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Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes

Abstract Interpretation of spatially structured population systems is critically dependent on levels of migration between habitat patches. If there is considerable movement, with each individual visiting several patches, there is one "patchy population"; if there is intermediate movement, with most individuals staying within their natal patch, there is a metapopulation; and if (virtually) no movement occurs, then the populations are separate (Harrison 1991, 1994). These population types actually represent points along a continuum of much to no mobility in relation to patch structure. Therefore, interpretation of the effects of spatial structure on the dynamics of a population system must be accompanied by information on mobility. We use empirical data on movements by ringlet butterflies, *Aphantopus hyperantus*, to investigate two key issues that need to be resolved in spatially-structured population systems. First, do local habitat patches contain largely independent local populations (the unit of a metapopulation), or merely aggregations of adult butterflies (as in patchy populations)? Second, what are the effects of patch area on migration in and out of the patches, since patch area varies considerably within most real population systems, and because human landscape modification usually results in changes in habitat patch sizes? Mark-release-recapture (MRR) data from two spatially structured study systems showed that 63% and 79% of recaptures remained in the same patch, and thus it seems reasonable to call both systems metapopulations, with some capacity for separate local dynamics to take place in different local patches. Per capita immigration and emigration rates declined with increasing patch area, while the resident fraction increased. Actual numbers of emigrants either stayed the same or increased with area. The effect of patch area on movement of individuals in the system are exactly what we would have expected if *A. hyperantus* were responding to habitat geometry. Large patches acted as local populations (metapopulation units) and small patches simply as locations with aggregations (units of patchy populations), all within 0.5 km^2. Perhaps not unusually, our study system appears to contain a mixture of metapopulation and patchy-population attributes.

Key words Area effects · Fragmentation · Patch · Mark-release-recapture · Scale

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Introduction

Despite widespread acceptance of metapopulation ideas in population biology and conservation (Gilpin and Hanski 1991; Hastings and Harrison 1995; Hanski and Gilpin, in press), serious questions about the approach remain. Part of the problem has been that empirical studies of metapopulations have usually concentrated on spatial patterns rather than on the processes generating these patterns. Harrison (1991, 1994), in particular, has argued that few spatially structured population systems in nature conform to a strict definition of a metapopulation, because there is either too much or too little migration of individuals between real habitat patches. She identified several key issues which require further study, of which we tackle two in this paper. First, limited information is available on exchange rates of individuals between habitat patches in presumed metapopulations. Localised groups of individuals can be generated in systems where individuals are highly mobile, provided that they show some sort of aggregative response (Hassel and May 1974) in favoured patches. Restricted movement is not the only cause of localised distributions. Thus, an aggre-

gated distribution, in itself, does not demonstrate meta-population structure. Despite the importance of good data on dispersal, to date there are few detailed studies of exchange between habitat patches to evaluate the relevance of metapopulation models to patchily distributed species (Baguette and Nève 1994; Hanski et al. 1994, 1995; Nève et al. 1996).

Second, we need to examine the effects of variation in habitat patch area on population structure and persistence. Harrison (1991, 1994) argued that survival of an entire metapopulation may be dominated by the survival of one or two very large populations and may not really depend on the existence of a whole network of local populations at all. Furthermore, any natural habitat network is likely to contain a wide range of habitat patch areas, so responses to patch area may be important determinants of population structure even when the largest patches are not persistent. This is also an important question when one considers that modern fragmentation changes the distribution of patch sizes in a system, usually making them smaller.

This paper presents an empirical assessment of dispersal in the ringlet butterfly, *Aphantopus hyperantus*. We examine exchange rates of individuals in a spatially structured population system in which breeding areas are localised, to evaluate the extent to which local habitat patches support partly independent local populations, the basic unit of a metapopulation, or whether habitat patches merely contain temporary aggregations of adults which move frequently among patches (Shorrocks et al. 1990; Harrison 1991). Distinguishing between these possibilities is essential if we are to understand and predict the dynamics of spatially structured populations. We also investigate migration in and out of local patches which vary in area, to evaluate the effects of this important aspect of the spatial structure of the landscape on migration. The results reveal a complexity of structure that we believe is typical of many spatially structured animal populations.

