictor et al. 2012).

Much of Europe now consists of agricultural land interspersed with plantation forests, urbanized areas, and remnant forest fragments. These fragments are characterized by reduced interior forest areas, increased edge habitat, increased isolation, and reduced connectivity between patches (Dolman et al. 2007, Riutta et al. 2011). In the United Kingdom, forest cover has declined from ~75% 6000 years ago to ~12% today, with three-quarters of forest patches currently <2 ha (Watts 2006). This fragmentation process results in population size reductions and disruptions to dispersal, particularly for forest specialists (Dolman et al. 2007, Callens et al. 2011).

Studies on butterflies have highlighted the importance of landscape connectivity and have provided some classic examples of metapopulation dynamics (e.g., Thomas et al. 1992, Hanski and Kuussaari 1995). They have also been used to document the effects of habitat

Manuscript received 7 August 2012; 11 December 2012; accepted 31 January 2013. Corresponding Editor: J. A. Jones.

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fragmentation, land-use change, and climate change (e.g., Summerville and Crist 2001, Thomas et al. 2001, Warren et al. 2001). In contrast, and despite their roles in terrestrial ecosystems as pollinators, herbivores, and as prey for birds, bats, and other taxa (Fox 2013), moths remain a relatively understudied group (but see beta-diversity studies in tropical landscapes [e.g., Beck et al. 2012] and in North American forests [e.g., Summerville and Crist 2008]). Habitat destruction, degradation, and fragmentation, along with climate change, are thought to be major drivers of the often severe population declines seen for two-thirds of the United Kingdom's once widespread and common species of moth (Fox 2013). Because of their ecological roles, such widespread declines are likely to cascade through whole ecosystems.

Recent studies at the field and farm scale have highlighted the importance of hedgerow trees and improved agricultural practices through agro-environment schemes (Merckx et al. 2012), and habitat connectivity has been found to be critical for moth movements within agricultural landscapes (Merckx et al. 2010). Several recent meta-analyses have also highlighted the importance of considering species' life-history traits when assessing their dispersal ability and responses to habitat fragmentation (Beck and Kitching 2007, Bommarco et al. 2010, Öckinger et al. 2010, Sekar 2012). However, moth movements have been rarely quantified at the landscape scale (but see Nieminen 1996, Betzholtz and Franzén 2011), and there are only a handful of dispersal-related studies for forest invertebrates, most of which are for ground beetles and butterflies (Brouwers and Newton 2009). Although an estimated 60% of the United Kingdom's moths are reliant on seminatural, broad-leaved lowland forest (Young 1997), the effects of forest fragmentation on moths are relatively unknown, and there have been no attempts to quantify moth movement patterns within and between remaining forest fragments. We believe it is of increasing conservation relevance to do so in order to be able to predict both the distribution of species within fragmented forest landscapes and their movement patterns between forest fragments.

The aim of this study was to detect if moth life-history traits and landscape characteristics affect the distribution and movement patterns of macro-moths among forest fragments set within an agricultural matrix. Specifically, we asked: (1) Are macro-moth life-history traits able to explain movement patterns across a landscape? (2) How do forest fragment size and forest edges affect macro-moth abundance and species composition? (3) Do forest macro-moths use linear landscape features (i.e., hedgerows) and stepping stones (i.e., isolated trees, small forest fragments) to move across the landscape?

METHODS

Experimental design

The study took place in a landscape encompassing 10 forest fragments around Wytham Woods, a 400-ha

seminatural broad-leaved forest in southern England (51°46' N, 01°20' W). Fragments differed in size (0.37–361 ha), but all were characterized by similar soil, topography, tree species composition, and management (see Appendices A and B; see also Butt et al. 2009).

A mark–release–recapture experiment was conducted across the fragments, and at solitary oak trees (either isolated or within a hedgerow) within the matrix. Light traps (heath-type actinic 6 W; Bioquip, Knutsford, Cheshire, UK) were permanently placed at 44 sampling sites, all within a 2 km radius from the center of the largest fragment (study area of 12.6 km²; Appendix A). Eight traps (four edge and four interior traps) were placed in the largest fragment (361 ha), four traps (two edge and two interior traps) in each of the larger fragments (4.8–21.7 ha), and two traps were placed at the edges of smaller fragments (0.3–3.5 ha). These fragments were so small that there was no true interior forest habitat and so we could not distinguish between edge and interior traps (Riutta et al. 2011). Edge traps were placed on the side nearest to neighboring fragments to increase the capture of movements between fragments. Traps were also placed within the agricultural matrix, at the base of 10 similarly sized solitary large oak trees (the study landscape's predominant solitary tree species): five at trees within linear hedgerows and five at isolated trees within fields (Appendices A and B). The average distance among all pairwise trap combinations was 1739 ± 20 m (mean ± SE; maximum = 4131 m, minimum = 45 m). Actinic 6W traps have an attraction radius of only 10 to 30 m (E. M. Slade and T. Merckx, *unpublished data*), and as such allow for a good representation of real movement patterns.

The experiment ran from 14 June 2009 until 24 July 2009 on 31 nights. Traps were divided across the landscape (i.e., 25 in the southern part, and 19 in the northern part). These two sets of traps were run on alternate nights, with traps lit before dusk and visited at dawn. Using data from Merckx et al. (2009, 2010) and Waring and Townsend (2009), a subset of 92 macro-moth species was selected based on their forest habitat use, flight period, common presence, identification ease, and ease of marking. Every individual from the selected species was marked at first capture by writing a unique number on the left forewing, using a fine (0.4 mm) nontoxic, waterproof, permanent marker pen (Lumocolor; Staedtler, Nurnberg, Germany). Three separate teams were needed to check all traps, and so three different pen colors (i.e., red, green, black) were used. After marking, moths were released in situ into nearby tall vegetation. For each capture, date, species, trap, and individual mark number were recorded. Recaptured individuals on which the mark could not be read reliably (22 individuals) were not included in analyses. All 31 nights met the sampling criteria of a minimum night temperature of 10°C, maximum wind speed of 20 km/h, and maximum precipitation risk of 50% (data from the Wytham Woods weather station of the Environmental

Change Network, Center for Ecology and Hydrology [CEH], UK, 2009).

Analyses

The data were split into two themes to analyze (1) the effect of life-history traits on movements and (2) the effects of landscape characteristics and forest fragmentation on movements, species richness, and abundance.

Life-history traits.—Each species was classified using Manley (2008) and Waring and Townsend (2009) for the following traits: (1) forest affinity (weak [i.e., ubiquitous species], medium [i.e., associated with forest, but not exclusively so], and strong [i.e., broad-leaved forest specialists]), (2) larval feeding guild (grass/herb feeders or shrub/tree feeders), (3) larval diet breadth (monophagous, oligophagous, polyphagous), (4) adult feeding (yes or no), (5) average wingspan (mm), and (6) wing shape (i.e., wing aspect ratio as broad or pointed). All species were also classified in terms of conservation status based on national population trends measured over 35 years: severely declining (i.e., declines >69%), moderately declining (i.e., declines 0–69%), increasing, unknown (Conrad et al. 2006) (see Appendix C).

A sound phylogeny is not yet established for Eurasian moths (Betzholtz and Franzén 2011), and we were therefore unable to use a phylogenetic tree to control for trait evolution (see Sekar 2012). Instead, we controlled for phylogenetic relatedness by fitting models with “family,” “subfamily,” and “subfamily nested within family” as random effects (Nieminen et al. 1999). Their effect was assessed using likelihood ratio tests comparing models with and without these error terms. “Family” was not included as a fixed effect in models as we were interested in the specific life-history traits that describe moth dispersal ability at the species level.

To answer the question of whether macro-moth life-history traits were able to explain movement patterns across a landscape, the effect of the trait variables on the total distance moved across the landscape for each recaptured individual was analyzed. Linear mixed effects and generalized least squares (GLS) models were used, including the trait variables as fixed effects and “days since marking” as an additional continuous variable. “Species” was fitted as a random factor in the models, both alone and nested within “subfamily” and “family.” Different variances among forest affinity classes were modeled using the *varIdent* weights function (Zuur et al. 2009). All two-way interactions were fitted and nonsignificant interaction terms and variables dropped from the model until the minimal adequate model was obtained, using AIC scores and likelihood ratio tests (LRT). Fixed effects of model parameters were also estimated using LRTs to assess the differences between models after sequentially deleting significant terms from the minimal model and adding nonsignificant terms (Zuur et al. 2009). Variables were log- or square-root-transformed where necessary to meet the assumptions of parametric testing, and continuous variables were

standardized using a *z*-transformation so that the magnitude of the coefficients were directly comparable (Schielzeth 2010). *P* values were calculated using adjusted sums of squares as models contained both categorical and continuous variables.

Movement distances between captures were calculated using GIS (ESRI 2008). Coefficients from the final model were then used to predict the mean distance traveled over seven days for all moth species, using their trait values.

