THE PERSISTENCE OF THE SANDHILL RUSTIC MOTH *LUPERINA NICKERLII* SSP. *LEECHI* (LEPIDOPTERA: NOCTUIDAE) AT AN ISOLATED SITE IN CORNWALL, UK

ADRIAN SPALDING[1] & MARK R. YOUNG[2]

[1] *Tremayne Farm Cottage, Praze, Camborne, Cornwall TR1 2LS UK,*
[2] *Institute of Biological and Environmental Science, Zoology Building, University of Aberdeen, Tillydrone Avenue, Aberdeen Scotland*

ABSTRACT

The colony of the nocturnal moth *Luperina nickerlii leechi* Goater was studied between 1995 and 2009 on Loe Bar in Cornwall, where it persists as an isolated population separated from the nearest populations by over 300km. This study investigates the population size using transect studies, linked to detailed mapping of individual moths and the larval foodplant Sand Couch-grass *Elytrigia juncea*. There has been remarkable persistence in this single, small, isolated population but long-term trends indicate that the population may be gradually declining. Seventy percent of the recorded moths are female and males may find it easy to find females in the relatively small area of larval foodplant, which at its most extensive covers less than 20,000 m^2. Residence time at around 3.79 days allows time for females to mate and lay eggs. Restricted mobility ensures that moths do not lose touch with their habitat. The earlier the emergence the longer the flight period, so that factors which affect early emergence are probably beneficial.

INTRODUCTION

The Sandhill Rustic moth *Luperina nickerlii* Goater is a medium sized noctuid moth occurring in Europe mainly on dry xerothermic slopes but also (in Britain and Ireland and formerly in Brittany) in coastal locations. The moth is univoltine, the eggs being laid in August and September on grasses, inside the stems of which the larvae feed over-winter, before moving down in early spring to feed on the crowns and roots; on softer substrates the larvae and the pupae are subterranean. The moths are nocturnal, flying in late summer. The type locality is Czechoslovakia (Emmet, 1991) and there are several subspecies throughout Europe (Karsholt & Razowski, 1996) including *nickerlii* Freyer in Germany, Prague and Bulgaria, *graslini* Oberthür and *tardenota* Joannis in France and *albarracina* Schwingenschuss in Spain. All, except possibly ssp. *tardenota,* occur widely in Europe. Four subspecies occur in Britain and Ireland, separated from each other by over 300km: *gueneei* Doubleday (found in north Wales and north-west England) (Doubleday, 1864); *knilli* Boursin (found in south-west Ireland) (Knill-Jones, 1965); *demuthi* Goater & Skinner (found in south-east England) (Goater & Skinner, 1995) and *leechi* Goater (restricted to Loe Bar in south-west Britain) (Goater, 1976). *Luperina nickerlii leechi* Goater, 1976 was first discovered in Cornwall in 1974 when it was considered an interesting form of *Luperina testacea*, but subsequently described as a new subspecies of *Luperina nickerlii* on the basis of its silvery brown colouration, not found in other forms of the species.

Luperina nickerlii gueneei occurs in large populations on sand dunes in north Wales and the west coast of Lancashire (e.g. Wallace & Finnegan, 1994: Wallace, 2006). *Luperina nickerlii knilli* occurs widely on cliff tops along the south coast of the Dingle Peninsula in Ireland ((Knill-Jones, 1965; A. Spalding unpublished data).

Luperina nickerlii demuthi occurs in extensive populations on saltmarshes in south-eastern England (e.g. Spalding, 2002). In contrast, *Luperina nickerlii leechi* is restricted to a small area about 500m × 240m, where its larval foodplant Sand Couch-grass *Elytrigia juncea* occurs as a monoculture covering an area of less than 20,000m^2 (Spalding, 1991a). *Luperina nickerlii leechi* is of high nature conservation value, being restricted to one site, and has been classified as RDB1 (Waring, 1993). It can be characterized as a non-eruptive or latent species (Veldtman, McGeoch & Scholtz, 2007), having fully-functional wings, no sexual dimorphism and no physical defences, and being cryptic, solitary and as a sub-species monophagous; as such, it would not be expected to show sudden population explosions. It has recently been added to the British Biodiversity Action Plan list (JNCC, 2007) as a unique subspecies currently under threat and declining, using information on distribution and current status based on the results of the present study, which is designed to investigate the factors which may be linked to the persistence of this isolated colony.

