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The butterfly assemblages of northeastern Spanish wetlands

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Summary

An ecological assessment of the butterfly assemblages of the last three relatively large wetlands existing in the northeastern Iberian Peninsula was carried out. Data were collected in 1988-1995 using the Butterfly Monitoring Scheme methodology. Four monitoring transect routes were considered, one in the Empordà Marshes Natural Park, two in Llobregat Delta Nature Reserves and one in the Ebro Delta Natural Park. Nearly 45,000 butterflies belonging to 59 species were recorded, of which only 35 breed regularly in the study areas. Despite the different number of regular breeders in the four transect routes, there was a very close coincidence in the number of species which form open populations. Some of these species (e.g., *Cynthia cardui, Vanessa atalanta, Pieris rapae, Pontia daplidice, Colias crocea*) are common migrants in the region, and northward migration was observed in the spring months, especially in May and June. The difference in the species' richness of the four areas was related to the different number of species with closed populations, which in the case of the Ebro Delta was exceedingly low. In comparison with other surrounding areas, the sites surveyed in this study are characterized by very poor butterfly faunas. Moreover, the extinction of at least four species was recorded in an eight years' period in the Empordà Marshes Natural Park, the richest of the four areas. Habitat fragmentation following the adoption of modern agricultural practices is identified as the main factor leading to the progressive impoverishment in the butterfly populations.

Resumen

El presente estudio analiza, desde una perspectiva ecológica, las comunidades de ropalóceros de las tres últimas grandes marismas que se conservan en el noreste de la Península Ibérica. Los datos se obtuvieron durante el período 1988-95, aplicando la metodología del Butterfly Monitoring Scheme en cuatro transectos distintos : uno en el Parque Natural de los Aiguamolls de l'Em-

pordà, dos en las Reservas Naturales del Delta del Llobregat y uno en el Parque Natural del Delta del Ebro. En total se contabilizaron unas 45,000 mariposas pertenecientes a 59 especies, de las cuales 35 pueden considerarse reproductoras regulares. A pesar de que entre las cuatro áreas existen marcadas diferencias en cuanto al número de especies que se reproducen regularmente, se observa una gran coincidencia respecto al número de mariposas con poblaciones de tipo abierto. Algunas de estas especies (e.g., *Cynthia cardui, Vanessa atalanta, Pieris rapae, Pontia daplidice, Colias crocea*) son migradoras comunes en el NE de la Península Ibérica, siendo frecuentes las migraciones hacia el norte durante los meses de primavera, especialmente en mayo y junio. Las diferencias en la riqueza específica se relacionan, por tanto, con el distinto número de especies con poblaciones cerradas, que en el caso del Delta del Ebro es extraordinariamente bajo. En comparación con otras áreas cercanas, las localidades estudiadas presentan una fauna lepidopterológica muy pobre. Hay que destacar, además, la extinción de un mínimo de cuatro especies en un período de ocho años en el Parque Natural de los Aiguamolls de l'Empordà, el área más diversa de las cuatro estudiadas. Se sugiere que este progresivo empobrecimiento de las comunidades de mariposas es una consecuencia directa de la fragmentación de los hábitats, resultante de la implantación de las técnicas agrícolas modernas.

Introduction

Largely as a result of the construction of infrastructure for the tourist industry, the Mediterranean coastline of the Iberian Peninsula has been dramatically transformed over the last few decades. In Catalonia (NE Spain) this process has been especially notable (Folch I Guillèn, 1976) and today only a few areas of the Catalan coastline possess well-preserved natural ecosystems (Orta *et al.*, 1992). Three of the most important of these remaining areas are the last relatively large wetlands left in the northeastern Iberian Peninsula : the Ebro Delta, the Llobregat Delta and the Empordà marshes (Fig. 1). These three areas were declared Natural Parks in the 1980s due to their importance as sites for breeding and migrating birds. Recent studies have shown, moreover, that these areas are also of high interest for plants as well as for other animal groups than birds.

The terrestrial invertebrate fauna of these wetlands has very special characteristics and a very limited range within Catalonia and, in general, within the Iberian Peninsula. This is the case for the distribution of some moth species (one of the best-studied groups) restricted to marsh and brackish environments (Pérez De-Gregorio, 1990 ; Stefanescu & Miralles, 1994).

