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Distributions of occupied and vacant butterfly habitats in fragmented landscapes

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Summary. We found several rare UK butterflies to be restricted to relatively large and non-isolated habitat patches, while small patches and those that are isolated from population sources remain vacant. These patterns of occurrence are generated by the dynamic processes of local extinction and colonization. Habitat patches act as terrestrial archipelagos in which long-term population persistence, and hence effective long-term conservation, rely on networks of suitable habitats, sufficiently close to allow natural dispersal.

Key words: Colonization – Biogeography – Extinction – Incidence function – Metapopulation

The processes of local extinction and colonization should apply to terrestrial "habitat islands" as well as to oceanic islands (e.g. Lovejoy et al. 1986; Wilcove et al. 1986; Simberloff 1988; Soulé et al. 1988; Gilpin and Hanski 1991; Taylor 1991). On oceanic islands, most extinction takes place on small islands (e.g. MacArthur and Wilson 1967; Schoener 1991), and colonization of relatively distant islands is slow (e.g. MacArthur and Wilson 1967; Simberloff 1976; Williamson 1981). This leads to patterns of occurrence (incidence functions) whereby most species occur disproportionately on large islands and on those near the mainland (e.g. Diamond 1975; Williamson 1981). By analogy, habitat specialists that inhabit fragmented, terrestrial landscapes could be expected to occur predominantly in relatively large habitat patches, and in patches which are close to others.

Although the theoretical effects of habitat isolation and patch size are well known (e.g. Lande 1988; Gilpin and Hanski 1991), their effects on individual species have rarely been studied in detail (e.g. Lovejoy et al. 1986; Wilcove et al. 1986; Simberloff 1988; Soulé et al. 1988; Lawton and Woodroffe 1991; Gilpin and Hanski 1991; Sjogren 1991; Taylor 1991), particularly for insects (Harrison et al. 1988). To construct incidence functions for habitat specialists in fragmented, terrestrial landscapes, it is essential to be able to distinguish between habitat and non-habitat, regardless of the presence or absence of the species in question (Harrison et al. 1988; Lawton and Woodroffe 1991; Sjogren 1991; Taylor 1991). We have defined suitable habitat precisely and unambiguously for several colonial United Kingdom butterfly species, and can now map the distributions of vacant habitat patches (within species geographic ranges) as well as the distributions of occupied habitat. In this paper, we bring together studies of the distributions of four butterfly species and present new analyses to show that the same general pattern of patch occupancy is consistent among species.

Methods and analysis

We mapped the distributions of four British butterfly species and of their habitats using the quantitative survey technique of Thomas (1983a). The species were *Plebejus argus* (Lycaenidae), *Hesperia comma* (Hesperiidae), *Thymelicus acteon* (Hesperiidae) and *Mellicta athalia* (Nymphalidae). We also studied colonization in a fifth species, *Strymonidia pruni* (Lycaenidae).

Using logistic regression (LOGIT, SYSTAT), we analysed the presence (1) and absence (0) of each species in relation to patch area and distance to the nearest other populated patch (the nearest potential source). Terms and interactions were dropped from the analysis by backwards elimination until only those that were significant ($P<0.05$) were left. In a second analysis, we used distance to the nearest habitat patch instead of distance to the nearest populated patch.

A potential problem arises in the independence of data for distance. If patch A is the nearest neighbour of B, and vice versa, the same measure of distance will be used twice. Therefore, in separate analyses, we dropped one member of all such pairs, and then dropped the other member of each pair. All subsets of the data produced overall models that were significant, and in each case the same model components were significant and gave very similar parameter estimates. Therefore, we present only the full analyses in this paper.

Study species and results

On limestone in North Wales, *Plebejus argus* occupies southerly-facing hillsides subject to intermediate intensi-

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ties of grazing (Thomas 1985a, b; Thomas and Harrison 1992). Here, *P. argus* lays its eggs along the margins between bare ground and the vegetation (Thomas 1985a). *P. argus* is found only in habitat patches which are within 1 km of other populated patches; it is absent from small (<0.05 ha) and isolated (>1 km) patches (Fig. 1a, Table 1a). Local extinctions and recolonizations take place predominantly in relatively small (0.05–1.00 ha) habitat patches (Thomas and Harrison 1992), and colonization is distance-dependent (Table 1b).