METHODS

Study area

The study was carried out on Loe Bar, Cornwall, UK, most intensively between 2002 and 2009, but using additional data collected at the same site between 1995 and 2001. The study area is a shingle beach facing south-west onto Mounts Bay, exposed to strong westerly winds and occasionally washed over by waves in major storm events (Fig. 1). The larval foodplant *Elytrigia juncea* occurs as a near monoculture over large parts of Loe Bar, especially near the sea, in NVC community SD4 (Rodwell *et al*., 2000).

Fig. 1

Mapping

Almost nightly visits were made during the flight period and the position of each individual *L. nickerlii* located during these visits was mapped from 2003 onwards using a Trimble GEOXT GPS unit (made by Trimble Navigation Ltd) with the linked BoB (Beacon on the Belt) (used with the software GPS Pathfinder Office) and the European satellite system Egnos (European Geostationary Navigation Overlay Service) when available, with information transferred into MasterMap© and placed over the Ordnance Survey Mastermap digital topography layer digital base layer. Data were also post-processed for greater accuracy using RINEX data files from a local station from the National GPOS Network web site at: *http://gps.ordnancesurvey.co.uk/active.asp* giving greater than 50cm accuracy.

Population trends

Moths were surveyed at night during the course of the flight period, generally mid - August to late September, between 2002 and 2009 inclusive. Searching for moths resting on the low-growing vegetation was by powerful battery-operated searchlight. Flying moths were also netted, identified and recorded, but the great majority were found at rest. Surveys generally started at 23.00h (previous work having indicated that this was the time of peak numbers (Spalding, 1991a)). A transect 464m long by 10m wide running SSE to NNW across the Bar was established in 1995 based on the Butterfly Monitoring Scheme methodology (Hall, 1981: Pollard, Hall & Bibby, 1986) and moths counted within this area. It made use of permanent site features to ensure consistency of orientation from year to year and was first monitored by the author in 1995 (Spalding, 1997), the first recorded use of this method for nocturnal moths (Birkenshaw & Thomas, 1999). From 2003 onwards, transect information was

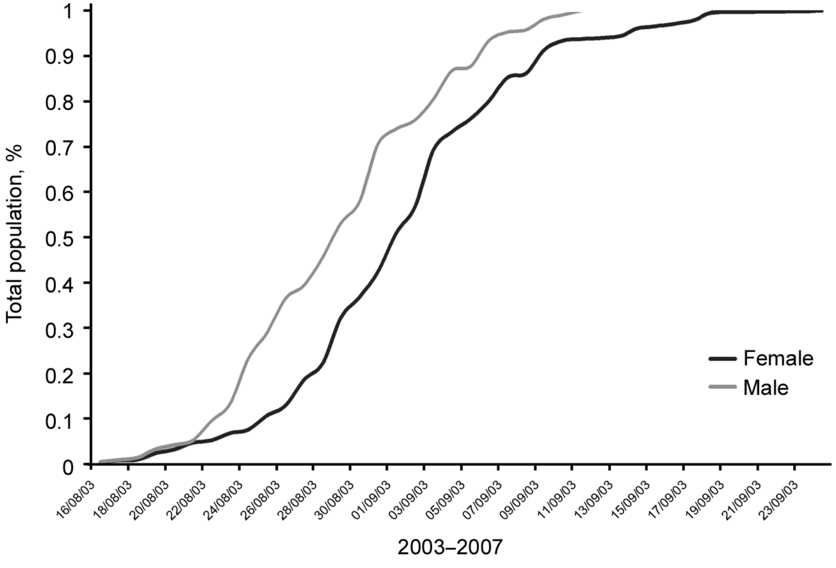

Fig 2. Cumulative totals for male and female Sandhill Rustics on Loe Bar 2003–2007

Table 1. Numbers of adult Sandhill Rustics recorded on Loe Bar 1995–2009

Year	Total recorded	Nos of females	Nos of males	Length of flight period (days)	Date first seen
1995	289	232	57	46	14 August
1996	237	165	72	31	15 August
1997	83	53	30	35	20 August
1998	64	37	27	34	11 August
1999	39	26	13	25*	24 August
2000	133	65	68	27*	20 August
2001	60	34	26	31	15 August
2002	126	82	44	36*	16 August
2003	167	124	43	39*	16 August
2004	246	192	54	34*	16 August
2005	195	130	65	37*	17 August
2006	172	132	40	32*	17 August
2007	77	57	20	36*	19 August
2008	43	32	11	27	22 August
2009	41	25	16	21*	23 August
Totals	1972	1386	586		

*Actual flight period; the other dates represent the minimum observed flight period.

obtained by extrapolation from detailed moth distributions mapped by GPS, a more accurate method than estimating whether individuals near the transect boundaries are within the transect. Weekly transect counts were collated for Sandhill Rustics and the Index of Abundance calculated from the sum of the weekly means according to the standard butterfly recording method (Pollard, Hall & Bibby, 1986).