The butterflies, on the other hand, are dominated by a small number of opportunistic species found throughout the Iberian Peninsula (e.g., Miralles & Stefanescu, 1994). Most of these species have been favoured by the transformation of the countryside and the replacement of natural ecosystems by cultivated and degraded areas. However, the study of these rather limited communities does provide the opportunity to analyze interesting and little-known aspects of the ecology of Mediterranean butterflies. It is also important to take into account the fact that some species migrate along the Mediterranean coast and a long-term study would provide much information on the nature of these migrations.

Furthermore, the different degrees of conservation of these three wetlands furnishes an excellent opportunity to study the responses of butterfly populations to the destruction and transformation of the countryside, a process which has severely affected butterflies over the last few decades.

The aim of this paper is to employ data collected in 1988-1995 using the British Butterfly Monitoring Scheme methodology, a standard technique for monitoring butterfly populations (Pollard & Yates, 1993), to analyze some of these issues.

Material and methods

Study sites

Three distinct geographical areas were covered by this study : Empordà Marshes Natural Park (EMNP), Llobregat Delta Nature Reserves (LLDNR) and Ebro Delta Natural Park (EDNP) (Fig. 1).

From a phytogeographic point of view, the three areas represent coastal wetlands (Riba *et al.*, 1980 ; Orta *et al.*, 1992) in which halophytic (*Phragmition*) and saltmarsh communities dominate. However, all of the areas are highly populated and contain large areas of agricultural land.

The EMNP covers 4824 ha to the north and south of the Muga river. The northern section corresponds almost exactly to the area formerly occupied by the Castelló d'Empúries lagoon and consists of extensive reedbeds and well-preserved halophytic vegetation, as well as the remains of the fluvial woodland which once surrounded the lagoon. To the south there is a series of saline coastal lagoons lying between the mouths of the Fluvià and Muga rivers, the neighbouring beach and the interior Cortalet lagoon. The vegetation mainly consists of saltmarsh

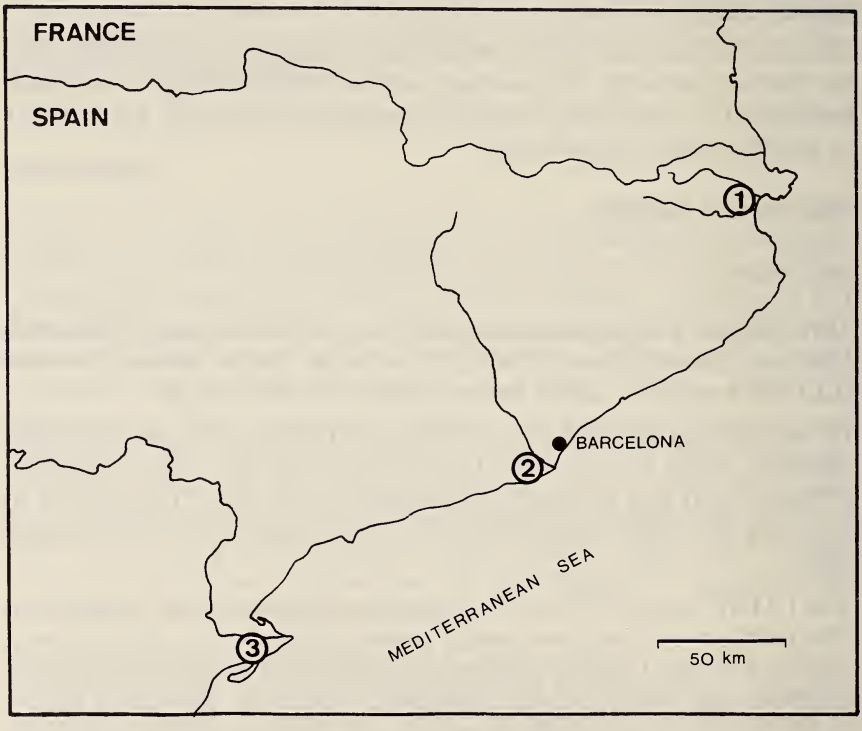

Fig. 1. Map of the study area. 1 : Empordà Marshes Natural Park ; 2 : Llobregat Delta Nature Reserves ; 3 : Ebro Delta Natural Park.