A subsidiary goal was to undertake a "metapopulation" study of a relatively common species. Previous studies of dispersal in butterfly metapopulations have concentrated on species in regions where they are unusually rare, at their range margins (Baguette and Nève 1994; Hanski et al. 1994, 1995; Nève et al. 1996; Hill et al., in press; and may not therefore be typical of less endangered species. To ensure that studies of migration in metapopulations are not based solely on marginal metapopulations, it is also important to study patchily distributed species where they are not critically endangered. *A. hyperantus* falls into this category; it is not rare or endangered in southern Britain at present, but it is patchily distributed (Heath et al. 1984). In this respect it appears typical of many butterfly species in northern Europe. This study was intended to test whether a metapopulation approach is really applicable to such a species.
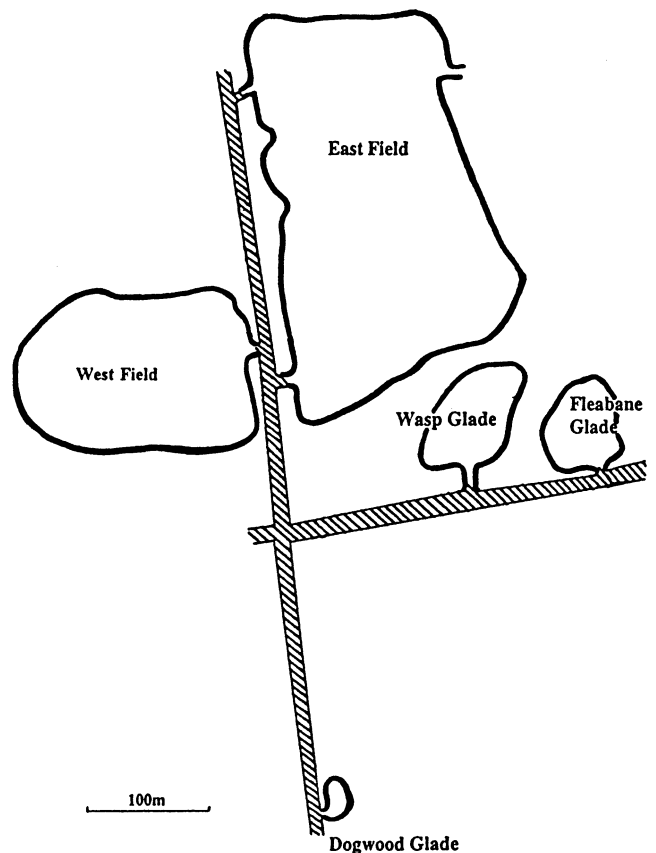
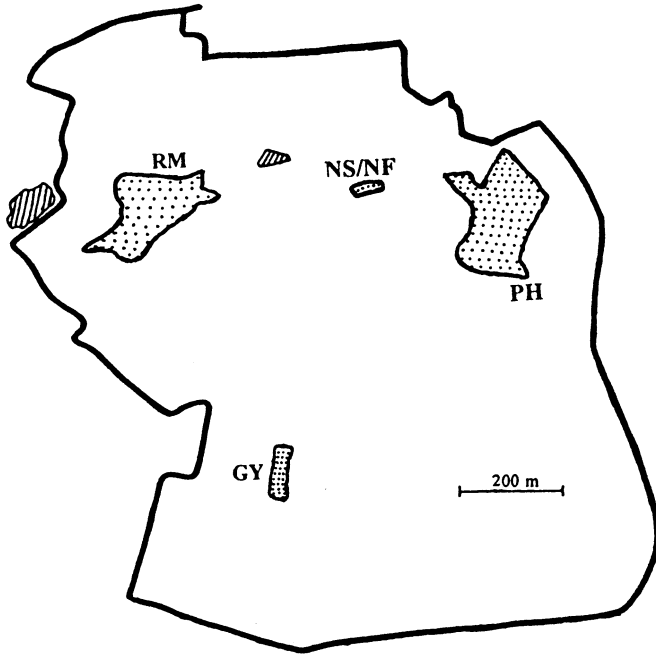## Materials and methods

Study organism

A. hyperantus occurs in lowland Wales, Ireland and southern lowland England, becoming more localized in northern England and Scotland. It is a common butterfly of shady woodland rides, edges and glades, although it is not confined to woods and may be seen on rough grassland (Thomas and Lewington 1991). The caterpillar feeds on a range of coarse grasses, particularly *Dactylis glomerata* and *Brachypodium sylvaticum* (Thomas and Lewington 1991). *A. hyperantus* has generally been considered to be quite sedentary, occurring in small, well-defined populations (Heath et al. 1984; Pollard and Yates 1993).

