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The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story

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Abstract

Many specialist species are declining as a result of habitat loss and fragmentation, such that conservation actions typically aim to stem rates of decline rather than bring about genuine recovery. Here, we document the recovery of a species from former population refuges. An extensive survey of the entire British range of *Hesperia comma*, conducted in 2000, recorded over three times the number of tetrads (2 km × 2 km grid squares) occupied in 1982. This was accompanied by a fourfold increase in the number of populations and a 10-fold increase in the habitat area occupied. The improving status of *H. comma* is the product of good habitat management, recovering rabbit populations and climate warming, which have improved the quality, and increased the availability, of suitable habitat. This has enabled remnant metapopulations to expand, via distance-dependent colonisation, through large networks of habitat. Metapopulation recovery in *H. comma* demonstrates that landscape-scale conservation can be successful.

Keywords: Agri-environment; Colonisation; Conservation; Distribution; Metapopulation

1. Introduction

In the modern landscape, numerous taxa are threatened by the destruction and fragmentation of their habitat, and have become increasingly restricted to relatively small or isolated patches of once extensive habitat (Saunders et al., 1991; Groombridge, 1992; Andrén, 1994; Gibbs and Stanton, 2001). Nevertheless, it is very rare that these fragments are completely isolated from one another and many species persist in a regional network of suitable habitat, connected via migration, as a metapopulation (Harrison et al., 1988; Kindvall and Ahlén, 1992; Thomas et al., 1992; Hanski et al., 1994; Bellamy et al., 1996; Hanski and Gilpin, 1997; Gaona et al., 1998). The long-term survival of such a metapopulation is dependent on a balance between the processes of local extinction and colonisation (Harrison, 1991; Gilpin and Hanski, 1991; Hanski and Gilpin, 1991; Harrison and Taylor, 1997; Hanski, 1998, 1999).

Given that long-term persistence is conditional on maintaining this balance, recovery depends on reducing extinction rates, increasing colonisation rates, or both. This metapopulation approach to conservation has often been advocated over the last decade (Thomas, 1995; Thomas and Hanski, 1997; Hanski, 1999;

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McCarthy and Lindenmayer, 1999; Akcakaya, 2000; Margules and Pressey, 2000). However, most literature pertaining to metapopulations in a conservation context detail species declines (Hanski et al., 1995; Lewis and Hurford, 1997; Thomas and Hanski, 1997; Kuussaari et al., 1998; Moilanen et al., 1998; Thomas et al., 2000) to the extent that the utility of the approach has been questioned (Harrison, 1991; Harrison and Taylor, 1997; Harrison and Bruna, 1999). During periods of decline, when local extinctions far exceed colonisations, the conservation focus is likely to concentrate on the processes giving rise to extinction. Yet, if species recoveries are to be achieved, it is equally important to understand the processes of colonisation.

Metapopulation theory predicts that rates of colonisation will increase as habitat patches become larger and better connected. To promote species re-expansion through the landscape, networks of suitable habitat patches are required in close proximity to existing refuge populations (Gilpin and Hanski, 1991; Hanski and Gilpin, 1991; Thomas and Jones, 1993; Wiens, 1997; Hanski and Gilpin, 1997; Harrison and Taylor, 1997; Etienne and Heesterbeek, 2001). This can be achieved by consolidating the management efforts of conservation agencies on protected sites and reserves, and by the management of habitat within the wider countryside (i.e., outside reserves) through government funded agri-environment schemes.

In this paper, we document rapid metapopulation recovery and range re-expansion in a species experiencing an increase in habitat availability. This case study illustrates that a metapopulation approach to landscape-scale conservation can indeed be successful.

2. Methods

2.1. Study system

During the last century, many species of butterfly became increasingly rare or were lost from entire regions of north-west Europe (Heath et al., 1984; van Swaay and Warren, 1999; Asher et al., 2001). One such species, the silver-spotted skipper *Hesperia comma* L., was reduced to fewer than 70 populations in the UK by 1982. In Britain, *H. comma* is on the north-western edge of its range and is thermally constrained to suitable habitat located in southern England. The extant refuge colonies remaining in 1982 conformed to a remnant metapopulation structure (Thomas and Jones, 1993) and were located in eight habitat networks: Kent and Surrey in the North Downs, Hampshire and East Sussex in the South Downs, the Chilterns and three in the south-west on the borders of Dorset, Wiltshire and west Hampshire (Barnett and Warren, 1995; Fig. 1).