Landscape characteristics.—A series of landscape variables was calculated for each trap site using GIS (ESRI 2008): (1) fragment area, (2) distance to fragment edge (for within-fragment sites) or to nearest fragment edge (for sites outside fragments), (3) fragment perimeter, (4) number of hedgerow connections/fragment perimeter, (5) hedge density (i.e., total hedgerow length/1 km radius around each fragment or tree), (6, 7) number and area of fragments within a 1 km radius, (8) fragment shape (calculated as $R = 0.282P/\sqrt{A}$ where *P* is perimeter, *A* is area, and 0.282 is the factor that ensures $R = 1$ for circular fragments; *R* values increase as fragments become more elongate [Usher and Keiller 1998]), (9) isolation (calculated as

$$I = 1 / \left[\sum_{i=1}^n (A_i/d_i^2) \right]$$

where *I* is calculated as *n* other fragments within a distance of 1 km of the study fragment, each of which has an area *A_i* and is separated by a margin to margin distance *d_i* from the study fragment [Usher and Keiller 1998]), and (10) dominant surrounding matrix type around fragment or tree (arable, A; short-grass pasture, SP; and long-grass pasture, LP).

A correlation matrix of the variables was constructed to check for collinearity. “Fragment area” and “distance to edge” were highly correlated (Pearson’s correlation coefficient = 0.9), which is unavoidable as the largest distances to the edge occur within the large fragments, and the smallest distances are from solitary oak sites (negative values), which have the smallest areas (see Appendix B). Consequently, we split the data set in two. To answer the question of how forest fragment size and forest edges affect macro-moth abundance and species composition, we considered only trap sites within fragments (“fragments-only” data set). To answer the question of whether forest macro-moths use linear landscape features (i.e., hedgerows) and stepping stones (i.e., isolated trees) to move across the landscape, we considered only solitary oak trap sites (“oaks-only” data set).

In the “fragments-only” data set there was also significant correlation among several of the continuous variables (fragment perimeter, number of hedgerow connections/fragment perimeter, area of fragments within a 1 km radius, fragment shape) and area (Pearson correlation values > 0.55). We therefore excluded these

TABLE 1. Minimum adequate model for distance moved with wingspan and wing shape as wing morphology traits and adult feeding, larval feeding guild, and forest affinity as life-history traits for the 87 moth species marked in this study in Wytham Woods, UK.

Trait	df	F	P
Intercept	1, 645	22.65	<0.0001
Days since marking	1, 645	23.24	<0.0001
Wingspan	1, 645	7.43	0.0066
Wing shape	1, 645	0.02	0.8905
Forest affinity	2, 645	6.46	0.0017
Larval feeding guild	1, 645	4.05	0.0446
Adult feeding	1, 645	4.77	0.0293
Wingspan \times forest affinity	2, 645	8.32	0.0003
Wing shape \times forest affinity	2, 645	8.81	0.0002

Note: Wing shape was described as broad or pointed using the wing aspect ratio; forest affinity was defined as weak (i.e., ubiquitous species), medium (i.e., associated with forest, but not exclusively so), or strong (i.e., broad-leaved forest specialists); larval feeding guild was described as grass/herb feeders or shrub/tree feeders; and adult feeding was described as yes or no.

continuous variables from the models. The fragments-only data set displayed only a marginal correlation between “area” and “distance to edge” (Pearson correlation coefficient = 0.4), and so both variables were included for analysis. For the oaks-only data set, only “distance to nearest forest edge” was included, as “area” was similar for all oak trees used in the study.

Linear mixed-effects and GLS models were used to model abundance and a measure of species richness as a function of forest affinity and the landscape variables. As we had preselected the species we marked, we could not use species richness per se, so instead, we used the proportion of species of the preselected species found in each trap for each forest affinity class (PropS). Abundances and PropS were summed across trap nights for each affinity class in each trap to avoid issues of temporal autocorrelation, and because we were not interested in the effects of date or weather conditions.

Thus, of the original variables calculated, only “hedge density,” “number of fragments within a 1-km radius,” “isolation,” “area,” and “distance to edge” were not correlated for the fragments-only data set, and hence were included as fixed effects, along with the categorical variables “matrix type” and “forest affinity.” For the oaks-only data set, “distance to nearest fragment edge,” “hedge density,” “number of fragments within a 1 km radius,” and “isolation” were not correlated, and hence were included as fixed effects. “Position” (i.e., hedgerow oak/isolated oak), “forest affinity,” and “matrix type” were included as the categorical variables.

Variables were log- or square-root-transformed where necessary, and continuous variables were standardized using a z-transformation as above in the subsection *Life-history traits*. For the fragments-only data set, “trap nested within site” was modeled as a random effect for both the abundance and PropS models. For the oaks-only data set, “site” fitted as a random factor did not

significantly improve the fit of the abundance model (LRT, $P > 0.05$), and hence was only included in the PropS model. Different variances among affinity classes were modeled using the *varIdent* weights function where necessary. The interactions between each main effect and “forest affinity,” and “position” (for the oaks-only data set), were modeled using LRTs and AIC values as above in the subsection *Life-history traits*. Coefficients from the final models were used to predict the abundance and PropS of moth species associated with different landscape characteristics. Spatial autocorrelation among sites was tested for abundance and species richness by calculating Moran’s I index using GIS (ESRI 2008).

The *lme*-function of the *nlme* package for R 2.10.1 (R Development Core Team 2006, Pinheiro et al. 2008) was used for all of the analyses.

RESULTS

A total of 14 719 individuals from 87 of the 92 preselected species were sampled, with 679 recaptures of 657 individuals comprising 41 species, resulting in a recapture rate of 5.17% (see Appendix D). There was no evidence of spatial autocorrelation between traps ($P > 0.05$ in all cases). The simplest model, without any phylogenetic component, was found to be the best (likelihood ratio tests, $P > 0.05$). In all cases, the variance explained by family, subfamily, and species (0.002, 0.872, and 1.29, respectively) was low compared to the residual variance (15.06), and the coefficient estimates changed little between the models.

Life-history traits

Overall, species with strong and medium forest affinity had nearly double the recapture rate of species with weak forest affinity (strong, 6.4%; medium, 6.7%; weak, 3.5%). There was a large variation in movements (overall mean = 348 m, overall median = 52 m). On average, species with weak forest affinity moved larger distances than species with strong and medium forest affinity (weak, 430 ± 52 m [$n = 220$]; medium, 314 ± 34 m [$n = 375$]; and strong, 261 ± 65 m [$n = 62$]).

Moths with pointed wings moved further than moths with broad wings, although this was only the case for species with either weak or strong forest affinity (Table 1, Fig. 1a). An increase in wingspan accounted for larger distances moved overall, but this was only significant for species with a strong forest affinity (Fig. 1a; Appendix E). Among all single traits considered, adult feeding was the strongest predictor of movement rate for moth species regardless of forest affinity (Appendix E). Moths that fed as adults and moths with shrub/tree-feeding larvae had larger predicted movement rates than those that did not feed as adults or with grass/herb-feeding larvae, and this pattern was similar among all forest affinity classes (Table 1, Fig. 1b, c; Appendix C). The predictive power of wingspan and wing shape was low, except for species with a strong forest affinity (Appendix E). The majority of species were predicted to move <500

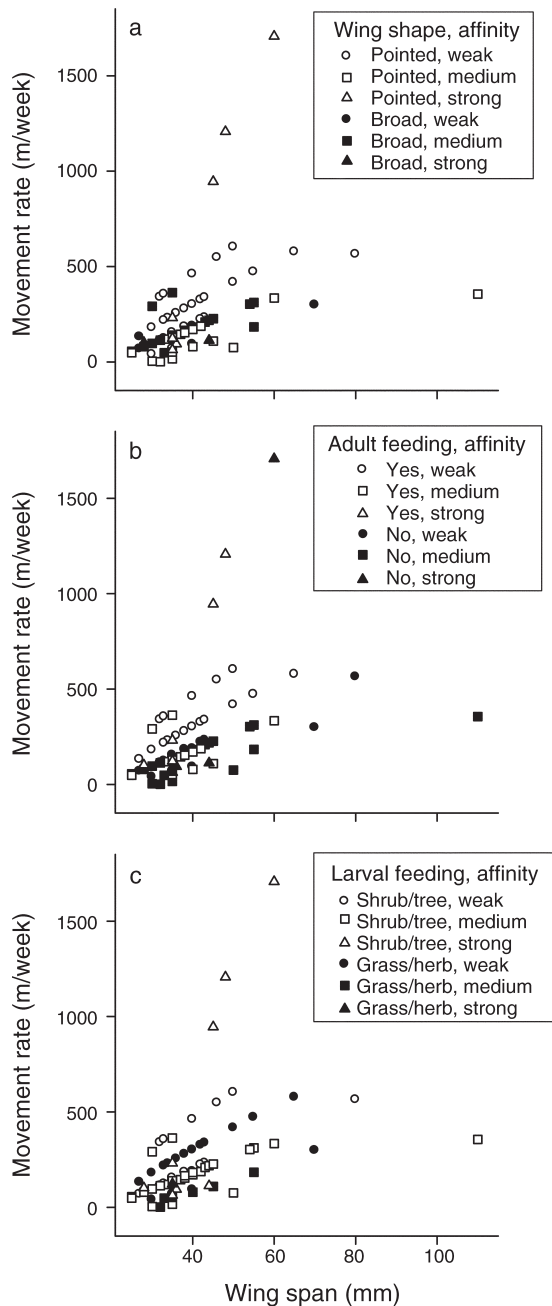


FIG. 1. Model-predicted movement rates for the 87 moth species marked in this study in Wytham Woods, UK. Movements are given for each forest affinity class (weak [i.e., ubiquitous species], medium [i.e., associated with forest, but not exclusively so], and strong [i.e., broad-leaved forest specialists]) as a function of wingspan and (a) wing shape (i.e., wing aspect ratio as pointed or broad), (b) adult feeding (yes or no), and (c) larval feeding guild (shrub/tree or grass/herb feeders).

m in a week, with the range increasing with wingspan. The three species with the largest predicted movement rates, i.e., lobster moth *Stauropus fagi*, green arches *Anaplectoides prasina*, and scarce silver-lines *Bena bicolorana*, were all forest species with pointed wings

(Fig. 1a; Appendix C). Species with medium forest affinity tended to have the smallest predicted movement rate for a given wingspan.