The skipper *Hesperia comma* also occurs on southerly-facing calcareous grasslands, but on chalk downs in southern England. *H. comma* lays its eggs only on small *Festuca ovina* plants which are adjacent to bare ground (Thomas et al. 1986). Formerly widespread, *H. comma* became restricted to 46 or fewer refuge localities when myxomatosis killed rabbits in the mid-1950s, and most of the downs became overgrown (Thomas et al. 1986). Conservation management and a gradual recovery by rabbits during the 1970s and 1980s (Trout et al. 1986; Trout and Tittensor 1989) have restored the habitat of *H. comma* to at least 144 sites in S.E. England. However, by 1991 *H. comma* had recolonized only 35 of these, and remains restricted to relatively large and non-isolated patches (Fig. 1b, Table 1a). Between 1982 and 1991, *H. comma* colonized 29 relatively large patches which were close to population sources and became extinct from 10 predominantly small, isolated patches (Thomas and Jones (in press)).

Another grassland skipper, *Thymelicus acteon*, occupies warm, >15 cm tall, grasslands dominated by its host plant *Brachypodium pinnatum* (Thomas 1983b). Many new patches of this habitat were created as domestic, and later rabbit, grazing declined on southern downland during the 50–100 year period preceding 1978 (when our survey was conducted). As a result, *T. acteon* colonized inland from its traditional undercliff refuges (Thomas 1983b). Re-evaluation of the survey shows that *T. acteon* failed to occupy the most isolated patches of suitable habitat within its historical range (Fig. 1c, Table 1a). Many other large patches of apparently suitable *B. pinnatum*-dominated downland are 50–250 km away from the nearest *T. acteon* population (in the South and North Downs), but they are not included in Fig. 1c because they are beyond the documented range of *T. acteon*.

In South East England, the fritillary *Mellicta athalia* inhabits the earliest successional stages of coppiced (regularly-cut) woodlands, and its larvae feed on *Melampyrum*