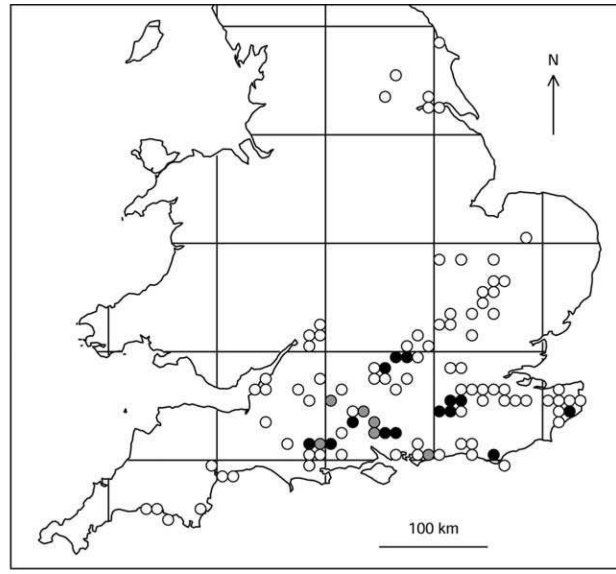

Fig. 1. The historical decline of *Hesperia comma* in the UK (from Thomas et al., 1986; Asher et al., 2001). Symbols show 10 km^2 records: empty circles, recorded pre-1970; grey filled circles, recorded 1970–81; black filled circles, refuge distribution recorded in the 1982 survey (Thomas et al., 1986). National 100 km grid lines are shown.

The declining status of this butterfly was a result of the widespread reduction of sparse, short-turfed calcareous grassland containing the species' sole larval host plant, sheep's fescue grass *Festuca ovina* L. (Thomas et al., 1986). Subsequently, the availability of suitable habitat within the species' former distribution has increased due to grazing management (Warren and Bourn, 1997), the recovery of wild rabbit *Oryctolagus cuniculus* L. populations after myxomatosis (Trout et al., 1986, 1992; Trout and Smith, 1995) and an increase in the range of aspects and vegetation that the butterfly can utilize due to climate change (Thomas et al., 2001a; Z. Davies et al., unpublished).

Hesperia comma females have specific ecological requirements for oviposition. Eggs are individually laid on the leaf blades of small tufts (1–5 cm tall) of *F. ovina*, generally situated in a warm hollow and growing adjacent to bare ground (Thomas et al., 1986; Warren et al., 1999). Plants that have been heavily nibbled by grazing animals tend to be avoided by egg-laying adults (Thomas and Jones, 1993; Warren et al., 1999).

2.2. Distribution of habitat and populations

Between July and September 2000, a comprehensive survey was conducted over the entire UK distribution of the species. Past records from a complete survey of the British distribution carried out in 1982 (Thomas et al., 1986), a re-survey of the North and South Downs during 1991 (Thomas and Jones, 1993; Fig. 2), and records obtained from Butterfly Conservation's "Butterflies for the New Millennium" (BNM) database