"steppes" and reedbeds depending on their distance from the coast and the salinity levels of the soil. Pastures liable to flood (known locally as "closes") and cultivated fields (principally maize, sunflowers and alfalfa) are common in both areas.

The LLDNR covers 500 ha to the south of the Llobregat river. Its proximity to Barcelona and the Barcelona/Baix Llobregat conurbation has meant that the original landscape has been radically altered. Today, only 5% of the area is covered by semi-natural vegetation, the remaining area being occupied by market gardening and orchards, built-up areas and industrial complexes. The fluvial woodland which once must have occupied a large area has been all but destroyed and only a very few elms and poplars still stand along the banks of the river and the irrigation channels.

The EDNP covers a total of 7736 ha on both sides of the Ebro river and penetrates 22 km into the Mediterranean Sea. The transformation of the Delta as a result of demographic growth goes back as far as the 14th Century, although the Delta underwent greatest change in the 19th Century. During this century rice cultivation expanded in the marsh areas which until then occupied a large part of the Delta and which currently only occupy 20% of the total area. As a result of the development of market gardening and orchards, fluvial woodland is non-existent.

Sampling methodology

The sampling procedure was based on the British Butterfly Monitoring Scheme (BMS) methodology (Pollard, 1977), a scheme used in Britain since 1976 to monitor butterfly abundance. The monitoring method has been previously well described (e.g., Hall, 1981 ; Pollard & Yates, 1993), and therefore only a brief description is given here.

The BMS consists of visual counts of butterflies along a fixed route. The transect is walked once a week and only those butterflies which come within 5 m in front of the recorder are counted. At the end of the season, an annual index of abundance is calculated for each species. This index is the sum of the weekly counts, including the estimated figures for missing values. Although the annual index does not provide the absolute population size of a species in a site, a close correlation between this measure and population estimates obtained with MRR methods has been shown on many occasions (e.g., Pollard, 1977 ; Thomas, 1983).

As most Spanish multi-brooded butterflies have overlapping flying periods, we have preferred to calculate a single annual index of abundance instead of a separate index for each generation, as is usually done in the British Butterfly Monitoring Scheme.

In this study, sampling started on March 1st and ended on September 26th, thus comprising a total of 30 weeks. Recording time was always restricted to the time between 10.00 am and 2.00 pm. When the temperature was lower than 15°C, transects were walked only if sunshine was higher than 75%.

Apart from a global analysis of the areas comprised within the transect routes, there is also a section dedicated to the migration of some butterfly species in 1995. Most of the data have been taken from the results of the transects, although observations by the authors and other people that work in the field are also included. This additional information has been very valuable in the case of *Danaus chrysippus*, a species which was recorded mainly in the EDNP on the "Illa de Buda" a few kilometres from the transect area, and once in the LLDNR and EMNP within the transect route.

Transect routes

In total four transect routes have been considered : one each in EMNP and EDNP and two in LLDNR. All of them are included in the Butterfly Monitoring Scheme which has been running in Catalonia since 1994, comprising 18 sites in 1995 (Stefanescu, 1994). Table 1 summarizes some characteristics of these transects.

Table 1

Some characteristics of the transect routes used in the present study.
EMNP : Empordà Marshes Natural Park ;
LLDNR : Llobregat Delta Nature Reserves ; EDNP : Ebro Delta Natural Park

Transect route	Location	Recording period	Number of sections	Transect length	Distance to the sea
El Cortalet	EMNP	1988-95	16	4.3 km	0.5-1.5 km
El Remolar	LLDNR	1994-95	9	3.0 km	0.1-2.0 km
Cal Tet	LLDNR	1994-95	10	4.0 km	0.2-2.5 km
La Marquesa	EDNP	1995	5	1.5 km	0.0-0.2 km

In EMNP, the transect route (here designated as "el Cortalet") is located around the Park information center, and mainly consists of a network of paths surrounded by fluvial woodland (elms, ash and oaks), hay meadows used for grazing, cultivated fields of sweet corn and sunflower, and ruderal habitats (see Miralles & Stefanescu (1994) for more details).