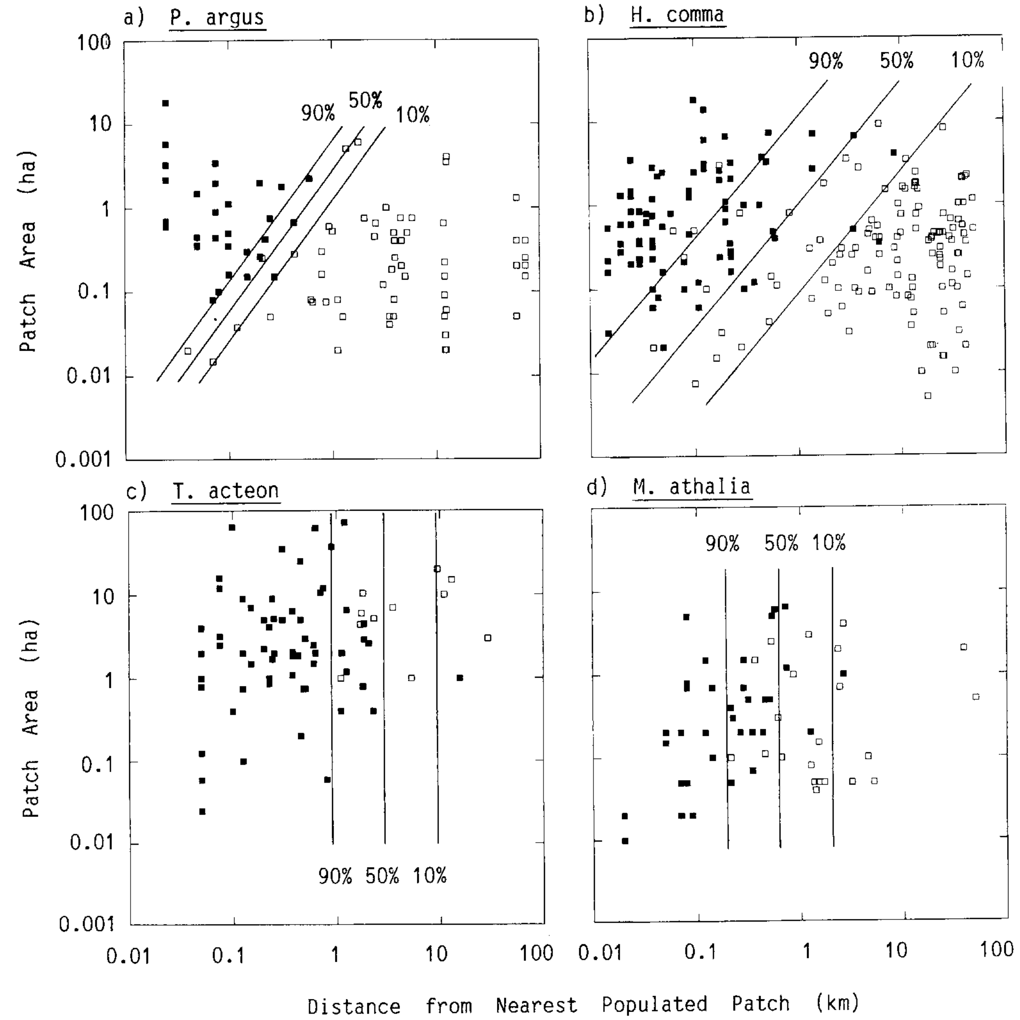

Fig. 1a–d. Distributions of occupied (*solid*) and vacant (*open*) habitat patches for four species of British butterfly. *Lines* give fitted 90%, 50% and 10% occupancy, from logistic equations in Table 1. **a** *Plebejus argus* on limestone grassland in North Wales, in 1990 (reanalysed from Thomas and Harrison 1992). **b** *Hesperia comma* on chalk grassland in the South and North Downs, S.E. England, in 1991 (from Thomas and Jones (in press)). **c** *Thymelicus acteon* on chalk and limestone grasslands in Dorset, in 1978 (data from Thomas 1983b, unpublished): the one occupied site >2.25 km from the nearest population is a separate refuge (which is currently threatened) and not a 20th-century colonist. **d** *Mellicta athalia* in woodland clearings, in Kent and Essex, SE England, in 1980 (data from Warren et al. 1984, unpublished)

Table 1. Logistic regression equations relating (a) butterfly occupancy and (b) colonization to patch area (ha) and to distance (m) from the nearest populated patch

Species	Constant	Log_{10}area	Log_{10}dist	Model[a] X^2	RHO^2-P	RHO^2-H	*n*
(a) Occupancy							
Plebejus argus	28.45**	6.18*	−10.40**	96.4***	0.850	0.158	77
Hesperia comma	9.09***	2.08***	−3.03***	183.7***	0.692	0.124[b]	197
Thymelicus acteon	14.96***		−4.33**	32.6***	0.524	0.187	74
Mellicta athalia	11.94***		−4.25***	36.9***	0.463	0.133	59
(b) Colonization							
P. argus[c]	8.15*		−4.01**	22.1***	0.561	0.017	62

* $P<0.05$; ** $P<0.01$; *** $P<0.001$

[a] 2 *df* in area and distance models, 1 *df* in distance-only models

[b] $n=162$ for this analysis

[c] measured over 7 years; only 3 extinctions were recorded on limestone, so *P. argus* extinctions could not be analysed by logistic regression

RHO^2-P is the proportion of variation explained by the models. RHO^2-H is the proportion of variation explained when distance is measured to the nearest habitat patch (equations not given). *n*, number of patches analysed

pratense (Warren et al. 1984; Warren 1987a, b, c, 1991). *Mellicta athalia* fails to colonize the most isolated patches of these ephemeral habitats (Fig. 1d, Table 1a), and often takes 2 or 3 years (generations) to colonize patches just 300–700 m from source populations (Fig. 2). In this species, local extinction is frequent and habitat- rather than area-dependent: succession eliminates *M. athalia* from individual habitat patches within 5–10 years of their creation (Warren 1987c).

The woodland hairstreak, *Strymonidia pruni*, lays its eggs on any *Prunus* species, but mainly on sheltered banks of *P. spinosa* (Thomas 1974, 1991). Historically, *S. pruni* was restricted to a belt of woodland in the East Midlands, where cutting was sufficiently infrequent (every 20–40 yrs) that *S. pruni* was able to disperse to new banks of *P. spinosa* as they became available. Elsewhere *S. pruni* was apparently unable to keep up with the shifting mosaic of its habitat. Support for this view is provided by the substantial delay shown by *S. pruni* in colonizing fresh patches of habitat that are more than a few hundred metres from source populations (Fig. 3). We have not mapped the distribution of vacant habitat in this species, but the habitat is clearly much more widespread than the historical distribution. Confirmation of this was provided by the successful introduction of *S. pruni* to Surrey in 1952, 90 km outside its previous range (Thomas 1991). This introduced population survives to the present day.