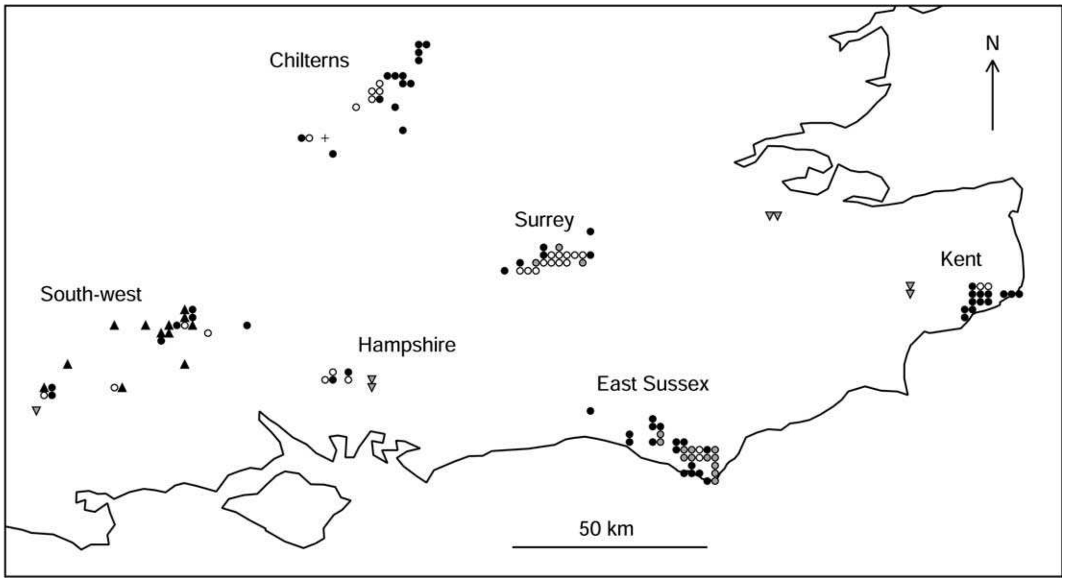

Fig. 2. Changes in the distribution of *Hesperia comma*, across the British range of the species. Symbols show tetrad (2 km × 2 km grid square) records: empty circles, occupied in 1982 and 2000; grey filled circles, occupied in 1991 and 2000; black filled circles, colonised by 2000; cross, extinct between 1982 and 2000; grey filled inverted triangles, occupied as a result of re-introduction between 1982 and 2000; black filled triangles, occupied records from the 1995 to 1999 "Butterflies for the New Millennium" database (R. Fox, pers. comm.; Asher et al., 2001). The 2000 survey was intensive in all networks apart from in the south-west which, though extensively searched, was unlikely to have been a complete census. Solid line outlines the coast of south-east England.

(R. Fox, pers. comm.; Asher et al., 2001) were collated. The intensive survey radiated out from these points. All chalk grassland within a 15 km radius of a known population (recorded in any of these past surveys) was examined in order to map every suitable habitat patch (regardless of whether it was occupied) and locate new colonisations. Given rates of colonisation recorded by previous surveys (Thomas and Jones, 1993), and rates of dispersal recorded in mark-release-recapture (MRR) studies (Hill et al., 1996), new colonisations more than 15 km from the current silver-spotted skipper distribution were deemed very unlikely. Whenever a new population was located during the 2000 survey, the search area was expanded to encompass all potential grassland habitats within 15 km of the new record.

In the south-west region, the spread of new colonies meant that extensive areas of potential habitat in southern central England were within a 15 km radius of an extant population. The primary focus in the south-west therefore became documentation of the number and size of previously recorded populations and, although the search was extensive, some new *H. comma* colonisations are likely to have been missed in this region.

2.3. Habitat patch definition

Potentially suitable habitat was defined as unimproved chalk grassland where *F. ovina* was growing in turf less than 10 cm tall, usually next to bare ground. A habitat patch was any area of suitable habitat, bounded either by a continuous barrier of woodland or scrub, or by at least 25 m of unsuitable grassland. This definition of a habitat patch was consistent with that of Thomas and Jones (1993), and Hill et al. (1996), although it is important to note that there may be substantial migration between populations that are such short distances apart (Hill et al., 1996). Habitat patch boundaries, and therefore the number of populations, recorded during 1982 and 1991 have been adjusted and re-calculated to be consistent with the habitat patch definition used in the 2000 survey in all networks apart from in the south-west region, where the survey was incomplete.

2.4. Estimation of population size

In each habitat network, a weekly "fixed" transect was walked at one large *H. comma* population, in accordance with the standard procedure described by Pollard (1977). As most populations in Surrey are small, weekly fixed transects were walked at two sites.

Once the flight period had begun, as determined by the weekly fixed transect in each respective network, the population size of *H. comma* in every habitat patch was estimated using the transect method described by Thomas (1983). The number of butterflies counted was converted into a standard measure of density per 100 m of transect walked, and a population index of abundance on the day of the transect was calculated by multiplying the density of adults by the area of the habitat patch. As these indices were obtained at different points during the flight period, the values were corrected to correspond to the expected abundance on the peak day of emergence; the index was adjusted by comparison with the recorded proportion of adults flying on the respective regional weekly fixed transect site, on the equivalent date.

Transect population indices of *H. comma* (x) were related to independent estimates of population size (y) calculated using MRR data collected in 1982 at two sites in Surrey and four in the south-west (J.A. Thomas, unpublished). We used regression through the origin to estimate adult population size (y) for each *H. comma* population:

$$y = 20.034x \quad (R^2 = 0.92,\ n = 6,\ p < 0.01).$$

If adults were not recorded on a particular site during the adult flight period, the habitat patch was visited at least once, after peak regional emergence, to search for eggs on *F. ovina* plants deemed suitable for egg laying. A habitat patch with one or more females, two or more males, or one or more eggs present was considered to be occupied by *H. comma*. However, it is important to note that some small populations would struggle to support breeding populations in the absence of immigration from other larger populations nearby.