Landscape characteristics

Most individuals moved relatively small distances and were recaptured within the same fragment. However, for isolated oaks, only 27% of recaptured individuals were marked and re-caught again at an isolated oak compared to 61% of individuals at hedgerow oaks and around 80% for small and large fragments. Hedgerow trees “captured” more marked individuals than did isolated trees (mean = 14 vs. 3 individuals/trap, respectively).

Most individuals of species with a weak forest affinity were recaptured at hedgerow trees, while most recaptures of medium affinity species were in small fragments. The majority of species with a strong forest affinity were captured in the large fragments (>5 ha; 94% of individuals and 89% of species), and were only recaptured in the largest fragments, or rarely at hedgerow trees, and never in smaller fragments or at isolated trees.

Effect of fragment size and distance to the edge: fragments-only data set.—“Distance to edge,” rather than “fragment area” was the most important predictor of moth abundance (Table 2, Fig. 2a, b). Predicted abundance increased with increasing distance to the edge, although this effect differed with forest affinity. The abundance of species with strong forest affinity significantly increased with distance to the edge, while there was no such effect for species with weak to medium forest affinity. Low numbers of forest specialists were found outside forests, and the edge effect was particularly pronounced up to 100 m from the edge (Fig. 2b). Moth numbers increased with increasing fragment area, but this was only marginally significant (Table 2, Fig. 2a).

This pattern for abundance was reversed for species richness (PropS). The predicted PropS differed among forest affinity classes only for fragment area (Table 2). The proportion of species captured increased with area

TABLE 2. Minimum adequate model for the abundance and proportion of species (PropS) of moths captured in the fragments.

Trait	df	F	P
Abundance			
Intercept	1, 64	725.73	<0.0001
log(area)	1, 8	4.67	0.0626
Distance to edge	1, 23	0.1	0.7538
Forest affinity	2, 64	213.49	<0.0001
Distance to edge × forest affinity	2, 64	9.2	0.0003
PropS			
Intercept	1, 62	594.05	<0.0001
log(area)	1, 8	1.01	0.3432
Distance to edge	1, 23	3.04	0.0946
Forest affinity	2, 62	0.29	0.7476
log(area) × forest affinity	2, 62	12.03	<0.0001
Distance to edge × forest affinity	2, 62	2.9	0.0593

Note: See Table 1 for a description of the traits.

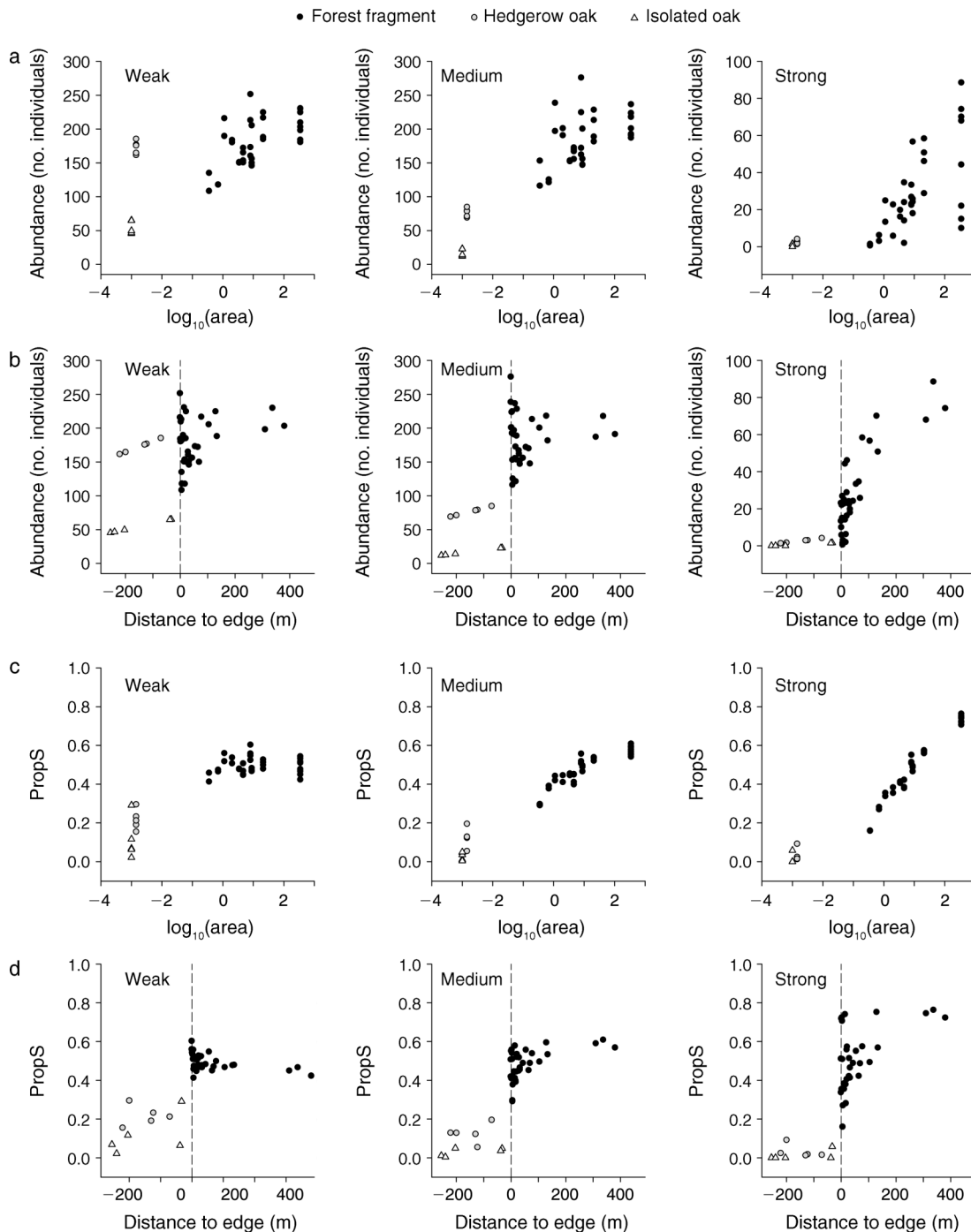


FIG. 2. Model predicted moth abundance and a species richness measure (PropS; see subsection *Landscape characteristics* in *Methods: Analyses* for details) of moths for the three forest affinity classes (weak, medium, and strong), in relation to (a, c) forest area (log-transformed; originally measured in hectares; hedgerow and isolated oaks were given a value of 0.0015 ha and 0.001 ha, respectively) and (b, d) distance from forest edge. Note that in panels (a) and (b), the y-axis has a different range for the strong forest affinity class. In panels (b) and (d), positive values are the distance from within (i.e., trap is placed inside the forest), and negative values are the distance from outside (i.e., trap is outside the forest at solitary oak trees).

for species with a medium or strong forest affinity, with a minimum fragment size of ~ 5 ha (0.7 at \log_{10} scale) needed for 50% of the species in those affinity classes to be present (Table 2, Fig. 2c). However, an increasing distance to edge only gave a marginally significant increase in the proportion of these species (Table 2, Fig. 2d). None of the other variables was found to affect moth abundance or PropS at within-fragment sites.

Linear landscape features and "stepping stones": oaks-only data set.—Moth abundance at isolated and hedgerow oaks differed among forest affinity classes. Very few moths with strong forest affinity were caught at either type of oak overall, and species with weak to medium affinity were more abundant at hedgerow oaks than at isolated oaks (Table 3, Fig. 3a). This was also true for the species richness measure (PropS; Table 3, Fig. 3b). Abundance, though not the PropS of species with weak forest affinity, was similar at hedgerow oaks and in many of the fragments (Fig. 2a, c). As distance to edge of the nearest fragment decreased, overall moth abundance increased, both for isolated and hedgerow oaks, with no significant difference between the forest affinity classes (Table 3, Fig. 2b). None of the other variables measured was found to affect moth abundance at isolated and hedgerow oak trees.

The type of matrix surrounding solitary oak trees, as well as the density of hedgerows in the surrounding area, affected the species richness (PropS) of some affinity classes, and the effect was the same regardless of whether the solitary oak was an isolated oak or a hedgerow oak (Table 3). There were significantly more species with weak or strong forest affinity at an oak when it was surrounded by long-grass pasture, rather than either arable or short-grass pasture (Table 3, Fig. 3c). However, only the PropS of species with strong forest affinity increased significantly with an increased density of hedgerows surrounding the oak, with the strongest effects being seen with increases in hedgerow densities above 4 km/km² (Fig. 3d). Distance to nearest forest edge had no effect on the PropS of any affinity class caught at oak trees.