Discussion

The patterns of occurrence (Fig. 1) are consistent with a stepping-stone model of island occupancy (Gilpin 1980). The probability of occupancy increases with patch size

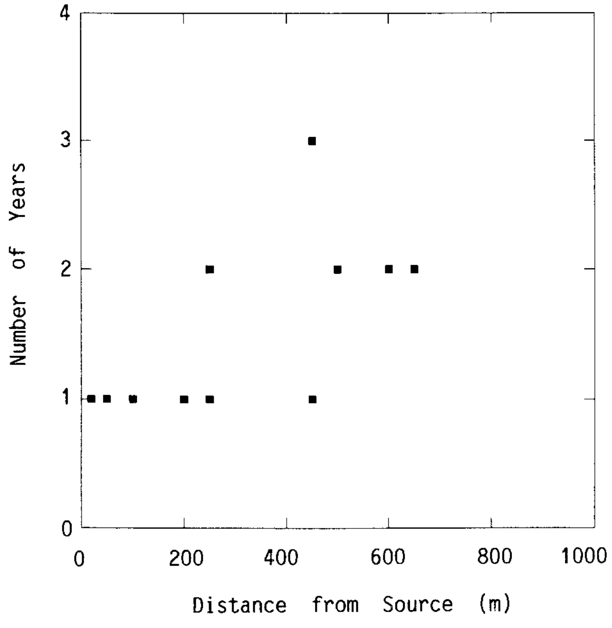

Fig. 2. Numbers of years (generations) taken by *M. athalia* to colonize temporary woodland clearings (coppices), at different distances from populated source patches; data from the Blean Wood complex, Kent. Time to colonize after habitat creation versus distance; Kendall tau = 0.569, $n=12$, $P<0.05$

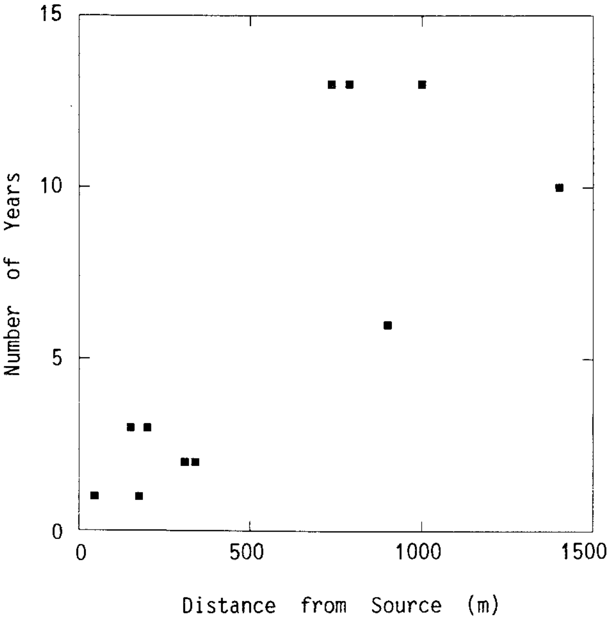

Fig. 3. Numbers of years (generations) taken by *S. pruni* to colonize vacant habitat patches, at different distances from populated source patches; data from Surrey, Monks Wood and Keysoe Park Wood. Years = 0.942 + 0.00937 Dist (m), $n=11$, $P=0.003$; $r^2=0.641$

and distance to the nearest occupied patch as a dynamic consequence of local extinction and colonization. The amount of variation for occupancy explained by the logistic regression models can be assessed by examining the RHO^2 values for the models. RHO^2 is the logistic equivalent of r^2 in normal linear regression, i.e. the proportion of variation explained. Since RHO^2 values between 0.2 and 0.4 are generally regarded as good fits of logistic models to data (Hensher and Johnson 1981), the higher values obtained here (0.46–0.85) show extremely good correspondence between the logistic regressions and the data. The importance of the effect of isolation from other populated patches can be seen by comparing RHO^2 values for the distance-to-nearest-population (RHO^2-P) and distance-to-nearest-habitat (RHO^2-H) models; the distribution of populations in habitat patches explains an additional 0.33–0.69 of the variation for occupancy. Present spatial patterns of habitat only weakly explain the distribution of occupied patches (RHO^2-H varies between 0.12 and 0.19). This implies that historical factors have played a major role in determining distributions, and that present distributions are not solely a consequence of the spatial characteristics of present habitat patches.

Area was significant only for *P. argus* and *H. comma* (Fig. 1), but this may reflect recording effort rather than a biological difference among the species: the smallest vacant patches were not mapped for *T. acteon* and *M. athalia*. Notice that the smallest patches that were occupied by *T. acteon* and *M. athalia* were close to neighbours.