Two different transect routes were defined in LLDNR. The first route (designated as "el Remolar") is located inside the Nature Reserve of "el Remolar-Filipines". While reed beds and ruderal vegetation are extensive along all the transect, some other habitats (e.g., patches of pines mixed with dry meadows and some remnants of dune vegetation) are also well represented. The second transect (designated as "cal Tet") is located inside the Nature Reserve of "la Ricarda-ca l'Arana" a small remnant of the original vegetation completely surrounded by irrigated fields. Ruderal vegetation is extensive along the entire transect, but meadows and paths through a patch of pine wood are also included.

The transect route in EDNP (designated as "la Marquesa") is located along the beach and is divided in two distinct areas, both dominated by salt-tolerant and ruderal plant species. In the first one ("platja de la Marquesa") there are still good remnants of the dune system, while in the second one ("bassa de les Olles") some patches of long turf grass mixed with *Medicago marina* are also sampled.

The four transects are representative of the dominant environments found in each area. Only in the EMNP, the most heterogeneous area from a phytogeographical point of view, do patches of typically Mediterranean vegetation exist, each with characteristic butterfly populations that are not represented in the transect routes. In broad terms, therefore, and with the exception mentioned above, the butterfly composition found in each site is very similar to that found in the whole of the protected areas.

Results

Butterfly assemblages at the different sites

In the period 1988-1995, 44,848 butterflies were recorded belonging to 59 different species (Table 2). Comparisons of species richness are difficult given the different sampling sizes of each area, a factor directly related to the number of recording years and the length of each transect (Table 1). Logically, a larger sample size leads to more observations of vagrant species which, due to their greater mobility, disperse far from their breeding areas. The relatively large number of vagrant species which have been recorded in "el Cortalet" once or only a very few times during the recording period (e.g., *Pieris mannii, Colias alfacariensis, Anthocharis cardamines, Charaxes jasius, Aglais urticae, Issoria lathonia, Hipparchia semele*, etc.) is worth remarking on. Presumably in years to come the number of such species recorded in the other areas will also increase considerably.

A more balanced analysis can be carried out if only the species which breed regularly in each area are considered. In Table 2 these species are listed in accordance with the observations accumulated over the recording periods. "El Cortalet" (EMNP, 29 spp.) has the greatest diversity, followed by "el Remolar" (LLDNR, 27 spp.), "cal Tet" (LLDNR, 22 spp.) and "la Marquesa" (EDNP, 14 spp.). In the EMNP and the LLDNR these totals are probably accurate, whereas in the EDNP where only one year's records are available, the total may be expected to change.

In broad terms, the breeding species can be divided in two distinct groups according to their different population structures : species having closed populations (species that form well-defined colonies within discrete areas) and species having open populations (species that range more widely or regularly migrate from one breeding area to another) (Thomas, 1984 ; Warren, 1992). The species belonging to each of these groups are indicated in Table 2, according to Thomas (1984) and Warren (1992) and, for the butterflies not considered by these authors, according to distributional data of the species within the transect routes and unpublished data of their movement patterns.

The proportion of the species within these two main groups is represented in Figure 2. Despite the different number of species breeding

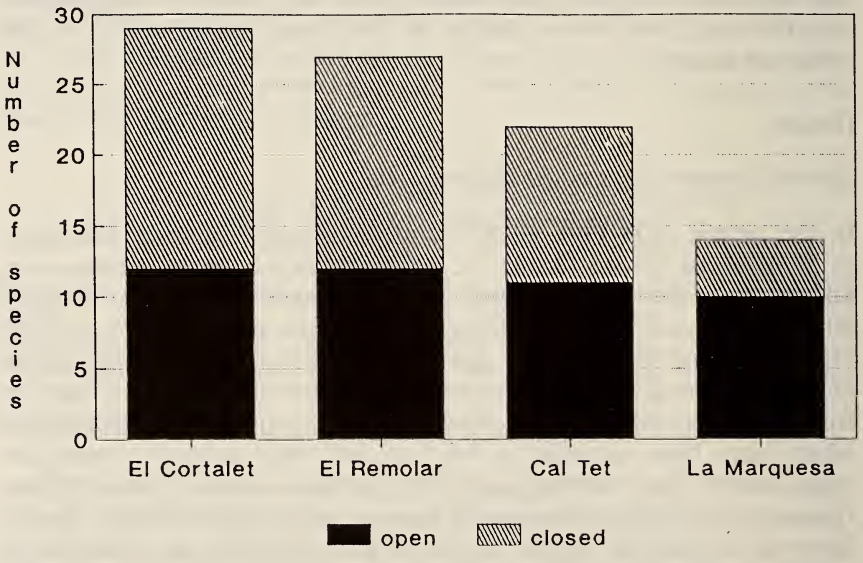

Fig. 2. Number of regular breeding species with open and closed populations in the four study areas.

regularly (resident) in the four areas, there is a very close agreement in the number of species with open populations. The difference in number of resident species is due, therefore, to the number of species with closed populations, which in the case of the Ebro Delta is exceedingly low (cf. Table 2).