DISCUSSION

How best to manage existing forest patches, mitigate the consequences of forest fragmentation, and enable landscape permeability so that biodiversity can adapt to climate change are key questions for conservation (Sutherland et al. 2006, Maclean 2010). Moreover, research specifically aimed at understanding the decline of the United Kingdom's moths and the action necessary to mitigate such declines was listed in the top 100 most important research priorities for informing conservation policy in Britain (Sutherland et al. 2006) and more recently listed in the top 25 key questions in ecology (Maclean 2010).

Understanding the widespread, and often severe declines, of once-common moth species requires a better understanding of the functional connectivity of land-

TABLE 3. Minimum adequate model for the abundance and proportion of species (PropS) of moths captured at oaks.

Trait	df	F	P
Abundance			
Intercept	1, 23	158.2	<0.0001
Distance to edge	1, 23	4.47	0.0456
Position	1, 23	15.1	0.0007
Forest affinity	2, 23	76.66	<0.0001
Position \times forest affinity	2, 23	7.74	0.0027
PropS			
Intercept	1, 10	45.77	<0.0001
Hedge density	1, 5	1.76	0.2423
Position	1, 5	5.15	0.0726
Forest affinity	2, 10	43.7	<0.0001
Matrix	2, 5	4.28	0.0825
Hedge density \times forest affinity	2, 10	4.93	0.0324
Position \times forest affinity	2, 10	6.2	0.0177
Matrix \times forest affinity	4, 10	7.99	0.0037

Note: Position was defined as an isolated oak or oak within a hedgerow; forest affinity was weak, medium, strong; hedge density was defined as total hedgerow length/1 km radius around each tree; matrix was the dominant surrounding matrix type around fragment or tree, described as arable (A), short-grass pasture (SP), or long-grass pasture (LP).

scapes, and how this connectivity is defined by species-specific dispersal propensity (i.e., willingness to leave a patch) and dispersal ability (i.e., matrix crossing and settlement) (Van Dyck and Baguette 2005). Previous studies have considered moth movements at the field scale (Merckx et al. 2009, 2010) and highlighted the importance of considering species' life-history traits (Beck and Kitching 2007, Bommarco et al. 2010, Öckinger et al. 2010, Sekar 2012). However, this study is the first to quantify moth movement patterns for a large number of species at a landscape scale. As most macro-moths show a continuous mode of dispersal during their adult life, their movement rates can be used as a measure of dispersal ability and potential dispersal success (Brouwers and Newton 2009). Such species-specific movement rates are important for modeling the impacts of land use and climate change on species distribution patterns (e.g., Walters et al. 2006).

Mobile forest specialists are most at risk from forest fragmentation

As has been found for other forest invertebrate groups (Brouwers and Newton 2009), in general, species with weak forest affinity moved larger distances than species with strong and medium forest affinity. However, our results also showed that species with a strong forest affinity and with large, pointed wings have a greater ability to disperse than similarly shaped species with medium to weak forest affinity. For instance, individuals of the forest specialist lobster moth *Stauropus fagi* are predicted to move a weekly mean distance of 1707 m, whereas roughly similarly sized and similarly shaped buff-tip *Phalera bucephala* and poplar hawk-moth *Laothoe populi* individuals, species with medium and weak forest affinity, respectively, are predicted to move

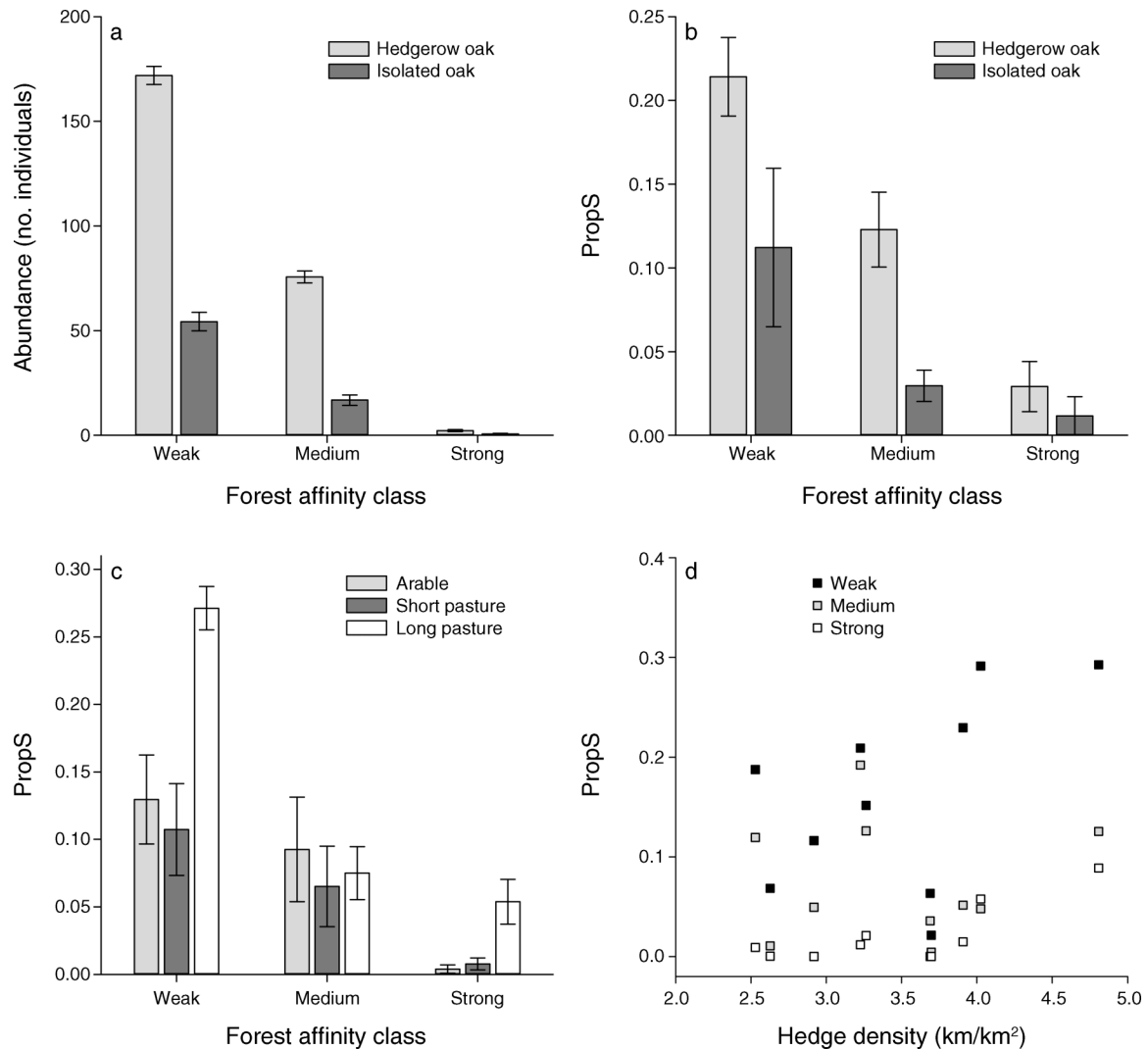


FIG. 3. Model predicted mean (\pm SE) moth (a) abundance and (b) species richness measure (PropS; see subsection *Landscape characteristics* in *Methods: Analyses* for details) in each forest affinity class (weak, medium, and strong) at hedgerow and isolated oaks. (c) Species richness (PropS) for each affinity class in relation to the matrix surrounding all solitary oak trees (hedgerow and isolated oaks combined as the final model showed no effect of position of the oak on PropS captured in the different matrices). (d) Model-predicted species richness (PropS) at all solitary oak trees (hedgerow and isolated oaks are not separated as the final model showed no effect of position of the oak on PropS) for each forest affinity class in relation to hedge density.

only 76 m and 563 m in the same amount of time. The observed high mobility of some macro-moth forest specialists may be a result of these forest specialists being exposed to stronger selection pressures for increased dispersal ability between remnant forest fragments due to the long history of forest fragmentation in the United Kingdom (Bergerot et al. 2012). Selection is predicted to switch direction from increasing to decreasing dispersal ability once species are unable to keep track with the pace of forest fragmentation (Bergerot et al. 2012). Thus, selection working in the opposite direction may currently be at work for those forest specialists that display low mobility. Such species would be predicted to have short movement rates and according flight-related morpholo-

gy. For example, the relatively small and round-winged black arches *Lymantria monacha* and maiden's blush *Cyclophora punctaria* have predicted mean weekly movement rates of 113 m and 102 m, respectively.