2.5. Assessing the impact of agri-environment schemes on populations

The Department for Environment, Farming and Rural Affairs (Defra) operates a number of agri-environment schemes, on behalf of the British Government, which provide financial support for farmers and other land managers to undertake environmentally beneficial management practices. Since their inception in the late 1980s, agri-environment schemes have become one of the primary mechanisms in the UK for implementing favourable nature conservation land management in locations that fall outside formal nature reserves (Ovenden et al., 1998). The two main schemes operating across the range of *H. comma* are the Countryside Stewardship Scheme (CSS) and The South Downs Environmentally Sensitive Area (ESA) programme, and their impact on the species has been monitored through transect data collected by Butterfly Conservation and the Centre for Ecology and Hydrology (CEH). Transect data was obtained from Butterfly Conservation for the period 1992–2000 and the agri-environment scheme status of each transect was obtained from Defra. Transects were chosen to ensure that populations, in both scheme ($n = 17$) and non-scheme ($n = 18$) locations, were evenly represented and spread across the species' distribution.

Annual population indices at each transect site were calculated by summing the weekly counts (Pollard, 1977). Population trends in (collated) indices at scheme and non-scheme sites were analysed by modelling year and site effects using a loglinear model, with Poisson errors incorporating adjustments for overdispersion and serial correlation, written in the freeware program "Trends and Indices for Monitoring Data" (TRIM) (Pannekoek and van Strien, 1996). A wald-test was used to determine whether there were statistically significant differences between the scheme and non-scheme sites.

3. Results

Hesperia comma populations were recorded in 109 tetrads (2 km × 2 km grid squares) in 2000 (Fig. 2), in contrast to the 30 documented in 1982. A further 12 tetrads have been added to Fig. 2 in the south-west, representing populations recorded as part of the BNM project between 1995 and 1999 (R. Fox, pers. comm.; Asher et al., 2001), as this region was not searched with the same degree of intensity as the other networks during the 2000 survey.

257 breeding populations were identified in 2000 across the entire species range, compared to 68 in 1982. However, over 90% of these were considered small or very small, with fewer than 500 adults estimated at peak emergence (Table 1). The total area of occupied habitat increased 10-fold to approximately 2100 ha (21 km^2; compared to 2.1 km^2 in 1982, Cowley et al., 1999) in the 18-year period between surveys.

Approximately 90% of colonisations were within 10 km of a 1982 population, excluding 13 small populations which have resulted from four re-introductions

Table 1
The number of *Hesperia comma* populations, grouped by estimated adult population size at peak emergence and habitat network. The survey was intensive in all networks apart from in the south-west which, though extensively searched, was unlikely to have been a complete census

Population size class (No. of adults on peak day)	Chilterns	Kent	Surrey	East Sussex	Hampshire	South-west	Total
Very large (>50000)	0	0	0	0	0	1	1
Large (3000–50000)	1	1	0	0	1	0	3
Medium (500–3000)	6	2	7	2	0	0	17
Small (100–500)	5	3	17	12	4	4	45
Very small (<100)	20	12	40	23	2	3	100
No transect data	12	16	10	42	5	6	91
Total	44	34	74	79	12	14	257

(two in Kent, one in Hampshire and one in the south-west). Nevertheless, colonisations were recorded over longer distances, up to 17 km in the Chilterns and 29 km in East Sussex. The maximum single-step colonisation distance observed was 9 km, assuming that colonisation had occurred via emigrants from the nearest occupied habitat patch. The North and South Downs were re-surveyed in 1991, and within these networks, the colonisation distances from 1991 to 2000 were comparable to those previously recorded between 1982 and 1991 (Fig. 3). The probability of a habitat patch being colonised by 1991 or 2000 rose significantly with increasing proximity to a patch occupied during a previous survey (Table 2).

Between 1992 and 2000, the size of *H. comma* populations on transects significantly increased at a mean rate of 14% per annum ($t = 6.59$, $p < 0.001$) Agri-environment scheme and non-scheme populations differed significantly ($X^2 = 27.43$, d.f. = 8, $p < 0.001$). On ESA and CSS sites, butterfly densities increased at an average rate of more than 22% per annum, compared to a 9% increase per annum on non-scheme sites (Fig. 4).