Table 2

Butterflies present at the four studied areas during the period 1988-95.
(1) : El Cortalet, EMNP (1988-95) ; (2) : El Remolar-Filipines, LLDNR (1994-95) ; (3) : Cal Tet, LLDNR (1994-95) ; (4) : La Marquesa-Ses Olles, EDNP (1995). Symbols used : + : regular breeding species ; * : vagrant species ; e : extinct species during the recording period ; – : species not detected at the study site ; o : species with open populations ; c : species with closed populations. Systematic order and nomenclature follow Higgins & Riley (1980).

	(1)	(2)	(3)	(4)	population structure
PAPILIONIDAE					
Papilio machaon	*	+	+	+	o
Iphiclides feisthamelii	–	*	–	–	o
PIERIDAE					
Pieris brassicae	+	+	+	+	o
P. rapae	+	+	+	+	o
P. mannii	*	–	–	–	c
P. napi	+	+	+	+	o
Pontia daplidice	+	+	+	+	o
Euchloe crameri	+	+	+	+	o
Anthocharis cardamines	*	–	–	–	o
A. euphenoides	–	*	–	–	o
Colias crocea	+	+	+	+	o
C. alfacariensis	*	–	–	–	o
Gonepteryx rhamni	*	–	–	–	o
G. cleopatra	*	*	–	–	o
Leptidea sinapis	e	–	–	–	c
LYCAENIDAE					
Strymonidia spini	e ?	–	–	–	c
S. w-album	+	–	–	–	c
Callophrys rubi	–	+	–	–	c
Lycaena phlaeas	+	+	+	*	c
Lampides boeticus	+	+	+	+	o
Syntarucus pirithous	+	+	+	–	o
Cacyreus marshalli	–	+	–	–	o
Everes argiades	e	–	–	–	o ?
Celastrina argiolus	+	–	–	–	o
Plebejus argus	+	–	–	–	c
Aricia cramera	+	–	–	–	c
Lysandra hispana	*	–	–	–	c
Polyommatus icarus	+	+	+	+	c

	(1)	(2)	(3)	(4)	population structure
NYMPHALIDAE					
(Nymphalinae)					
Charaxes jasius	*	*	*	–	o
Nymphalis antiopa	–	*	*	–	o
Inachis io	*	*	–	–	o
Vanessa atalanta	+	+	+	+	o
Cynthia cardui	+	+	+	+	o
Aglais urticae	*	–	–	–	o
Polygonia c-album	+	–	–	–	o
Issoria lathonia	*	–	–	–	o
Melitaea phoebe	*	–	–	–	c ?
M. didyma	*	–	–	–	c ?
(Satyrinae)					
Melanargia lachesis	+	+	–	–	c
Hipparchia semele	*	–	–	*	c
Neohipparchia statilinus	e ?	–	–	–	c
Brintesia circe	e	–	–	–	c
Maniola jurtina	e	+	–	–	c
Pyronia tithonus	+	+	+	–	c
P. cecilia	+	+	+	+	c
P. bathseba	*	–	–	–	c
Coenonympha pamphilus	+	+	+	–	c
Pararge aegeria	+	+	+	*	c
Lasiommata megera	+	+	+	–	c
(Danainae)					
Danaus chrysippus	*	*	–	*	o
HESPERIIDAE					
Pyrgus malvoides	+	+	–	–	c
P. armoricanus	+	–	+	–	c
Spialia sertorius	*	*	–	–	c
Carcharodus alceae	+	+	+	+	c
C. boeticus	+	–	–	–	c
Thymelicus acteon	+	+	–	–	c
T. lineola	*	–	–	–	c
Ochlodes venatus	+	+	+	–	c
Gegenes nostrodamus	–	+	+	+	c
Total individuals	27561	6797	9335	1155	
Total species	53	36	24	18	
Resident species	29	27	22	14	
Vagrant species	18	9	2	4	
Extinct species	6	–	–	–	