Despite the relative high mobility of some forest specialists, they were only rarely found within the matrix at hedgerow oaks and isolated oaks. However, the density of hedgerows in the vicinity of an oak tree (whether hedgerow or isolated oak) was found to increase the species richness of forest specialists at that tree, suggesting that forest specialists are heavily dependent on forest connectivity in order to cross the agricultural matrix. Thus, despite their potentially high dispersal capability, the most mobile species of these forest

specialists appear to be confined mostly to the largest of the forest patches due to their strong forest affinity. Together, these findings contradict the ideas that species with a high degree of habitat specialization are necessarily poor dispersers and that species with low mobility are most likely to be affected by habitat fragmentation and lack of connectivity (Brouwers and Newton 2009, Öckinger et al. 2010). We suggest that forest specialists are the most vulnerable to forest fragmentation, not because of their low mobility, but rather because of their high habitat affinity. Indeed, abundance and species richness of forest specialists increased linearly with fragment area and distance from the edge. As wingspan is generally related to body size, and body size inversely related to population size (Nieminen et al. 1999), viable populations of small-bodied, sedentary forest specialists, such as maiden's blush *Cyclophora punctaria* and nut-tree tussock *Colocasia coryli* could be maintained, even within relatively small fragments, without direct need for rescue by a wider meta-population. However, it is the more mobile, larger species, such as lobster moth *Stauropus fagi* that are at risk from local extinction in smaller fragments, particularly if hedgerow connectivity in the landscape is reduced. This study suggests that fragments need to be larger than five hectares and need to have interior forest >100 m from the edge, in order to sustain populations of mobile forest specialist species (Fig. 2; see also Usher and Keiller 1998).

*Small forest fragments and solitary oaks act
as "stepping stones"*

The lower affinity to forest of weak and medium forest affinity species allows them to move more freely into and out of smaller fragments and through the matrix. These species seemed to be particularly associated with the smaller fragments, perhaps also using them as "stepping stones" to cross the landscape. Isolation was not a significant factor for any of the forest affinity classes and this may in part be due to the "stepping-stone" effect of smaller fragments, hedgerows, and isolated trees in the landscape (Usher and Keiller 1998). Previous studies have also highlighted the importance of small patches of forest and the amount of forest cover (within a 1–1.4 km radius), for several taxa including moths (Ricketts et al. 2001, Summer-ville and Crist 2004, Dolman et al. 2007, Fuentes-Montemayor et al. 2011). Many farm woodland schemes conserve small patches of forest (i.e., <2 ha) within the agricultural landscape. While such schemes may not benefit true forest specialists, this study suggests that small forest fragments may provide key habitat resources for many other species, such as blood-vein *Timandra comae*, lackey *Malacosoma neustria*, and pretty chalk carpet *Melanthia procellata*, all of which are severely declining in Britain (Conrad et al. 2006).

Ubiquitous species, such as the nationally declining bright-line brown-eye *Lacanobia oleracea*, heart and dart *Agrotis exclamationis*, flame shoulder *Ochropleura plecta*,

and flame *Axylia putris*, were relatively abundant at hedgerow oak trees in particular, suggesting that they are using hedgerows as corridors when crossing the agricultural landscape. In fact, hedgerow oaks approached small fragments in terms of abundance and species richness of species with weak to medium forest affinity. Species with weak to medium forest affinity were also frequently captured at isolated oaks, and low recapture rates at the same tree suggest that they were being used as "stepping stones," enabling movement across the landscape. The land use of the surrounding matrix was also found to have an effect on the number of both ubiquitous and forest specialist species using oak trees. Long-grass pastures were associated with higher moth numbers than short-grass pastures and intensively managed arable crops. Reduced vegetation structure and plant species composition, with fewer nectar sources and reduced shelter in grazed and arable fields, have been shown to be detrimental to many moth species (Littlewood 2008).

A previous study found that hedgerow trees were only effective in increasing the abundance of less mobile moth species (Merckx et al. 2010). However, as that study was conducted at the field scale only, the absence of an effect for the more mobile species was probably due to these species moving at a larger scale than the study could capture. The current study provides evidence that hedgerow trees are important for the movement of moths through agricultural landscapes at a large spatial scale, and that this is true for species of all mobility and forest affinity classes. Moreover, we show that for some moth species general landscape characteristics, such as the hedgerow density and the matrix surrounding solitary trees, may be almost as important as whether an individual tree is isolated or directly connected to a hedgerow.

Predicting moth dispersal from species life-history traits

Phylogenetic relatedness was not found to be causing the differences in the life-history traits and mobility between species measured in the study. Similarly, Nieminen et al. (1999) found that phylogenetic relatedness did not qualitatively affect the outcome of their studies on moth migration rates. Thus, both these studies suggest that dispersal in moths evolves independently of phylogeny, but is dependent instead on the ecological and life-history traits of the species.

Wingspan is often used as a surrogate for body size and as a proxy for dispersal ability (Nieminen et al. 1999, Beck and Kitching 2007, Öckinger et al. 2010, Sekar 2012). However, as has been found for butterflies (Sekar 2012) and sphingid moths (Beck and Kitching 2007), the overall predictive power of wingspan and wing shape for dispersal ability in this study was low, as it was dependent on forest affinity, and thus should be interpreted cautiously. However, the true distance travelled was probably underestimated as we used the minimum straight-line distance travelled between mark-release and recaptures. Also, some large and partly

migratory moths, such as *Noctua* species, were probably moving at a greater scale than this study, and were hardly ever recaptured, despite large numbers being marked, which indicates an underestimation of their dispersal ability. These moths, and other migratory moth species, such as the silver Y *Autographa gamma*, have been recorded to move distances of several hundred kilometers in a night (Chapman et al. 2010, 2012). The largest recorded movement in this study was for a broad-bordered yellow underwing *Noctua fimbriata*, which was recaptured outside the study area, having moved 13.7 km in two months (see also Betzholtz and Franzén 2011).

The importance of considering wing shape as well as wingspan is also highlighted, as the most mobile species were those with pointed wings, rather than those with the largest wingspan (e.g., the weekly movement rate of green arches *Anaplectoides prasina* [48 mm wingspan, pointed wings] was 1207 m whereas that of the garden tiger *Aretia caja* [70 mm wingspan, rounded wings] was 297 m). We have, however, no clear explanation why this pattern was most prevalent in forest specialists and to a lesser extent in ubiquitous species, while species with a medium forest affinity showed no difference in distance moved with wing shape or wingspan. In contrast to the extensively studied butterflies, the mobility of the majority of moth species is largely unknown, and for many species these data represent some of the first records of their dispersal ability.

Larval host plant, adult habitat specificity, and adult feeding have been shown to affect Lepidoptera dispersal ability (Nieminen et al. 1999, Beck and Kitching 2007, Betzholtz and Franzén 2011, Sekar 2012). In contrast to these studies, adult feeding rather than larval food plant specificity was the strongest predictor of mobility. Moths that feed as adults and moths with larvae that feed on shrubs and/or trees were more mobile than those that do not feed as adults or with grass/herb-feeding larvae (e.g., the weekly movement rate of scorched wing *Plagodis dolabraria* [adult feeder with shrub/tree feeding larvae] was 363 m whereas that of the white ermine *Spilosoma lubricipeda* [adults do not feed and larvae are grass/herb-feeders] was 92 m). Adult moths dependent on nectar resources may need to be more mobile in order to locate enough of these energy resources, while the adults of shrub/tree-feeding larvae may be more mobile than grass/herb-feeding species in order to locate sufficient host plants because shrubs and trees are generally more dispersed within a landscape than the more ubiquitous grasses and herbs. Similarly, it has been suggested for tropical hawk-moths that adult feeders are typically longer lived and therefore may disperse further and be less habitat specific (Beck et al. 2006, Beck and Kitching 2007).

Citizen science in action

We believe that this is the largest ever mark–release–recapture experiment, in terms of species involved, individuals released, and area covered. One reason that a study such as this has not been conducted before is the

large workforce it takes to monitor such large numbers of light traps and moths across a landscape. Our study was unique in that it involved teams of citizen scientists, allowing large quantities of data on a large number of moth species to be collected on a landscape scale. However, the use of volunteers to carry out scientifically sound research is not easy and studies need to be designed so that volunteers can make a meaningful contribution or enable research that would otherwise be unfeasible (Lovell et al. 2009). Many invertebrates are difficult to sample at large scales or across long time periods and these issues have been identified as particular challenges to invertebrate conservation (Lovell et al. 2009).

Monitoring of butterflies through citizen science based programs within Europe has enabled large amounts of data to be collected on their distributions, making butterflies useful indicators of biodiversity change and flagships for conservation (Kuhn et al. 2008, van Swaay et al. 2008). Recently, moths were also proposed as an excellent group to engage citizen scientists, as they occur in large numbers and are relatively easy to trap and identify in temperate regions (Fox et al. 2010). Moreover, because of their high species richness and ecological diversity, they are thought to represent terrestrial insects as a whole better than butterflies (Fox et al. 2010). This large-scale mark–release–recapture study serves as an example of labor-intensive and time-consuming research where the use of volunteers greatly increased the numbers of individuals and species recorded and the spatial scale sampled.

Conservation implications

Both forest size and forest connectivity are important when considering how to conserve moth diversity in fragmented landscapes. Different groups of forest-associated species will require different degrees of habitat connectivity, and it has been suggested that physical links, such as corridors, may be important both for forest specialists (Bailey 2007) and for generalists (Dolman et al. 2007). This study highlights that even small fragments and isolated trees have a fundamental role to play, and act as crucial “stepping stones” for moths as they move through the landscape. Furthermore, the higher the landscape connectivity surrounding trees, through their positioning within hedgerows or within a favorable matrix, the higher their “stepping-stone” capacity, both for forest specialist and ubiquitous moth species. Such connectivity is particularly important in light of climate change, which means that species are moving, and will need to move, in order to stay within their climatic envelopes (Devictor et al. 2012). We suggest that increasing the landscape connectivity between patches of remaining forest should be a key priority (e.g., for national agro-environment schemes). The extent of forest cover in the United Kingdom is now increasing (Mason 2007), and agro-environmental schemes, combined with farm business models that

include sustainable forest revenue streams, have the potential to be used to increase connectivity and create forest networks at the landscape level leading to ecologically functional landscapes. However, in order to maintain the full complement of species within the landscape, and forest specialists in particular, it is necessary to maintain both connectivity and large patches of suitable forest habitat. Our results thus have important implications for the landscape-scale management of forest patches and their connectivity within agricultural landscapes.