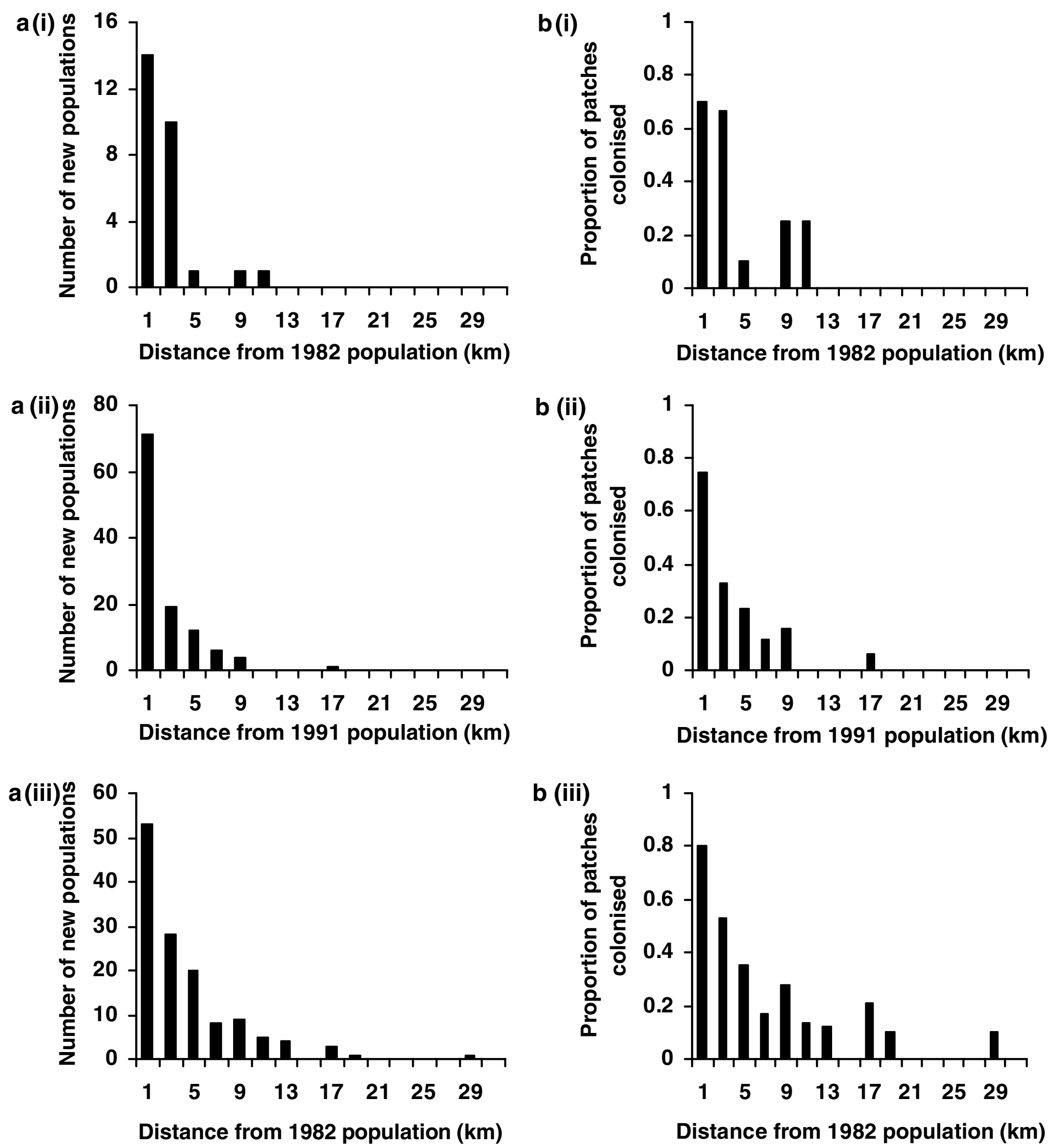

Fig. 3. (a) The distance of newly colonised *Hesperia comma* populations in the North and South Downs (Surrey and Kent networks and Hampshire and East Sussex networks respectively): (i) recorded in 1991 from the nearest population in 1982; (ii) recorded in 2000 from the nearest population in 1991; (iii) recorded in 2000 from the nearest population in 1982. (b) The proportion of suitable habitat patches in the North and South Downs colonised by *H. comma* : (i) by 1991 from the nearest population in 1982; (ii) by 2000 from the nearest population in 1991; (iii) by 2000 from the nearest population in 1982. Populations which are assumed to have resulted from re-introductions have been excluded.