Methods

The main study was carried out on *A. hyperantus* at Monks Wood National Nature Reserve, a 157 ha oak-ash woodland in Cambridgeshire, eastern England. The sampling area, as shown on the map (Fig. 1), encompassed five grassland areas which are all managed by irregular, rotational cutting of both the herb and scrub layers. Interchange of individuals among habitat patches was assessed using mark-release-recapture (MRR) techniques. The approximate areas of the five patches are: East Field, 50,000 m²; West Field, 20,800 m²; Fleabane Glade, 3,520 m²; Wasp Glade 4,620 m²; and Dogwood Glade 445 m². All five patches are connected via a series of wide rides (grassy tracks) which are controlled by a complex management regime: the central strip of all rides is mown once or twice a year; the strips on either side of the ride are cut ro-

Fig. 1 Sampling area at the Monks Wood site. The interconnecting ride system is *shaded*. The intervening habitat is shady woodland, without *Aphantopus hyperantus*.

number caught in patch$_i$ and recaptured anywhere else), number of immigrants (I_i; number recaught in patch$_i$ that had previously been marked elsewhere), and number of residents (R_i; number marked and recaptured in patch$_i$). The second is the fraction of individuals that emigrate (*E*-fraction), immigrate (*I*-fraction), and remain (*R*-fraction). These were calculated as follows:

$$E\text{-fraction}_i = \frac{E_i}{E_i + R_i}$$

$$I\text{-fraction}_i = \frac{I_i}{I_i + R_i}$$

$$R\text{-fraction}_i = \frac{R_i}{R_i + I_i + E_i}$$

Results

At Monks Wood 732 recaptures (558 males and 174 females) were obtained from 1711 individuals marked during the study period. Most British butterflies are thought to have equal numbers of males and females in each generation (Shreeve 1992). However, it is common in field situations to encounter a higher proportion of males than females, and our results should not be taken as evidence that the sex-ratio is biased. The higher number of male *A. hyperantus* caught during this study is probably a result of butterfly behaviour – males are active throughout the day seeking mates. The mean distance moved by male *A. hyperantus* (calculated from recaptures over the whole sampling period) was 93 m directly, or 120 m indirectly via rides, which is the route they would usually have taken (Sutcliffe and Thomas, in press). Average female movement was similar at 90.5 m directly and 116 m via rides, showing no significant difference between the sexes. Mean time between captures was 3.2 days for males and 4 days for females. Mean residence time for males was 3.97 days, and for females 4.61 days (following methods of Cook et al. 1967; Watt et al. 1977). The maximum distance recorded by an individual was 458 m (710 m via rides) for a male and 410 m (600 m via rides) for a female. The longest movements recorded are similar to the maximum dimensions of the MRR study, suggesting some truncation of the distances moved. Pairwise edge-to-edge distances between patches varied between 31 and 312 m (97–532 m via rides), indicating considerable potential for population connectivity.

Fig. 2 Silwood Park site. The *dotted areas* are the four sampled fields. The *hatched areas* also have *A. hyperantus*, but were not sampled. Intervening habitats are largely dry meadows and shady woodland without *A. hyperantus*

tationally every 2–4 years; the belts of scrub immediately adjoining the rides are managed every 5–10 years by selective thinning and coppicing (cutting) (Warren 1985; Massey 1994). Sampling was carried out daily from 28 June to 4 August 1994, although daily sample effort varied, mainly because of the weather. Sampling time was allocated proportional to patch area. Irregular routes were followed through each patch and all butterflies encountered were given an individual mark using a code of coloured dots applied to the ventral hind wing surfaces using Staedtler Lumocolor fine-tipped permanent pens. For each individual caught, the following data were collected: time and date of capture; sex; mark number; and geographical position of capture (marked on map). Having been marked, each butterfly was released immediately at its position of capture.