The observed patterns of patch occupancy are apparently the dynamic consequence of local colonizations and extinctions. Local extinction is most frequently observed in small patches in *P. argus* (Thomas and Harrison 1992) and *H. comma* (CD Thomas and TM Jones, unpublished). This would lead to reduced occupancy of relatively small habitat patches, as was observed. However, extinction can hit habitat fragments of any size, especially if habitat quality deteriorates (Thomas 1985b; Thomas and Harrison 1992; Thomas 1991; Thomas et al. 1986; Warren 1991, in press). For *M. athalia* and *S. pruni*, local extinction depends more on the time since habitat creation than on patch area since both species rely on the successional stages of woodlands.

Even the largest habitat patches in the fragmented landscapes we studied were <100 ha, and most were <10 ha (Fig. 1), so none of the patches in the present study systems can be regarded as immune from extinction. Therefore, the five species considered here do not conform to a Boorman and Levitt (1973) metapopulation model, in which the largest patches are regarded as eternally populated. Harrison et al. (1988) and Schoener (1991) described invertebrate metapopulations that did appear to fit the Boorman-Levitt model, but the largest patches/islands in their studies (100–2000 ha) were much larger than the habitat fragments we examined. The butterflies we studied do not conform exactly to a Levins (1969, 1970) type metapopulation model either, in which all patches are equally susceptible to local extinction. The two types of theoretical model can be regarded as opposite ends of a continuum. The real situation for these colonial butterflies in fragmented landscapes is intermediate between these two extreme models: some patches (generally the largest) are more important to persistence than are others, but no patch can be regarded as eternally populated. The time- rather than area-dependent extinctions of *M. athalia* and *S. pruni* place them close to Levins-type models.

Colonization of suitable habitat apparently depends mostly on isolation. The more isolated a patch, the less likely it is to be colonized (Table 1b; Thomas and Jones (in press)), and the greater the gap between habitat patches, the longer it takes for a vacant patch to be colonized from one that is populated (Figs. 2 and 3). This will lead to reduced occupancy of relatively isolated habitat patches.

If vacant habitat remains vacant simply because it is too isolated for colonization to be possible, human-mediated establishment of species in isolated patches should meet with success. Outcomes have been documented for >3 years following introduction for 28 species of British butterfly (Oates and Warren 1990; see also Holdren and Ehrlich 1981; Harrison 1989); 18 species have been successfully established on at least one occasion, including *P. argus* (Thomas and Harrison 1992), *M. athalia* (Warren 1991), and *S. pruni* (Thomas 1991). Ten species have failed. Seven of the ten failures involved species that were released just once or twice, some into poor habitat, and two of the remaining three were nationally extinct species for which Britain may no longer be suitable.

Many of the habitat patches which are now vacant were formerly populated, but the populations in them became locally extinct, usually when the habitat was temporarily unsuitable (Thomas 1985b; Thomas and Harrison 1992; Thomas 1991; Thomas et al. 1986; Warren 1991, in press). The scope for recolonization will then depend on the distribution of population refuges and on the ability to recolonize through a network of habitat patches. Maximum natural single-step colonization distances that have been observed or deduced for the species considered here are: 0.60–1.00 km for *P. argus* (Thomas and Harrison 1992), 8.65 km for *H. comma* (CD Thomas and TM Jones, unpublished), 2.25 km for *T. acteon*, 0.65–2.50 km for *M. athalia* (Warren 1987c), and 1.40 km for *S. pruni*. Depending on the species, a lack of suitable habitat patches for a few to tens of kilometres would prevent spread from occupied regions into those where all habitat patches are vacant.

The importance of stepping-stone habitat patches to sedentary species can be seen in *S. pruni* and *P. argus*. Following its introduction to Surrey, *S. pruni* spread 4 km from the release point in 36 years, even though the maximum known single-step colonization distance was only 1.4 km. Following the successful introduction of *P. argus* to an unoccupied part of North Wales in 1942 (Thomas and Harrison 1992), this species also spread further (≥1.8 km in 30 years, 2.5 km in 41 years) than was achieved in any single step (each step ≤0.6 km).

The contagious distributions of occupied patches (Fig. 1) have important implications for the conservation of colonial species. Populations in single, isolated patches rarely persist in the long term, say for 100 years or more, unless patches are much larger than most remaining habitat fragments. Conservation must, therefore, cater for the protection of metapopulations occupying networks of habitat patches, not all of which will lie within a single protected area. Integrated protection and management of viable networks of patches is needed, rather than independent patch-by-patch measures. The approach taken here, in which vacant as well as occupied habitats are mapped (Fig. 1, Table 1), will allow conservation managers to predict whether freshly-created habitat will become populated or not, and whether introductions and reintroductions are likely to result in long-term population persistence in vacant networks of patches.

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