Movement

Mark–release–recapture observations were conducted on Loe Bar in 2003 and 2004, when most moths (a few were not marked, e.g. mating pairs) were given an unique pattern of painted spots using acrylic paints on one or both forewings, allowing them to be recognized if recaptured and their movement over a number of nights traced back to the time and position of first capture.

Residence time

Residence time for moths was calculated by plotting the best-fit line on the recapture results (numbers of days between the first and last capture) and using the equation residence time b^{-1} where $b = (y - c)/x$ ($b =$ the rate of decline; $c =$ the intercept point on the y axis; $y =$ the corresponding point on y equal to the intercept point on the x axis; $x =$ days since first recapture).

RESULTS

Flight period and male:female ratio

A total of 1972 adult moths was recorded on Loe Bar between1995 and 2009 (Table 2). These results include all data from surveys and transect counts based on variable year to year effort and as such do not show exact population trends. The

Table 2. Numbers of Sandhill Rustics recorded along the transect across Loe Bar 1995–2007 and estimates of abundance

Year	Total seen on the transect over the flight period	Maximum number of moths per transect	Index of Abundance (the sum of the weekly means)
1995	95	12	32
1996	57	18	58
1997	33	9	33
1998	10	4	10
1999	13	5	13
2000	36	13	36
2001	14	7	14
2002	53	11	23.8
2003	20	4	5.3
2004	46	5	7.6
2005	31	6	10.3
2006	22	5	11
2007	11	3	7.5
2008	17	4	10
2009	26	8	17.5
Total	484		

flight period generally lasted just over 30 days (mean 32.7 days), with mean peak numbers in early September. The total does not include recaptured marked moths, but may include some unmarked moths seen more than once, e.g. on successive nights. The earlier the appearance, the longer the flight period ($r = 0.876$; $p \leqslant 0.01$) (taken from the data when the actual flight period was recorded). Males emerged earlier than females (Fig 1). The female: male ratio varied between 4:1 and 0.77:1. Only in 2000 were more males seen than females; female numbers appear to fluctuate more widely than male numbers.

Note that in 2003 and 2004 greater effort was devoted to survey work, including the use of MRR, and large numbers of moths were found then. Nevertheless, there must be real concern over the recent very low numbers, allowing for the fact that there were equally low numbers in 1998 and 1999.

Transect results

A total of 484 moths was recorded along the constant effort transect between 1995–2009 (Table 2) and the annual index of abundance calculated. The numbers of moths along the transect appear to have been decreasing since the early years of 1995 to 1997, but note the low numbers recorded in 1998 and 1999.

The trend in the highest numbers seen on the transect shows a gradual decline to lower counts interspersed with occasional higher counts. With 20% positive and negative potential error values relative to each sample point (Fig 3), the trend line ($r^2 = 0.334$) passes through 6 of the 15 sample points; analysis of variance of the regression indicates that the decline is significant ($p = 0.024$). Further sampling over the years is required to establish whether there is an ongoing decline, or whether it has declined to a period of relatively constant but low numbers since 2003.

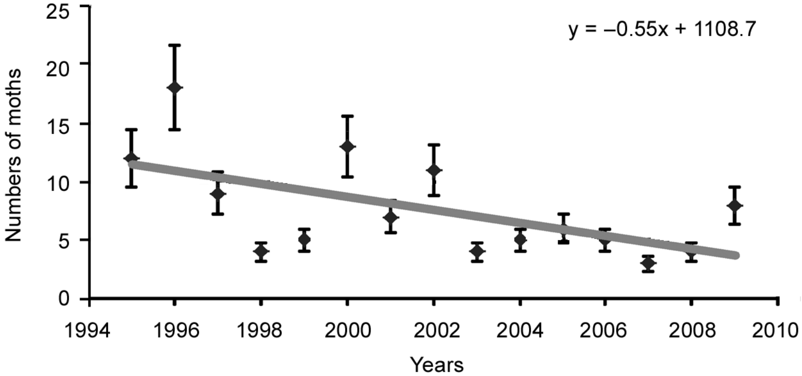

Fig. 3. Regression analysis of the highest numbers of moths seen on the transect 1995–2009 against years since the counts started