The second study site was Silwood Park, Ascot (Fig. 2). The area consists mainly of dry meadows and shady woodlands, and *A. hyperantus* was sampled in the four areas shown. Sampling was carried out from 6 to 24 July 1992, on all days with suitable weather conditions.

Emigration, immigration and residence

For each patch, we use two measures of emigration, immigration and residence. The first is simply the number of emigrants (E_i;

Table 1 Monks Wood data, male and female data combined

Patch	Approx area (m²)	No. recaptured in same patch (residents)	No. recaptured elsewhere (emigrants)	No. first captured in different patch or ride (immigrants)	Emigration fraction	Immigration fraction	Resident fraction	Proportion recaptured
EF	50,000	129	46	28	0.26	0.18	0.64	0.33
WF	20,800	101	48	35	0.32	0.26	0.55	0.52
WG	4,620	25	40	28	0.61	0.53	0.27	0.50
FG	3,520	33	30	49	0.48	0.60	0.29	0.56
DWG	445	19	18	14	0.49	0.42	0.37	0.60

Table 2 Monks Wood data, male and female data separated

Patch	No. recaptured in same patch (residents)		No. recaptured elsewhere (emigrants)		No. first captured in different patch or ride (immigrants)		Emigration fraction		Immigration fraction		Resident fraction		Proportion recaptured	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
EF	10	119	6	40	3	25	0.38	0.25	0.23	0.17	0.53	0.65	0.13	0.40
WF	17	84	9	39	4	31	0.35	0.32	0.19	0.27	0.57	0.55	0.37	0.57
WG	7	18	9	31	4	24	0.56	0.63	0.36	0.57	0.35	0.25	0.34	0.59
FG	12	21	10	20	16	33	0.45	0.49	0.57	0.61	0.32	0.28	0.44	0.65
DWG	6	13	4	14	6	8	0.40	0.52	0.50	0.38	0.38	0.37	0.53	0.63

Table 3 Silwood Park data. *Numbers in parentheses* represent males, all other numbers combined males and females

| Patch name	Approx area (m²)	No. recaptured in same patch (residents)	No. recaptured elsewhere (emigrants)	No. first captured in different patch (immigrants)	Emigration fraction	Immigration fraction	Resident fraction
PH	9000	78 (72)	7	12	0.08	0.13	0.80
RM	7500	9 (8)	4	7	0.31	0.44	0.45
GY	2190	1 (1)	4	1	0.80	0.50	0.17
NS/NF	90	5 (4)	9	4	0.64	0.44	0.28

Emigration, immigration and residence

Table 1 summarizes the overall capture and movement data for each patch at Monks Wood; Table 2 shows the separate contributions made by males and females. Chi-square tests showed no significant differences between the movement behaviour of males and females, so analysis was carried out with combined, in addition to separate, male and female data. Table 3 contains combined-sex data for *A. hyperantus* collected at Silwood Park, Ascot. Data for males are in brackets.

Area effects

For the Monks Wood data, the resident fraction is relatively low in smaller patches whereas the immigration and emigration fractions are relatively high in small patches (Fig. 3). Combining sexes, there were significant differences among patches in numbers of residents, emigrants and immigrants ($\chi^2 = 71.4$, $df = 8$, $P < 0.001$), and the differences are associated with patch area (Fig. 3). The results were similar when just the data from male recaptures were used ($\chi^2 = 62.2$, $df = 8$, $P < 0.001$), but were not significant for females ($\chi^2 = 11.3$, $df = 8$, $P = 0.18$) – probably due to low recapture numbers in females (Table 1). Grouping the two large patches together, and the three small patches (to produce larger expected values), suggested significant differences for females too ($\chi^2 = 6.46$, $df = 2$, $P = 0.046$).