Table 2
The availability and colonisation of suitable habitat patches in the North and South Downs (Surrey and Kent networks and Hampshire and East Sussex networks respectively) between distribution surveys. Colonisations which are assumed to have resulted from re-introductions have been excluded. Logistic regression was used to determine whether the probability of colonisation was a function of distance from the 1982 or 1991 *Hesperia comma* distribution

Time period	Number of colonisations	Number of habitat patches	−2 Log Likelihood	X^2	R^2	P
1982 to 1991	27	84	69.177	36.317	0.491	<0.001
1991 to 2000	113	431	357.476	138.455	0.402	<0.001
1982 to 2000	132	453	402.724	143.949	0.388	<0.001

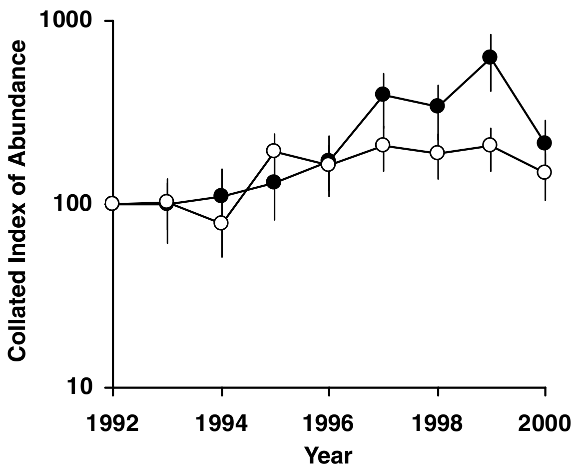

Fig. 4. Collated index of abundance for *Hesperia comma* populations, between 1992 and 2000, on agri-environment scheme (Environmentally Sensitive Area and Countryside Stewardship Scheme) sites ($n = 17$; black filled circles) and non-scheme sites ($n = 18$; empty circles). Bars indicate standard error. The mean rate of increase was 22% and 9% per annum on scheme and non-scheme sites respectively.

4. Discussion

4.1. Metapopulation expansion 1982–2000

Twenty years ago, *H. comma* had just undergone an alarming decline and was thought to be at risk of extinction in the UK, surviving in fewer than 70 generally small populations (Thomas et al., 1986). In the 18 years (generations) between 1982 and 2000, the number of populations grew fourfold from 68 to 257, and the area of occupied habitat rose 10-fold. The principal reason for this discrepancy in the magnitude of these increases is that half the occupied habitat area recorded in 2000 was located on one site (Porton Down Ministry of Defence Range in the south-west region; this can be attributed to the recovery of the rabbits rather than to conservation management). Excluding this one massive site, the average flight area at all other *H. comma* populations rose fivefold, from 2 km^2 in 1982 to 10 km^2 in 2000. A proportion of the remaining difference (fourfold versus fivefold increase) can be attributed to the expansion in area of individual habitat patches through improved management. For example, in 1982, the refuge populations in the Surrey network occupied an area of 0.46 km^2, which had expanded to 0.52 km^2 by 2000.

Since 1982, a number of factors have contributed to the increase in the quantity and quality of habitat. Firstly, spring and summer temperatures in Britain have risen by approximately 1.5 and 1 °C, respectively, since the mid-1970s (Roy and Sparks, 2000), increasing the amount of habitat thermally suitable for breeding. The species, which was traditionally restricted to very sparse vegetation (Thomas et al., 1986), can now utilise a wider range of *F. ovina* plants for egg-laying, as the microclimate of denser swards has become warmer (Z. Davies et al., unpublished). Furthermore, *H. comma* is no longer restricted to hot, south-facing slopes, with populations now found over an increasingly wide range of aspects (Thomas et al., 2001a). This means that more remnant grasslands are suitable for the species than they used to be, even without any change of grazing management. In East Sussex, the utilisation of habitat over a greater range of aspects effectively doubled the area of habitat available to the species within the network, leading to an approximate threefold increase in expansion rate (Thomas et al., 2001a).