ACKNOWLEDGMENTS

We thank Marc Botham, Rita Gries, Darren Mann, Claire McLaughlan, Alison Slade, Richard Sylvester, Chloe Wells, and the Earthwatch/HSBC Climate Champions for help with data collection. Richard Lewington gave us permission to use his plates from Waring and Townsend (2009). Martin Harvey, Darren Mann, and Martin Townsend provided advice on species selection and identification, and Richard Comont provided advice on data analyses. Nigel Fisher and Phil Smith provided support and access to forest fragments. The Food Animal Initiative and Mr. Barnett allowed us access to their fields. We thank Darren Mann and two anonymous reviewers for their comments on earlier versions of the manuscript. The study was funded by the HSBC Climate Partnership Programme through the Earthwatch Institute. The manuscript was in part written while E. M. Slade was funded by an Academy of Finland grant: number 138346. E. M. Slade, T. Merckx, and T. Riutta designed the experiment. E. M. Slade was responsible for coordinating the research, and E. M. Slade, T. Merckx, T. Riutta, and D. Redhead were responsible for data collection. E. M. Slade, T. Merckx, T. Riutta, and D. P. Bebber analyzed the results. D. W. Macdonald and P. Riordan conceived the research program within which this work fits. E. M. Slade wrote the first draft of the paper, and all authors contributed to revisions.

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SUPPLEMENTAL MATERIAL

Appendix A

Study landscape with trap locations ([Ecological Archives E094-138-A1](#)).

Appendix B

Trap and site details ([Ecological Archives E094-138-A2](#)).

Appendix C

Life-history traits for the 87 species marked in the study ([Ecological Archives E094-138-A3](#)).

Appendix D

Recapture rates and distances moved for 41 recaptured species ([Ecological Archives E094-138-A4](#)).

Appendix E

Coefficients table for distance moved with wingspan and wing shape as wing morphology traits and adult feeding, larval feeding guild, and forest affinity as life-history traits ([Ecological Archives E094-138-A5](#)).

Ecological Archives E094-138-A1

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APPENDIX A. Study landscape with trap locations.



FIG. A1. Study landscape with trap locations. See [Appendix B](#) for trap and fragment details.

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APPENDIX B. Trap and site details.

Trap	Fragment	*Fragment code	Area (ha)	†Distance to edge (m)	‡Matrix	Species richness	Total abundance
1	Woodview	SF	0.73	8	SP	36	225
2	Woodview	SF	0.73	19	SP	35	234
3	Godstow	SF	3.57	34	LP	42	374
4	Godstow	SF	3.57	22	LP	37	331
5	Wytham	W	361.02	312	SP	47	432
6	Wytham	W	361.02	382	SP	38	447
7	Wytham	W	361.02	4	SP	50	442
8	Oak	HO	0.0015	-121	LP	28	243
9	Oak	IO	0.001	-33	LP	33	161
10	Keepers	LF	8.33	6	SP	47	551
11	Keepers	LF	8.33	56	SP	54	366
12	Keepers	LF	8.33	31	SP	42	273
13	Keepers	LF	8.33	1	SP	50	675
14	Oak	HO	0.0015	-128	SP	31	340
15	Wytham	W	361.02	2	SP	47	282

16	Oak	IO	0.001	-255	SP	13	47
17	Oak	HO	0.0015	-219	SP	32	195
18	Oak	IO	0.001	-240	SP	8	35
19	Redhouse	SF	2.10	1	A	40	388
20	Redhouse	SF	2.10	12	A	44	458
21	Stimpsons	SF	1.16	1	A	42	617
22	Stimpsons	SF	1.16	12	A	43	546
23	Oak	HO	0.0015	-198	LP	37	344
24	Oak	IO	0.001	-38	A	17	87
25	Higgins	LF	4.83	16	A	31	281
26	Higgins	LF	4.83	66	A	41	417
27	Higgins	LF	4.83	30	A	43	362
28	Higgins	LF	4.83	1	A	38	255
29	Bean Wood	LF	21.72	22	A	44	363
30	Bean Wood	LF	21.72	136	A	42	380
31	Bean Wood	LF	21.72	79	LP	45	515
32	Bean Wood	LF	21.72	23	LP	50	604
33	Wytham	W	361.02	16	SP	55	584
34	Wytham	W	361.02	339	SP	51	612

35	Wytham	W	361.02	131	SP	50	569
36	Wytham	W	361.02	5	SP	42	299
37	Oak	HO	0.0015	-69	A	36	165
38	Oak	IO	0.001	-204	A	22	70
39	S Edge	SF	0.37	7	SP	23	180
40	S Edge	SF	0.37	1	SP	29	266
41	Stroud	LF	9.25	34	SP	36	271
42	Stroud	LF	9.25	71	SP	41	293
43	Stroud	LF	9.25	106	A	41	560
44	Stroud	LF	9.25	45	A	45	311

*Fragment code: SF = small fragment, LF = large fragment, W = Wytham woods, HO = hedgerow oak, IO = isolated oak. Hedgerow oaks were given a slightly larger area than isolated oaks to account for their connectivity.

†Distance: Distance to the nearest woodland edge. Positive values: distance from within, trap is placed in the woodland. Negative values: distance from outside, trap is outside of the woodland at oak trees.

‡Matrix: SP = short pasture, LP = long pasture, A = arable.

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Ecological Archives E094-138-A3

Eleanor M. Slade, Thomas Merckx, Terhi Riutta, Daniel P. Bebber, David Redhead, Philip Riordan, and David W. Macdonald. 2013. Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. *Ecology* 94:1519–1530. <http://dx.doi.org/10.1890/12-1366.1>

APPENDIX C. Life-history traits for the 87 species marked in the study.

Each species was classified using Manley (2008) and Waring and Townsend (2009) for the following traits: (i) forest affinity: weak (i.e., ubiquitous species), medium (i.e., associated to forest, but not exclusively so) or strong (i.e., broadleaved forest specialists), (ii) larval feeding guild: grass/herb-feeders or shrub/tree-feeders, (iii) larval diet breadth: mono-, oligo- or polyphagous, (iv) adult feeding: yes or no, (v) average wingspan (mm), and (vi) wing shape (i.e., wing aspect ratio): broad or pointed. All species were also classified in terms of conservation status, based on national population trends measured over 35 years: severely declining (i.e. declines >69%), moderately declining (i.e. declines 0-69%), increasing or unknown (Conrad et al. 2006). Model predicted mean distances moved in seven days for each species were calculated from the coefficients of the final model, using their trait values.

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Species	Scientific name	Family	Subfamily	Forest affinity	Wingspan (mm)	Wing shape	Larval feeding guild	Larval diet breadth	Adult feeding	Conservation status	Predicted distance moved (m)
Angle Shades	<i>Phlogophora meticulosa</i>	Noctuidae	Amphipyriinae	weak	50	pointed	shrub/tree-feeders	poly	Y	increasing	601
August Thorn	<i>Ennomos quercinaria</i>	Geometridae	Ennominae	medium	38	broad	shrub/tree-feeders	olig	N	severely declining	166
Beautiful Golden Y	<i>Autographa pulchrina</i>	Noctuidae	Plusiinae	weak	40	pointed	grass/herb-feeders	poly	Y	moderately declining	301
Beautiful Hook-tip	<i>Laspeyria flexula</i>	Noctuidae	Plusiinae	medium	30	pointed	shrub/tree-feeders	mono	N	moderately declining	4
Black Arches	<i>Lymantria monacha</i>	Lymantriidae	Lymantriinae	strong	44	broad	shrub/tree-feeders	olig	N	increasing	113
Blood-vein	<i>Timandra comae</i>	Geometridae	Sterrhinae	medium	33	broad	grass/herb-feeders	olig	N	severely declining	48
Blue-bordered Carpet	<i>Plemyria rubiginata</i>	Geometridae	Larentiinae	medium	28	broad	shrub/tree-feeders	olig	N	increasing	80
Bright-line Brown-eye	<i>Lacanobia oleracea</i>	Noctuidae	Hadeninae	weak	38	pointed	shrub/tree-feeders	poly	N	moderately declining	183
Brimstone Moth	<i>Opisthographis luteolata</i>	Geometridae	Ennominae	weak	35	broad	shrub/tree-feeders	olig	N	moderately declining	140
Broad-bordered Yellow Underwing	<i>Noctua fimbriata</i>	Noctuidae	Noctuinae	medium	60	pointed	shrub/tree-feeders	poly	Y	increasing	334
Brown Rustic	<i>Rusina ferruginea</i>	Noctuidae	Amphipyriinae	weak	38	pointed	grass/herb-feeders	poly	Y	moderately declining	277
Buff Arches	<i>Habrosyne pyritoides</i>	Thyatiridae	Thyatirinae	medium	40	pointed	shrub/tree-feeders	mono	Y	moderately declining	170
Buff Ermine	<i>Spilosoma luteum</i>	Arctiidae	Arctiinae	weak	40	broad	shrub/tree-feeders	poly	N	severely declining	187
Buff Footman	<i>Eilema depressa</i>	Arctiidae	Lithosiinae	medium	35	pointed	shrub/tree-feeders	mono	N	increasing	17
Buff-tip	<i>Phalera bucephala</i>	Notodontidae	Phalerinae	medium	50	pointed	shrub/tree-feeders	poly	N	moderately declining	76
Burnished Brass	<i>Diachrysia chrysitis</i>	Noctuidae	Plusiinae	weak	40	pointed	grass/herb-feeders	olig	Y	moderately declining	301
Clay	<i>Mythimna ferrago</i>	Noctuidae	Hadeninae	weak	38	pointed	grass/herb-feeders	olig	Y	moderately declining	277
Clouded Border	<i>Lomasipilis marginata</i>	Geometridae	Ennominae	weak	27	broad	shrub/tree-feeders	olig	N	moderately declining	69
Clouded Brindle	<i>Apamea epomidion</i>	Noctuidae	Amphipyriinae	medium	40	pointed	grass/herb-feeders	olig	Y	unknown	80
Clouded Silver	<i>Lomographa temerata</i>	Geometridae	Ennominae	medium	28	broad	shrub/tree-feeders	poly	N	moderately declining	80
Clouded-bordered Brindle	<i>Apamea crenata</i>	Noctuidae	Amphipyriinae	weak	42	pointed	grass/herb-feeders	olig	Y	moderately declining	325