The Silwood Park data gives further support to the effects of area on Immigration, Emigration and Resident fractions (Table 3). Analysis was restricted to data from males only because there were few female recaptures. In several cells the expected values in a chi-square test
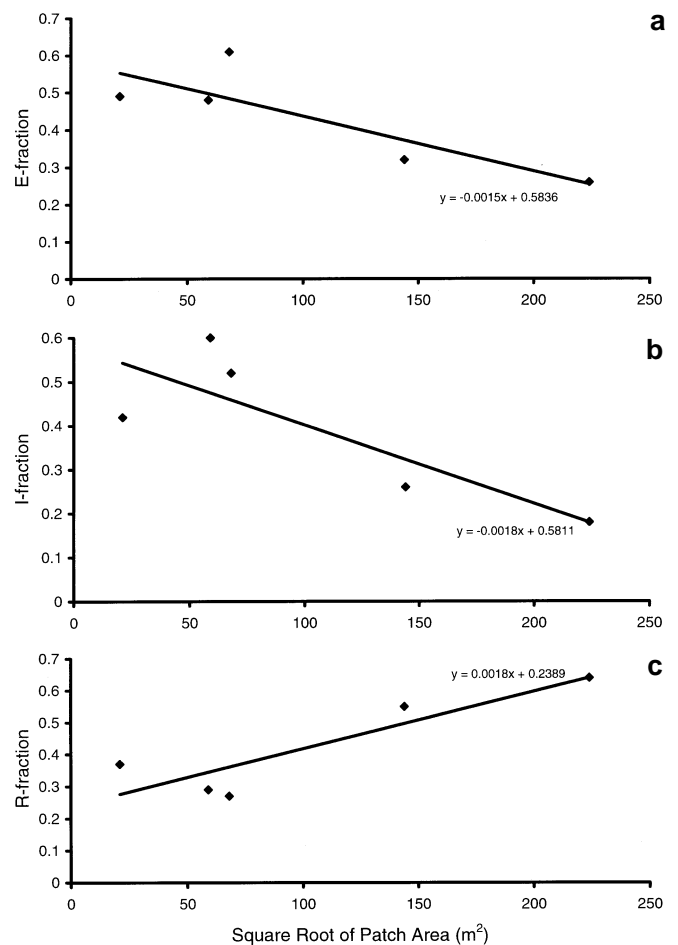
Fig. 3 Effect of square root of patch area at Monks Wood on: **a** emigration fraction, **b** immigration fraction, **c** residence fraction

would be small, so the columns of emigrants and immigrants were combined. The resulting analysis showed a significant effect of patch area on residence ($\chi^2 = 30.9$, $df = 3$, $P < 0.001$). Since the recapture numbers in the two smallest patches were very low, these were added together in a second analysis, but this made little difference to the result ($\chi^2 = 30.8$, $df = 2$, $P < 0.001$). At both sites, there is a significant effect of patch area on the fraction of individuals resident (R-fraction), immigrating (I-fraction) and emigrating (E-fraction). Overall, R-fraction increases with patch area, while immigration and emigration fractions both decline.

These fractions correspond to per capita residence, immigration and emigration. Even though per capita emigration and immigration rates are relatively small in large patches, large patches could still generate more emigrants and receive more immigrants in total because total population size in them is larger. Catching effort was similar – per unit area – in each patch, so the number of captures in each patch ($R + I + E$) should be correlated with local population size. Tables 1 and 2 show that local population size increased with patch area. Figure 4 shows actual numbers of immigrants (I) and emigrants (E) plotted against square-root of patch area. The number of emigrants increases with patch area ($F = 6.14$, $r^2 = 0.67$, $df = 4$, $P < 0.1$). The immigrants plot shows no pattern. The *number* of emigrants either stays the same or increases with area, even though the *fraction* of emigrants and immigrants declines with area (Fig. 3). Therefore, large patches may be important sources of migrants at the level of the entire system. However, immigration and emigration are more important determinants of local population size in small patches than in large ones.
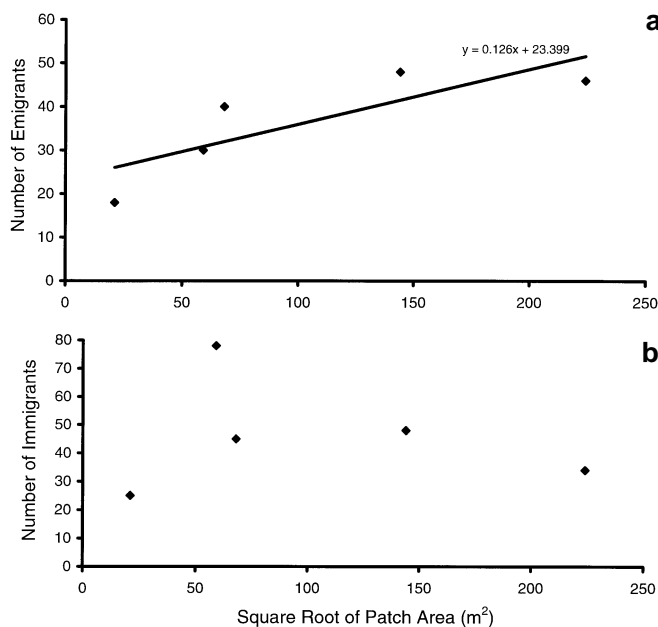
Fig. 4 **a** Number of emigrants plotted against square root of patch area, **b** number of immigrants plotted against square root of patch area: Monks Wood data