Logically, the most abundant species in all of the sites are also resident butterflies. Although these experience annual fluctuations in numbers and, therefore, changes in the dominance between the recording years (Miralles & Stefanescu, 1994), each site can be characterized by a subset of its most common butterfly species. In Table 3 a rank list of the five butterfly species with the highest annual indices in 1995 is given. These

Table 3

The most abundant species in each of the sample sites, listed according to their annual indices in 1995. The percentage of the species' annual index with respect to the sum of the annual index of all species is given in brackets

El Cortalet		La Marquesa	
P. aegeria	832.5 (20.6)	*P. rapae*	335.0 (29.0)
P. rapae	686.5 (17.0)	*C. cardui*	287.5 (24.9)
P. napi	678.5 (16.8)	*P. daplidice*	212.0 (18.4)
P. icarus	604.0 (14.9)	*C. crocea*	115.0 (10.0)
M. lachesis	181.5 (4.5)	*P. icarus*	64.5 (5.6)
El Remolar		**Cal Tet**	
P. rapae	1456.0 (37.2)	*P. rapae*	1627.0 (31.9)
P. cecilia	725.5 (18.5)	*P. napi*	1196.0 (23.5)
C. alceae	358.0 (9.1)	*P. aegeria*	413.0 (8.1)
P. napi	336.5 (8.6)	*L. megera*	355.0 (7.0)
P. icarus	160.0 (4.1)	*C. cardui*	345.0 (6.8)

species have the highest population sizes at each site and their annual indices account for nearly 75% or even more of the sum of the annual indices of all species (73.8% in EMNP, 77% in both transect routes in LLDNR, and 87.8% in EDNP).

Extinctions

In "el Cortalet", where data have been gathered for over eight years, the extinction of some species has been recorded. We consider that a population has become extinct when no individuals were seen in two successive recording years, after a period with two or more years with regular records. Although the criteria established by Pollard & Yates (1992) are more conservative, the patterns of annual fluctuations of the species detailed below undoubtedly indicate that local populations have disappeared.

During the recording period, the breeding populations of at least four species are assumed to have become extinct (Table 2) : *Leptidea sinapis, Everes argiades, Brintesia circe* and *Maniola jurtina.* Two other species, *Nordmannia spini* and *Neohipparchia statilinus* may also have become extinct during this period, although the presence of breeding populations when they were recorded in the transect has not been proved. For all these butterflies populations showed declining numbers that eventually led to their extinction. This is especially true for *B. circe* and *M. jurtina*, two species which became gradually scarcer after an increase in 1989, and disappeared completely from the area in 1994 (Fig. 3).

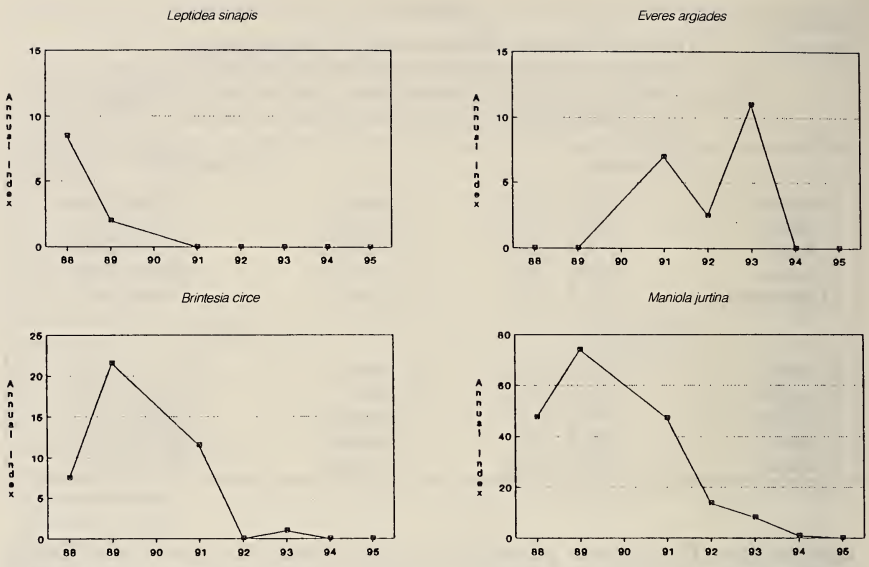

Fig. 3. Extinctions of butterfly species recorded in "el Cortalet" (EMNP) during the period 1988-95. No data were available in 1990.