Common Emerald	<i>Hemitea aestivaria</i>	Geometridae	Geometrinae	medium	30	broad	shrub/tree-feeders	poly	Y	moderately declining	291
Common Footman	<i>Eilema lurideola</i>	Arctiidae	Lithosiinae	weak	32	pointed	shrub/tree-feeders	olig	Y	increasing	339
Common Swift	<i>Hepialus lupulinus</i>	Hepialidae	Hepialinae	weak	30	pointed	grass/herb-feeders	olig	N	moderately declining	38
Coronet	<i>Craniophora ligustri</i>	Noctuidae	Acronictinae	medium	37	pointed	shrub/tree-feeders	olig	Y	unknown	145
Dark Arches	<i>Apamea monoglypha</i>	Noctuidae	Amphipyriinae	weak	50	pointed	grass/herb-feeders	olig	Y	moderately declining	417
Dingy Footman	<i>Eilema griseola</i>	Arctiidae	Lithosiinae	medium	35	pointed	shrub/tree-feeders	mono	Y	increasing	128
Dot Moth	<i>Melanchra persicariae</i>	Noctuidae	Hadeninae	weak	40	pointed	shrub/tree-feeders	poly	Y	severely declining	461
Double Square-spot	<i>Xestia triangulum</i>	Noctuidae	Noctuinae	medium	42	pointed	shrub/tree-feeders	poly	Y	moderately declining	187
Drinker	<i>Euthrix potatoria</i>	Lasiocampidae	Pinarinae	medium	55	broad	grass/herb-feeders	olig	N	moderately declining	184
Dun-bar	<i>Cosmia trapezina</i>	Noctuidae	Amphipyriinae	medium	34	pointed	shrub/tree-feeders	poly	Y	moderately declining	120
Early Thorn	<i>Selenia dentaria</i>	Geometridae	Ennominae	medium	43	broad	shrub/tree-feeders	poly	N	moderately declining	210
Elephant Hawk-moth	<i>Deilephila elpenor</i>	Sphingidae	Macroglossinae	weak	65	pointed	grass/herb-feeders	olig	Y	unknown	577
Eyed Hawk-moth	<i>Smerinthus ocellata</i>	Sphingidae	Smerinthinae	weak	80	pointed	shrub/tree-feeders	olig	N	unknown	563
Figure of Eighty	<i>Tethea ocellaris</i>	Thyatiridae	Thyatirinae	medium	38	pointed	shrub/tree-feeders	olig	Y	unknown	154
Flame	<i>Axylia putris</i>	Noctuidae	Noctuinae	weak	34	pointed	grass/herb-feeders	poly	Y	moderately declining	229
Flame Shoulder	<i>Ochroleuca plecta</i>	Noctuidae	Noctuinae	weak	30	pointed	grass/herb-feeders	poly	Y	moderately declining	180
Garden Tiger	<i>Arctia caja</i>	Arctiidae	Arctiinae	weak	70	broad	grass/herb-feeders	poly	N	severely declining	297
Gold Swift	<i>Hepialus hecta</i>	Hepialidae	Hepialinae	medium	32	pointed	grass/herb-feeders	Mon	N	unknown	1
Green Arches	<i>Anaplectoides prasina</i>	Noctuidae	Noctuinae	strong	48	pointed	shrub/tree-feeders	poly	Y	increasing	1207
Green Silver-lines	<i>Pseudoips prasinana</i>	Noctuidae	Chloephorinae	strong	36	pointed	shrub/tree-feeders	poly	N	increasing	94
Heart and Dart	<i>Agrotis exclamationis</i>	Noctuidae	Noctuinae	weak	38	pointed	grass/herb-feeders	poly	Y	moderately declining	277
Herald	<i>Scoliopteryx libatrix</i>	Noctuidae	Ophiderinae	weak	46	pointed	shrub/tree-feeders	olig	Y	unknown	547
Ingrailed Clay	<i>Diarsia mendica</i>	Noctuidae	Noctuinae	strong	35	pointed	shrub/tree-feeders	poly	Y	moderately declining	231
July Highflyer	<i>Hydriomena furcata</i>	Geometridae	Larentiinae	weak	32	broad	shrub/tree-feeders	poly	N	increasing	113
Lackey	<i>Malacosoma neustria</i>	Lasiocampidae	Malacosomatinae	medium	32	broad	shrub/tree-feeders	poly	N	severely declining	114
Large Emerald	<i>Geometra papilionaria</i>	Geometridae	Geometrinae	medium	55	broad	shrub/tree-feeders	olig	N	increasing	312
Large Nutmeg	<i>Apamea anceps</i>	Noctuidae	Amphipyriinae	weak	43	pointed	grass/herb-feeders	olig	Y	severely declining	337
Large Yellow Underwing	<i>Noctua pronuba</i>	Noctuidae	Noctuinae	weak	55	pointed	grass/herb-feeders	poly	Y	increasing	472
Light Arches	<i>Apamea lithoxylaea</i>	Noctuidae	Amphipyriinae	medium	45	pointed	grass/herb-feeders	olig	Y	moderately declining	110
Light Emerald	<i>Campaea margaritata</i>	Geometridae	Ennominae	medium	40	broad	shrub/tree-feeders	poly	N	increasing	184
Lobster Moth	<i>Stauropus fagi</i>	Notodontidae	Heterocampinae	strong	60	pointed	shrub/tree-feeders	olig	N	unknown	1707