Residence time and the movement of moths across Loe Bar

There were 10 recaptures in 2003 and 14 in 2004 (Table 3) and all but one involved female moths. Distances moved ranged from 4m to 349m with a mean movement of 86.6m. Moths may actually move more indirectly between capture and recapture sites and hence may have travelled greater distances. One moth was recaptured twice, living at least 10 days and moving 88m and then 17m. Residence time (b^{-1}) of individual moths equated to 3.79 days ($b = (y-c)/x$) (Fig 4). The 10 days survived by a single moth indicates that individual residence time may be longer than that estimated as mean survival.

DISCUSSION

Persistence and flight period

The flight period varied between 21 and 46 days with a mean of 32.7 days. Flight period length can be highly variable in some butterflies (e.g. (Brakefield, 1987; Warren 1987a). Lepidopteran species with short flight periods may be more prone to extinctions, especially when combined with monophagy (Mattila *et al.*, 2006) or a narrow habitat breadth (= single habitat association) on low fertility sites (Nilsson, Franzén & Jönsson, 2008). Short flight periods will reduce the opportunity for Lepidoptera to outlast short-term bad weather events or habitat changes (e.g. Nilsson, Franzén & Jönsson, 2008). Possible threats to *L. nickerlii* on Loe Bar include stochastic events such as stormy weather and flooding and this species certainly has narrow habitat-breadth and is on a low fertility site. Early emergence is probably beneficial if leading to longer flight periods which may enable moths to better survive short-term influences. As a result, factors encouraging early emergence are likely to lead to long-term persistence of the population.

Persistence and residence time

Residence time on Loe Bar for individual Sandhill Rustics moths was 3.8 days. In captivity adults may survive for up to 17 days (females) and 5 days (males) (Spalding, 1991b). Published residence times for nocturnal moths are hard to come by, although some data are available for diurnal species, e.g. the residence time for *Dysauxes*

Table 3. The residence time and movement of marked moths on Loe Bar 2003–2004

Date marked	Sex	Date recaptured	Date 2nd recapture	Days between captures	Distance moved metres (m)
27.viii.03	F	1.ix.03	–	5	19
28.viii.03	F	30.viii.03	–	2	4
28.viii.03	M	30.viii.03	–	2	24
29.viii.03	F	30.viii.03	–	1	255
29.viii.03	F	30.viii.03	–	1	7
30.viii.03	F	31.viii.03	–	1	34
31.viii.03	F	1.ix.03	–	2	30
31.viii.03	F	2.viii.03	–	2	152
1.ix.203	F	2.ix.03	–	1	23
2.ix.03	F	3.ix.03	–	1	67
16.viii.04	F	21.viii.04	26.viii.04	5 & 5	88.3 & 17.2
23.viii.04	F	24.viii.04	–	1	2.35
27.viii.04	F	28.viii.04	–	1	53.6
27.viii.04	F	29.viii.04	–	2	349
28.viii.04	F	30.viii.04	–	2	16.5
29.viii.04	F	30.viii.04	–	1	71.5
30.viii.04	F	1.ix.04	–	2	11.7
30.viii.04	F	1.ix.04	–	2	9.92
30.viii.04	F	1.ix.04	–	2	44.5
31.viii.04	F	1.ix.04	–	1	143
29.viii.04	F	2.ix.04	–	4	107
2.ix.04	F	3.ix.04	–	1	260
5.ix.04	F	6.ix.04	–	1	279
5.ix.04	F	10.ix.04	–	5	9.62