The recovery of rabbit populations after myxomatosis (Trout et al., 1986, 1992; Trout and Smith, 1995) and, more recently, the widespread growth in conservation management of species-rich calcareous grassland, have both played a substantial role in the re-expansion of this short-turf butterfly. To counteract the loss of biodiversity and the degradation of landscape quality, stemming from agricultural intensification, the Department for Environment, Farming and Rural Affairs (Defra) has developed a number of agri-environment schemes in the UK. Both of Defra's flagship land management schemes, the ESA programme and the CSS, run within the distribution of *H. comma*. The South Downs ESA extends for 673 km^2 over the chalk hills (Defra, 2003) and has been successful in promoting traditional grassland grazing management (Lobley and Potter, 1998). In Surrey, Kent, and areas of East Sussex and Hampshire outside The South Downs ESA, 698 CSS management agreements were signed between 1992 and 2000, recruiting an area of 116 km^2 of land under the scheme (Defra, 2003). Although only a small fraction of the land under both schemes is current or potential *H. comma* habitat, the species should continue to benefit considerably from such initiatives, having shown a 22% annual increase in population size on monitored scheme sites, compared to 9% on non-scheme sites, during the main growth period for these agri-environment schemes between 1992 and 2000.

Colonisations were apparent in all regions within the species' range. However, the networks witnessing the most notable expansion were East Sussex, Kent and to a lesser extent the Chilterns, where the greatest increases in habitat availability had occurred. Such increases in habitat area and patch connectivity, in conjunction with improved habitat quality, have permitted the species to re-colonise historically occupied habitat within the species' former distribution (Thomas and Jones, 1993; Thomas et al., 2001a). The 14% per annum average growth in population densities between 1992 and 2000, together with the increased number of populations, will have assisted this recovery by generating more emigrant individuals and thus potential colonists. Nonetheless, most colonisations occurred over relatively short distances, and over 80% of suitable habitat patches between 5 and 15 km from a 1982 refuge population remained uncolonised by *H. comma* in 2000. This illustrates that, despite the increase in habitat availability, the fragmented nature of the landscape is still likely to be limiting the rate of recovery.

Over the period studied, colonisations were frequent and extinctions were rare. Several extinctions were recorded in the Surrey network between 1982 and 1991 (Thomas and Jones, 1993), but these habitat patches were re-colonised in the subsequent nine year period. Only two habitat patches occupied in 1982 were vacant in 2000. Both of these populations were lost from the same tetrad at the southern end of the Chilterns network, where there was very little expansion during the eighteen years between surveys.

4.2. Conservation implications

Hesperia comma still remains far rarer than it was one hundred years ago (Asher et al., 2001) despite the successful conservation of the species; most extant populations are small, and some may depend on immigration to persist. Thus, conservation management should continue within the core metapopulations (Thomas et al., 2001b). Habitat loss and fragmentation were the major contributory factors in the decline in status of *H. comma* (Thomas et al., 1986; Barnett and Warren, 1995; Asher et al., 2001) and still inhibit its recovery. In the North (Surrey and Kent networks) and South Downs (Hampshire and East Sussex networks), 90% of new populations established since 1991 were within 5 km of the 1991 distribution, and a great deal of apparently suitable habitat remains unoccupied. This implies that further deliberate conservation actions for this species should concentrate on attempting to increase the rate of expansion.

There are four approaches that can be adopted in order to promote further re-expansion. The primary strategy should be to ensure that conservation management actions are taken within a 5 km zone around the edge of the current range, so as to maximise habitat availability for further colonisation. Secondly, management of habitat to increase population sizes within core networks will result in larger numbers of migrant individuals being available to establish new populations.

The third approach relates to the few long-distance colonisations observed, up to 29 km from the 1982 distribution. These long distances are a product of smaller "stepping stone" colonisations between neighbouring habitat patches; new populations are founded from which, in subsequent generations, migrants leave and colonise more distant habitat patches. Assuming that colonisation occurred from the nearest occupied patch, the maximum single-step distance recorded was 9 km. These rare colonisations are likely to have a major impact on the future spread of the species, provided the migrants arrive in substantial new habitat networks. Therefore, managing large habitat networks further afield should also be included in the overall recovery programme.