Discussion

At Monks Wood and Silwood Park respectively, 63% and 79% of recaptures were individuals remaining within the patch where they were first marked. This suggests that separate large habitat patches can support partially separate "local populations" with at least some capacity for local dynamics. In this respect the study system resembles a metapopulation. However, the exchange of individuals among patches was quite high (37% and 21%), and dynamics are likely to be linked. Small patches, with high rates of immigration and emigration, do not contain separate local populations and are much more akin to resource patches (*sensu* Harrison 1991) in which individuals regularly enter and leave the patch. Only about 30% of butterflies were recorded as resident in the three smallest patches at Monks Wood, and only 25% were residents in the two smallest patches at Silwood Park (Tables 1–3). Our present study system thus appears to be intermediate between a metapopulation and a patchy-population type of system (many individuals are resident but many disperse), and the pattern observed is scale dependent (only large habitat patches contain local populations). This is the same as the pattern observed in another butterfly, the skipper *Hesperia comma* (Hill et al., in press). We conclude that both of these butterfly species exist as "mixed" population systems with a mixture of "patchy" and metapopulation attributes.

The effects of patch area on residency, immigration and emigration are exactly what would be expected if *A. hyperantus* were responding to habitat geometry. Individuals are more likely to leave small than large patches because small patches have high perimeter to area ratios. Even if patch edges have low permeability (i.e. most individuals turn back at the edge), high encounter rates with margins in small patches should increase the probability of emigration from small patches. Butterflies may also be more likely to arrive in large than small patches because large patches make larger targets (Table 3). Actual numbers of immigrants did not seem to be related to patch area (Fig. 4), but this may be due to the over-riding effects of more dominant factors; for example an exceptionally high number of immigrants into Fleabane Glade occurred later in the flight period when most species of flower used for nectaring were fading, but fleabane (*Pulicaria dysenterica*) was coming out in profusion in Fleabane Glade. This implies that the flowers either attracted a large number of butterflies, or that the presence of flowers resulted in the retention of most immigrants (i.e. re-emigration was low). However, there is higher per capita immigration into small than large patches, because immigrants are diluted by larger local populations in large patches (immigration is likely to be proportional to the linear dimensions of a patch, and resident population size is likely to be proportional to area). These overall patterns are likely to be found in a wide variety of motile animals where patch sizes vary sufficiently (e.g., Kareiva 1985; McCauley 1991), unless patch boundaries are completely impermeable, in which

case there will be separate populations with no migration between them.

Habitat patch areas vary greatly in almost all field systems, so mixed patchy and metapopulation spatial structures are likely to be widespread. The interesting question is not in the definition of a particular population system as a "metapopulation" or a "patchy population", which seems rather irrelevant in the light of these data (the data fit neither definition), but in the relative contribution of local versus regional processes to population dynamics. This can be considered for each patch and for the system as a whole. Given the potential partial independence of local populations in some habitat patches, we continue to use the term metapopulation to focus attention on spatial structure in a patchy landscape, although we accept that others may prefer not to use the term for this type of population system. How local extinction and colonization dynamics, which are characteristic of metapopulations, contribute to persistence in such a connected system is unknown. If mixed patchy/metapopulation systems are common for motile animals, and we think that they are, then the contribution of local versus regional processes to population dynamics requires much more empirical and theoretical work. We address these questions empirically in a companion paper (Sutcliffe et al., in press).

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