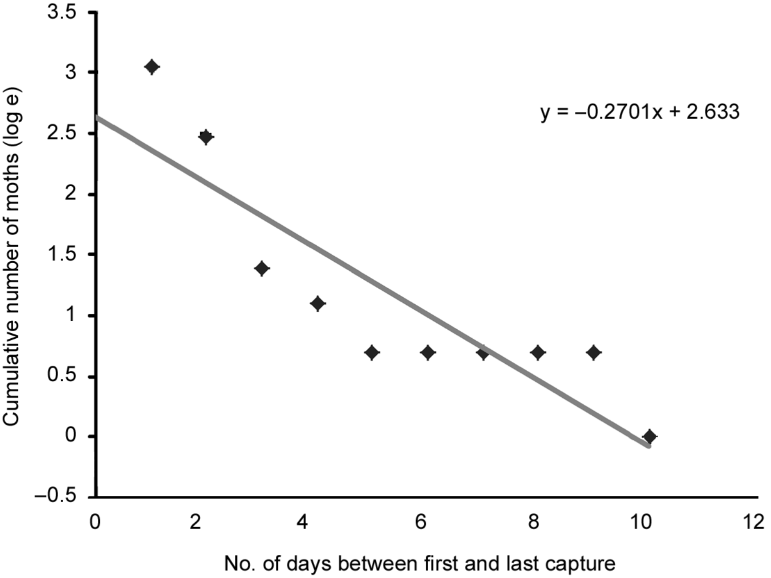

Fig 4. Residence times (days) of adult moths on Loe Bar 2003–2004

ancilla (L.) (Lepidoptera: Ctenuchidae) has been calculated as 2.6 days for males (Betzholtz, 2002). For butterflies residence times for non-overwintering species may range from 2 days for *Mellicta athalia* (Rottemburg) (Lepidoptera: Nymphalidae) (Warren, 1987b) to 34 days for males and 33 days for females of *Lycaena helle* (D. & S.) (Lepidoptera: Lycaenidae) in western Germany (Fischer, Beinlich & Plachter, 1999); the modal residence time from mark-release-recapture studies on butterflies is below 10 days (García-Barros & Fartmann, 2009). Residence time for Sandhill Rustics is within this range. Females in captivity emerge with large numbers of eggs within their abdomens, mate on the first night if males are available, start laying within 2 days and will lay up to about 300 eggs (pers. obs.) if they survive long enough. Egg-laying is rapid, eggs being laid in batches of up to 60 eggs at a time (pers. obs.). Residence time of 3.8 days is therefore long enough to ensure at least some population replacement, even if the full egg load is not laid.

The movement of adult moths

Distances moved were generally very small, the average movement being 86m. The distances moved by Lepidoptera can be very small e.g. less than 45m for *Yponomeuta padellus* (Brookes & Butlin, 1994) and 61m for *Lycaena helle* (Fischer, Benlich & Plachter, 1999). The majority of the Sandhill Rustic movements were localised and longitudinal across the habitat with very little lateral movement; one moth travelled almost the entire length of the site (349m). Similar within-habitat movement may occur with the moth *Agrotis ripae* (Hübner) (Lepidoptera: Noctuidae) which stays within its long thin habitat along the high tide mark on sandy shores (Young, 1997). Small within-site movement ensures that females stay in touch with their prospective mates and their habitat and foodplant. It also acts to reduce the risk of displacement beyond the habitat in very exposed and windy sites.

Persistence and male – female ratio

At Loe Bar many more females than males were seen, although the precise sex ratio changed over the course of the flight period. Uneven male: female ratios are generally unusual in Lepidoptera (Clarke, 1984; Shreeve, 1992) but it is likely that the effect observed is a real one – transect recording schemes often result in bias towards males as females fly less and are less noticeable when egg-laying (Dennis & Sparks, 2006). (However, in this case many of the recorded moths were noted at rest, rather than in flight, as usually applies to most butterflies recorded on transects). High female ratios are beneficial in small discrete populations where females are densely spaced and where males can easily find females. High female ratios can also occur where there are different levels of activity between males and females, e.g. where males broaden their temperature tolerance range and their heightened activity compensates for their lower numbers (Casula & Nichols, 2003). This may be true of Sandhill Rustics, where the males fly more readily (Spalding & Young, in press) and are likely therefore to cover a greater part of the habitat than females. Males also appear to emerge earlier than females and are ready to mate when females appear, enhancing the chances of successful pairing. They can also mate more than once, so reducing any adverse effect of a female-biased sex ratio.

Persistence and habitat area

The total habitat area (i.e. the area of *Elytrigia juncea*) available for Sandhill Rustics at Loe Bar is just under 2ha. The actual breeding habitat at Loe Bar may be less than this total area, as often plants do not represent usable resources unless they grow in suitable microhabitats (e.g. Roy & Thomas, 2003); in some areas of Loe Bar (perhaps 20–40%) Sandhill Rustics are never found, even though the larval foodplant is present. The actual breeding habitat may therefore be about 1ha. Sixteen of the British butterfly species (all with closed populations) can apparently survive in a minimum breeding area of 0.5–1ha (Warren, 1992), and the Sandhill Rustic territory is well within this range. Some moth species can survive for long periods in small areas. For example, a colony of *Pareulype berberata* (D. & S.) (Lepidoptera: Geometridae) survived for over 100 years from the 1860s to the 1990s (when the population was destroyed by fire) in a small length of narrow hedgerow not more than a few hundred metres long (e.g. Waring, 2000). The small habitat area is therefore unlikely in itself to be critical in reducing persistence of Sandhill Rustics here, but does significantly reduce the maximum population size.