The fourth option is re-introduction. Translocations into unoccupied habitat may be considered for patch networks that are too isolated to be re-colonised naturally, and which are large enough that the initial release has the potential to establish a viable metapopulation. This strategy has made some contribution to the recovery of *H. comma*. The re-introduction programmes in Hampshire and Kent appear to have been successful, thus far, with numbers at the release sites increasing and the species beginning to colonise new habitat patches nearby. However, this has been only a very minor element of the overall recovery and potentially detracts from the ability to use this species as an indicator of biodiversity recovery in managed grasslands as a whole (other short-turf invertebrates that are less well known may continue to suffer the ill effects of habitat fragmentation unnoticed). Habitat management to encourage natural re-colonisation should therefore be considered to be of much greater importance than translocations.

There is growing evidence highlighting the need to manage at a landscape-scale as opposed to focusing conservation efforts on protected reserves in isolation of their surroundings (Saunders et al., 1991; Warren, 1993; Pickett and Cadenasso, 1995; Wiens, 1997; Baillie et al., 2000; Cabeza, 2003; Rodriguez and Delibes, 2003). The importance of landscape structure in the recovery of *H. comma* is emphasised by its highly distance-dependent colonisation. A greater density of habitat patches within networks has resulted in "stepping stone" colonisation away from remnant metapopulations. To assist the movement of species through the wider countryside, mosaics of suitable habitat need to be managed (Roland et al., 2000; Ricketts, 2001; Hill et al., 2001; Sutcliffe et al., 2003), either by conservation agencies or under agri-environment schemes.

The landscape-scale approach to conservation will also facilitate shifts in species distributions as they track current climate warming. This is a particularly important consideration for habitat specialists that may be unable to keep pace with climate change (Warren et al., 2001; Hill et al., 2002; Travis, 2003); many specialists exhibit relatively poor colonisation ability and have declined over the last century (Thomas et al., 1994; Carlson, 2000; Maes and van Dyck, 2001; Asher et al., 2001; Warren et al., 2001; Robinson and Sutherland, 2002; Medellin, 2003; Kotze and O'Hara, 2003). An added complication is that climate change may alter realised niches due to the direct effects of temperature and moisture, and indirect effects resulting from changing community composition (Thomas et al., 2001a; Roy and Thomas, 2003). The habitat associations of a species may change through time and conservation management must be responsive to this. For example, as the realised niche of *H. comma* has broadened, habitat management should shift away from focusing solely on southerly facing slopes and become more generalised with regard to aspect. Managing habitats for a species based on a prescription that is out of date may even have detrimental affects on the populations the management is attempting to conserve. In this regard, habitat heterogeneity may be advantageous (Kindvall, 1996; Sutcliffe et al., 1997). A mosaic of grassland at various sward heights will provide the butterfly with ideal breeding conditions, whatever the prevailing temperature, and will improve the probability of a population surviving either extreme dry and hot, or cold and wet summers. The maintenance of more diverse vegetation conditions on calcareous grassland sites would also promote increased biodiversity as a whole (Andrén, 1994; Zschokke et al., 2000).

Hesperia comma is currently designated as a category 3 (rare) species in the British Red Data Book for Insects (Shirt, 1987) and as a priority species in the UK Biodiversity Action Plan (UK Biodiversity Group, 1995). If the recovery and re-expansion of *H. comma* continues, it may become appropriate to re-assess the conservation priority status of this species in Britain (Barnett and Warren, 1995). It is hoped that, in the future, this butterfly will be seen as an indicator of species-rich calcareous grasslands rather than as a threatened species in its own right.

The "classic" metapopulation consists of a set of local populations that are all subject to extinction and persist at the metapopulation level through recolonisation (Levins, 1969; Gilpin and Hanski, 1991), but few systems in nature actually conform to this definition (Harrison, 1991; Harrison and Taylor, 1997). The regional persistence of *H. comma* within networks of habitat corresponds to a broader definition of the metapopulation concept; Thomas and Jones (1993) reported the occurrence of both local colonisation and extinction events, and Hill et al. (1996) found that the majority of butterflies remained within the larger habitat patches (i.e., they support local populations), and between-patch movements were most likely among large patches situated close together. Patch to patch colonisations, as observed in *H. comma*, fall within the framework for metapopulation responses to increased habitat availability, and the re-expansion has been accurately predicted using metapopulation models (e.g., Hanski et al., 1994; Thomas et al., 2001a). Not only has the metapopulation approach provided a valuable insight into the dynamics of the species, but it has also contributed to the development of successful landscape-scale conservation management recommendations for the *H. comma* Biodiversity Action Plan (Barnett and Warren, 1995).

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