Maiden's Blush	<i>Cyclophora punctaria</i>	Geometridae	Sterrhinae	strong	28	broad	shrub/tree-feeders	mono	Y	increasing	102
Nut-tree Tussock	<i>Colocasia coryli</i>	Noctuidae	Pantheinae	strong	35	pointed	shrub/tree-feeders	poly	N	increasing	63
Oak Hook-tip	<i>Watsonalla binaria</i>	Drepanidae	Drepaninae	medium	30	broad	shrub/tree-feeders	olig	N	severely declining	97
Pale Prominent	<i>Pterostoma palpina</i>	Notodontidae	Notodontinae	weak	43	pointed	shrub/tree-feeders	olig	N	moderately declining	232
Pale Tussock	<i>Calliteara pudibunda</i>	Lymantriidae	Lymantriinae	weak	42	pointed	shrub/tree-feeders	poly	N	moderately declining	222
Peach Blossom	<i>Thyatira batis</i>	Thyatiridae	Thyatirinae	medium	35	pointed	shrub/tree-feeders	mono	Y	moderately declining	128
Pebble Hook-tip	<i>Drepana falcataria</i>	Drepanidae	drepaninae	medium	35	broad	shrub/tree-feeders	olig	N	moderately declining	140
Peppered Moth	<i>Biston betularia</i>	Geometridae	Ennominae	medium	55	broad	shrub/tree-feeders	poly	N	moderately declining	312
Plain Golden Y	<i>Autographa jota</i>	Noctuidae	Plusiinae	weak	40	pointed	grass/herb-feeders	poly	Y	moderately declining	301
Poplar Hawk-moth	<i>Laothoe populi</i>	Sphingidae	Smerinthinae	weak	80	pointed	shrub/tree-feeders	olig	N	moderately declining	563
Pretty Chalk Carpet	<i>Melanthia procellata</i>	Geometridae	Larentiinae	medium	40	broad	shrub/tree-feeders	mono	N	severely declining	184
Privet Hawk-moth	<i>Sphinx ligustri</i>	Sphingidae	Sphinginae	medium	110	pointed	shrub/tree-feeders	olig	N	unknown	356
Purple Thorn	<i>Selenia tetralunaria</i>	Geometridae	Ennominae	medium	44	broad	shrub/tree-feeders	poly	N	moderately declining	218
Ruby Tiger	<i>Phragmatobia fuliginosa</i>	Arctiidae	Arctiinae	weak	35	pointed	shrub/tree-feeders	poly	N	increasing	154
Rustic Shoulder-knot	<i>Apamea sordens</i>	Noctuidae	Amphipyriinae	weak	40	pointed	grass/herb-feeders	olig	Y	moderately declining	301
Scalloped Oak	<i>Crocallis elinguaris</i>	Geometridae	Ennominae	medium	38	broad	shrub/tree-feeders	poly	N	moderately declining	166
Scarce Silver-lines	<i>Bena bicolorana</i>	Noctuidae	Chloephorinae	strong	45	pointed	shrub/tree-feeders	olig	Y	unknown	946
Scorched Carpet	<i>Ligdia adustata</i>	Geometridae	Ennominae	medium	25	broad	shrub/tree-feeders	mono	N	moderately declining	56
Scorched Wing	<i>Plagodis dolabraria</i>	Geometridae	Ennominae	medium	35	broad	shrub/tree-feeders	olig	Y	increasing	363
Setaceous Hebrew Character	<i>Xestia c-nigrum</i>	Noctuidae	Noctuinae	weak	36	pointed	grass/herb-feeders	poly	Y	increasing	253
Shears	<i>Hada plebeja</i>	Noctuidae	Hadeninae	medium	35	pointed	grass/herb-feeders	poly	Y	increasing	52
Shuttle-shaped Dart	<i>Agrotis puta</i>	Noctuidae	Noctuinae	weak	30	pointed	grass/herb-feeders	poly	Y	increasing	180
Silver Y	<i>Autographa gamma</i>	Noctuidae	Plusiinae	weak	40	pointed	grass/herb-feeders	poly	Y	moderately declining	301
Slender Brindle	<i>Apamea scolopacina</i>	Noctuidae	Amphipyriinae	strong	35	pointed	grass/herb-feeders	olig	Y	increasing	123
Small Angle Shades	<i>Euplexia lucipara</i>	Noctuidae	Amphipyriinae	weak	33	pointed	shrub/tree-feeders	poly	Y	moderately declining	354
Small Emerald	<i>Hemistola chrysoptasaria</i>	Geometridae	Geometrinae	medium	35	broad	shrub/tree-feeders	mono	N	severely declining	140
Small Fan-foot	<i>Herminia grisealis</i>	Noctuidae	Hermininae	medium	25	pointed	shrub/tree-feeders	poly	Y	moderately declining	49
Spectacle	<i>Abrostola tripartita</i>	Noctuidae	Plusiinae	weak	33	pointed	grass/herb-feeders	mono	y	increasing	217
Swallow-tailed Moth	<i>Ourapteryx sambucaria</i>	Geometridae	Ennominae	medium	54	broad	shrub/tree-feeders	poly	N	moderately declining	304
Treble Lines	<i>Charanyca trigrammica</i>	Noctuidae	Amphipyriinae	weak	35	pointed	grass/herb-feeders	poly	N	increasing	69
White Ermine	<i>Spilosoma lubricipeda</i>	Arctiidae	Arctiinae	weak	40	broad	grass/herb-feeders	poly	N	severely declining	92

White Satin Moth	<i>Leucoma salicis</i>	Lymantriidae	Lymantriinae	medium	45	broad	shrub/tree-feeders	olig	N	unknown	227
White-pinion Spotted	<i>Lomographa bimaculata</i>	Geometridae	Ennominae	medium	28	broad	shrub/tree-feeders	olig	N	increasing	80
Yellow Shell	<i>Camptogramma bilineata</i>	Geometridae	Larentiinae	weak	27	broad	grass/herb-feeders	poly	Y	increasing	130
Yellow-tail	<i>Euproctis similis</i>	Lymantriidae	Lymantriinae	weak	33	broad	shrub/tree-feeders	poly	N	moderately declining	122

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APPENDIX D. Recapture rates and distances moved for 41 recaptured species.

Species	Scientific name	Forest affinity	No. marked	No. recaptured	Recaptured (%)	Mean distance (m)	Max. distance (m)	Min. distance (m)
Beautiful Golden Y	<i>Autographa pulchrina</i>	weak	28	2	7.1	411	426	396
Beautiful Hook-tip	<i>Laspeyria flexula</i>	medium	15	1	6.7	134	134	134
Black Arches	<i>Lymantria monacha</i>	strong	419	39	9.3	82	298	0
Bright-line Brown-eye	<i>Lacanobia oleracea</i>	weak	82	3	3.7	576	1053	54
Brown Rustic	<i>Rusina ferruginea</i>	weak	54	2	3.7	357	714	0
Buff Arches	<i>Habrosyne pyritoides</i>	medium	166	4	2.4	733	1993	109
Buff Ermine	<i>Spilosoma luteum</i>	weak	106	1	0.9	61	61	61
Buff-tip	<i>Phalera bucephala</i>	medium	49	5	10.2	88	322	0
Burnished Brass	<i>Diachrysia chrysitis</i>	weak	153	12	7.8	463	2774	0
Clay	<i>Mythimna ferrago</i>	weak	70	6	8.6	0	0	0
Clouded Border	<i>Lomaspilis marginata</i>	weak	14	2	14.3	0	0	0
Clouded Brindle	<i>Apamea epomidion</i>	medium	105	1	1.0	0	0	0
Common Footman	<i>Eilema lurideola</i>	weak	867	58	6.7	546	4269	0
Common Swift	<i>Hepialus lupulinus</i>	weak	132	3	2.3	0	0	0
Coronet	<i>Craniophora ligustri</i>	medium	190	6	3.2	66	200	0
Dark Arches	<i>Apamea monoglypha</i>	weak	630	10	1.6	584	3083	0
Dingy Footman	<i>Eilema griseola</i>	medium	970	34	3.5	244	2702	0
Double Square-spot	<i>Xestia triangulum</i>	medium	1029	152	14.8	348	3311	0
Drinker	<i>Euthrix potatoria</i>	medium	613	37	6.0	255	2440	0
Dun-bar	<i>Cosmia trapezina</i>	medium	1323	127	9.6	317	3563	0
Flame	<i>Axylia putris</i>	weak	107	5	4.7	83	288	0
Flame Shoulder	<i>Ochropleura plecta</i>	weak	228	2	0.9	768	1535	0
Garden Tiger	<i>Arctia caja</i>	weak	3	1	33.3	2387	2387	2387
Heart and Dart	<i>Agrotis exclamationis</i>	weak	787	39	5.0	545	2938	0
Ingrailed Clay	<i>Diarsia mendica</i>	strong	177	14	7.9	406	1985	0

July Highflyer	<i>Hydriomena furcata</i>	weak	904	24	2.7	51	223	0
Large Yellow Underwing	<i>Noctua pronuba</i>	weak	721	6	0.8	867	2740	0
Light Emerald	<i>Campaea margaritata</i>	medium	446	8	1.8	343	1595	0
Lobster Moth	<i>Stauropus fagi</i>	strong	74	4	5.4	1364	1976	619
Nut-tree Tussock	<i>Colocasia coryli</i>	strong	90	2	2.2	71	141	0
Pale Prominent	<i>Pterostoma palpina</i>	weak	69	4	5.8	528	1357	0
Poplar Hawkmoth	<i>Laothoe populi</i>	weak	162	16	9.9	619	2634	0
Pretty Chalk Carpet	<i>Melanthia procellata</i>	medium	47	1	2.1	223	223	223
Purple Thorn	<i>Selenia tetralunaria</i>	medium	99	4	4.0	183	486	0
Scalloped Oak	<i>Crocallis elinguarina</i>	medium	165	8	4.8	362	1022	0
Setaceous Hebrew Character	<i>Xestia c-nigrum</i>	weak	185	1	0.5	690	690	690
Shears	<i>Hada plebeja</i>	medium	4	1	25.0	183	183	183
Slender Brindle	<i>Apamea scolopacina</i>	strong	128	4	3.1	520	1782	0
Swallow-tailed Moth	<i>Ourapteryx sambucaria</i>	medium	46	1	2.2	1102	1102	1102
Treble Lines	<i>Charanyca trigrammica</i>	weak	22	1	4.5	0	0	0
Yellow-tail	<i>Euproctis similis</i>	weak	726	25	3.4	169	1021	0

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APPENDIX E. Coefficients table for distance moved with wingspan and wing shape as wing morphology traits and adult feeding, larval feeding guild, and forest affinity as life-history traits.

	Coefficient	SE	<i>t</i> value	<i>p</i> value
Intercept	10.90	2.29	4.75	<0.0001
Log(days)	2.73	0.57	4.82	<0.0001
Log(wingspan)	2.60	0.95	2.73	0.0066
Wing shape pointed	0.55	3.97	0.14	0.8905
Forest affinity strong	-10.52	3.33	-3.16	0.0016
Forest affinity medium	-0.10	3.45	-0.03	0.9763
Larval feeding guild grass/herb-feeders	-4.11	2.04	-2.01	0.0446
Adult feeding Yes	7.24	3.31	2.18	0.0293
Log(wingspan): Forest affinity strong	9.13	2.27	4.03	0.0001
Log(wingspan): Forest affinity medium	-0.15	1.63	-0.09	0.9252
Wing shape pointed: Forest affinity strong	10.96	4.31	2.54	0.0112
Wing shape pointed: Forest affinity medium	-8.28	4.11	-2.01	0.0447

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