Persistence and isolation

Many populations of Lepidoptera species exist in a network of suitable habitats in a metapopulation structure (Hanski & Gilpin, 1991) and their survival may depend on the protection of these metapopulations (e.g. Thomas & Jones, 1993; Hanski, 1994; Thomas, 1995; Saccheri *et al.*, 1998; Wahlberg, Klemetti & Hanski 2002); local populations within colonisation range may be regarded as belonging to a single metapopulation (e.g. Thomas & Harrison, 1992). This may be true of the other subspecies of *L. nickerlii*: *gueneei* in northern Britain where new colonies are occasionally founded (Burkmar & Jones, 2008), *demuthi* on the saltmarshes of south-east England and *knilli* on the cliffs of south-west Ireland. Metapopulations are characterised by colonisations and extinctions (Thomas, 1995) and lepidopteran species normally existing in metapopulations may not survive in isolation (Menéndez & Thomas, 2000). Sandhill Rustics at Loe Bar are completely isolated from all other known sites and may therefore not be able to survive in the long term. Unfortunately there is no knowledge of how long this population has survived at Loe Bar, although the sand bar may have been formed as a barrier beach moving onshore as Holocene sea levels rose after the last glacial period (May, 2007) and the moth has developed consistent racial characteristics, which itself suggests long persistence. The annual Index of Abundance indicates that the population varies from year to year; extinction may be most likely at its lowest point.

Persistence and population fluctuation

The reasons underlying the fluctuations in the population of *Luperina nickerlii leechi* are unknown. Stochastic elements may be important in small scale habitats (such as occurs on Loe Bar), where stochastic "noise" may push species into extinction (Southwood & Comins, 1976; Lande, 2002; Wilson & Roy, 2009), especially changes in weather which may be considered responsible for causing many of the fluctuations in insect populations (e.g. Davidson & Andrewartha, 1948; Singer & Thomas, 1996; Webb & Pullin, 1996). Isolation from other populations may also be critical, leading to loss of genetic variability (Nève, 2009) and loss of viability through inbreeding (e.g. Saccheri *et al.*, 1998; Cassel *et al.*, 2001; Nieminen *et al.*, 2001). Demographic stochasticity may be significant where the effective population size is limited by an unequal sex ratio (e.g. Gerber, 2006). It is suggested here that limited adult movement and the relative abundance of females contributes to the persistence of Sandhill Rustics at Loe Bar, and that factors leading to an early flight period are beneficial to its survival, but it remains highly threatened and vulnerable to adverse and unpredictable habitat factors.

REFERENCES

Betzholtz, P.-E. 2002. Population structure and movement patterns within an isolated and endangered population of the moth *Dysauxes ancilla* (Lepidoptera: Ctenuchidae): implications for conservation. *Journal of Insect Conservation* **6**: 57–66.

Birkenshaw, N. & Thomas, C. D. 1999. Torch-light transect surveys for moths. *Journal of Insect Conservation* **3**: 15–24.

Brakefield, P. M. 1987. Geographical variation in, and temperature effects on, the phenology of *Maniola jurtina* and *Pyronia tithonus* (Lepidoptera, Satyrinae) in England and Wales. *Ecological Entomology* **12**: 139–148.

Brookes, M. I. & Butlin, R. K. 1994. Population structure in the small ermine moth *Yponomeuta padellus*: an estimate of dispersal. *Ecological Entomology* **19**: 97–107.

Burkmar, R. & Jones, G. 2008. The Sandhill Rustic: A Conservation Flagship *Atropos* **35**: 38–44.

Cassel, A., Windig, J., Nylin, S. & Wiklund, C. 2001. Effects of population size and food stress on fitness-related characters in the scarce heath, a rare butterfly in western Europe. *Conservation Biology* **15**: 1667–1673.

Casula, P. & Nichols, J. D. 2003. Temporal Variability of Local Abundance, Sex Ratio and Activity in the Sardinian Chalk Hill Blue Butterfly. *Oecologia* **136**: 374–382.

Clarke, C. 1984. Upsets in the sex-ratio of some Lepidoptera. In R. I. Vane-Wright, & P. R. Ackery (Eds). *The Biology of Butterflies*. Symposium of the Royal Entomological Society. Academic Press. London.

Davidson, J. & Andrewartha, H. G. 1948. The influence of rainfall, evaporation and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). *Journal of Animal Ecology* **17**: 200–222.

Dennis, R. L. F. & Sparkes, T. H. 2006. When is a habitat not a habitat? Dramatic resource use changes under differing weather conditions for the butterfly *Plebejus argus*. *Biological Conservation* **129**: 291–301.

Doubleday, H. 1864. Luperina Gueneei, H. Dbl. n. sp. *Entomologist's Manual* 123–124.

Emmet, A. M. 1991. *The Scientific Names of the British Lepidoptera. Their History and Meaning*. Harley Books. Colchester.

Fischer, K., Beinlich, B. & Plachter, H. 1999. Population structure, mobility and habitat preferences of the violet copper *Lycaena helle* (Lepidoptera: Lycaenidae) in Western Germany: implications for conservation. *Journal of Insect Conservation* **3**: 43–52.

García-Barros, E. & Fartmann, T. 2009. Butterfly oviposition: sites, behaviour and modes. In J. Settle, T. Shreeve, M. Konvièka & H. Van Dyck (eds). *Ecology of Butterflies in Europe*. Cambridge University Press. Cambridge.

Gerber, L. R. 2006. Including behavioural data in demographic models improves estimates of population viability. *Frontiers in Ecology and the Environment* **4**: 419–427.

Goater, B. 1976. A new sub-species of *Luperina nickerlii* (Freyer) (Lep: Noctuidae) from Cornwall. *Entomologist's Gazette* **27**: 141–143.

Goater, B. & Skinner, B. 1995. A new subspecies of *Luperina nickerlii* Freyer, 1845 from south-east England, with notes on the other subspecies found in Britain, Ireland and mainland Europe. *The Entomologist's Record and Journal of Variation* **107**: 127–131.

Hall, M. L. 1981. *Butterfly Monitoring Scheme. Instructions for independent recorders*. ITE (NERC). Cambridge.

Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**: 151–162.

Hanski, I. & Gilpin, M. 1991. Metapopulation dynamics: a brief history an conceptual domain. *Biological Journal of the Linnean Society* **42**: 3–16.

JNCC. 2007. Biodiversity Action Plan Species. *http://www.ukbap.org.uk/PrioritySpecies*

Karsholt, O. & Razowski, J. (eds). 1996. *The Lepidoptera of Europe. A Distributional Checklist*. Apollo Books. Stenstrup.

Knill-Jones, S. A. 1965. The discovery of an Irish sub-species of *Luperina nickerlii* Freyer (Lep., Noctuidae). *Entomologist's Gazette*. **16**: 3–6.

Lande, R. 2002. Incorporating stochasticity in population viability analysis. In S. R. Bessinger & D. R. McCullough (eds). *Population Viability Analysis*. University of Chicago Press. Chicago.

Mattila, N., Kaitala, V., Komonen, A., Kotiaho, J. S. & Päivinen, J. 2006. Ecological determinants of distribution decline and risk of extinction in moths. *Conservation Biology* **20**: 1161–1168.

May, V. J. 2007. Loe Bar. *Geological Conservation Review* **28**: 1–5.

Menéndez, R. & Thomas, C. D. 2000. Metapopulation structure depends on spatial scale in the host-specific moth *Wheeleria spilodactylus* (Lepidoptera: Pterophoridae). *Journal of Animal Ecology* **69**: 935–951.

Nève, G. 2009. Population genetics of butterflies. In J. Settle, T. Shreeve, M. Konvièka & H. Van Dyck (eds). *Ecology of Butterflies in Europe*. Cambridge University Press. Cambridge.

Nieminen, M., Singer, M. C., Fortelius, W., Schöps, K. & Hanski, I. 2001. Experimental confirmation that inbreeding depression increases extinction risk in butterfly populations. *American Naturalist* **157**: 237–244.

Nilsson, S. G., Franzén, M. & Jönsson, E. 2008. Long-term land-use changes and extinction of specialised butterflies. *Insect Conservation and Diversity* **1**: 197–207.

Pollard, E., Hall, M. L. & Bibby, T. J. 1986. *Monitoring the abundance of butterflies 1976–1985*. Research and survey in nature conservation No. 2. NCC, Peterborough.

Rodwell, J. S., Pigott, C. D., Ratcliffe, D. A., Malloch, A. J. C., Birks, H. J. B., Proctor, M. C. F., Shimwell, D. W., Huntley, J. P., Radford, E., Wiggington, M. J. & Wilkins, P. 2000. *British Plant Communities. Volume 5*. Cambridge University Press. Cambridge.

Roy, D. B. & Thomas, J. A. 2003. Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologica* **134**: 439-444.

Saccheri, I, Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W. & Hanski, I. 1998. Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**: 491–494.

Shreeve, T. G. 1992. Adult behaviour. In R. L. H. Dennis. (Ed). 1992. *The Ecology of Butterflies in Britain*. Oxford University Press. Oxford.

Singer, M. C. & Thomas, C. D. 1996. Evolutionary responses of a butterfly metapopulation to human-caused and climate-caused environmental variation. *American Naturalist* **148**: 9–39.

Southwood, T. R. E. & Comins, H. N. 1976. A synoptic population model. *Journal of Animal Ecology* **45**: 949–965.

Spalding, A. 1991a. Notes on the behaviour of *Luperina nickerlii leechi* (the Sandhill Rustic, Lep: Noctuidae) at its site in Cornwall. *The Entomologist's Record and Journal of Variation* **103**: 323–325.

Spalding, A. 1991b. Notes on the population of *Luperina nickerlii leechi* Goater (Lepidoptera: Noctuidae) at its site in Cornwall, 1987-89. *The British Journal of Entomology & Natural History* **4**: 133–137.

Spalding, A. 1997. The use of the butterfly transect method for the study of the nocturnal moth *Luperina nickerlii leechi* Goater (Lepidoptera: Noctuidae) and its possible application to other species. *Biological Conservation* **80**: 147–152.

Spalding, A. 2002. In the Field: Searching for Sandhill Rustic. *Atropos* **17**: 50–52.

Spalding A. & Young M. in press. The effect of weather on the activity of the moths – the case of *Luperina nickerlii* (Lepidoptera: Noctuidae) under field conditions. *Entomologist's Gazette*.

Thomas, C. D. 1995. Ecology and conservation of butterfly metapopulations in the fragmented British landscape. In A.S. Pullin (ed). *Ecology and Conservation of Butterflies*. Chapman & Hall. London.

Thomas, C. D. & Harrison, S. 1992. Spatial dynamics of a patchily-distributed butterfly species. *Journal of Animal Ecology* **61**: 437–446.

Thomas, C. D. & Jones, T. M. 1993. Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: lessons for conservation in a fragmented landscape. *Journal of Animal Ecology* **62**: 472–481.

Veldtman, R., McGeoch, M.A. & C.H. Scholtz. 2007. Can life-history and defence traits predict the population dynamics and natural enemy responses of insect herbivores? *Ecological Entomology* **32**: 662–673.

Wahlberg, N., Klemetti, T. & Hanski, I. 2002. Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. *Ecography* **25**: 224–232.

Wallace, I. 2006. *The Sandhill Rustic Moth* Luperina nickerlii guenéei *on Gronant Dunes: Establishing a baseline for Common Standards Monitoring*. CCW Contract Science No 764. National Museums. Liverpool.

Wallace, I. & Finnegan, P. 1994. Talacre Dunes Management Plan: the 1993 Status of the Sandhill Rustic Moth in the Prestatyn to Point of Ayr Dune System. Unpublished report. Environmental Resources Management. London.

Waring, P. 1993. *National Moth Conservation Project: News Bulletin* 5. JNCC. Peterborough.

Waring, P. 2000. Conserving the Barberry carpet moth. *British Wildlife* **11**: 175–182.

Warren, M. S. 1987a. The ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. I. Host selection and phenology. *Journal of Applied Ecology* **24**: 467–482.

Warren, M. S. 1987b. The ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. II. Population dynamics and the effect of habitat management. *Journal of Applied Ecology* **24**: 499–513.

Warren, M. S. 1992. Butterfly Populations. In R. L. H. Dennis (Ed). *The Ecology of Butterflies in Britain*. Oxford University Press. Oxford.

Webb, M. R. & Pullin, A. S. 1996. Larval survival in populations of the large copper butterfly *Lycaena dispar batavus*. *Ecography* **19**: 279–286.

Wilson, R. J. & Roy, D. B. 2009. Butterfly population structure and dynamics. In J. Settle, T. Shreeve, M. Konvièka & H. Van Dyck (eds). *Ecology of Butterflies in Europe*. Cambridge University Press. Cambridge.

Young, M. 1997. *The Natural History of Moths*. Poyser Natural History. London.