Everes argiades colonized in small numbers one section of the transect in 1991, but after an increase in 1993 it disappeared in the following year. *Leptidea sinapis* was recorded in the first two years in small numbers, and afterwards disappeared from the area.

Migration

An important proportion of the species that regularly breed in the four areas are common migrants over their entire distribution range. As defined by Baker (1969) and Shreeve (1992), a species can be considered as a migrant when a part of its population is involved in predictable seasonal and directional movements. This type of behaviour is well exemplified by multi-brooded species such as *Cynthia cardui, Vanessa atalanta, Pieris rapae, Colias crocea* and *Pontia daplidice*, which show directional flights northward in spring and summer, and southward in late summer and autumn (Williams, 1951 ; Baker, 1969).

In 1995 the migration of some species was detected in the four sites. Table 4 summarizes the dates of the main migrations observed during the recording period (March 1st-September 26th). Other minor migrations were observed more or less regularly throughout the spring months.

Unlike the normal pattern of weekly counts observed for the generation of a butterfly with a typically closed population (a steady rise to a peak during the brood's emergence, followed by a decline as individuals die), the data of Table 4 refer to abrupt changes in abundance that can only be explained by the mass arrival of migrants. In most cases the butterflies were recorded with a clear directional flight towards the north, indicating that a migratory process was actually taking place.

Migration events were observed for all the species mentioned above, and were especially important in the EDNP. In this area the arrival of migrants is not only much more frequent, but also more intense than in the rest of the sites. Moreover, in some cases there were mixed butterfly migrations, with several species involved. The most evident was observed on 16th June, when high counts of *P. rapae, C. cardui, C. crocea* and, to a lesser extent, *V. atalanta*, were recorded (Fig. 4). Other mixed migrations were detected in LLDNR on 27th May and in EMNP on 2nd June (Table 4).

Unfortunately the BMS recording period ends on 26th September, and therefore most autumn migrations such as those described by Lack & Lack (1951), Williams (1951), Baker (1969) and Templado (1977) are lacking from our study. However, it is interesting to note one

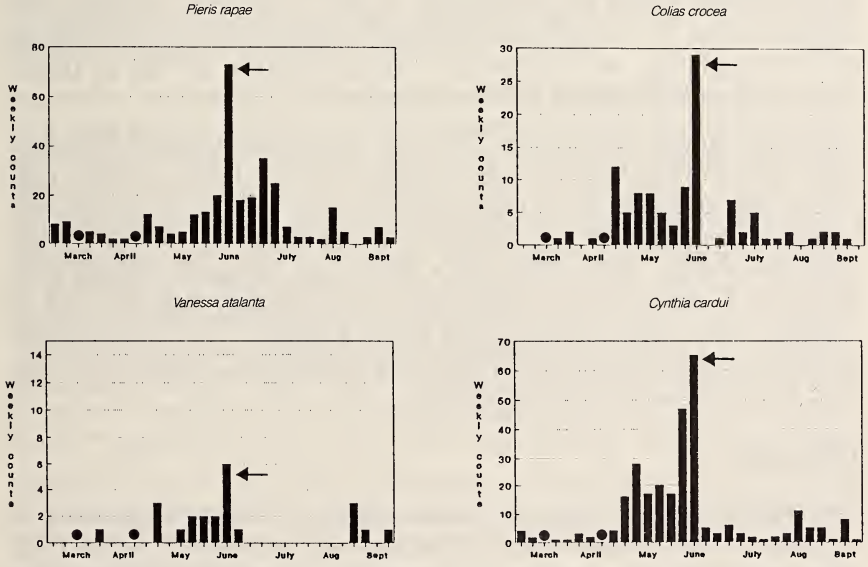

Fig. 4. Weekly counts of four migrants in "la Marquesa" (EDNP), in 1995. A dot indicates no count in that week. Note the mixed migration that took place on 16th June (shown by an arrow).

Table 4

Dates of the main migrations detected in 1995 at the four study areas during the recording period (March 1st-September 26th). In brackets, the number of butterflies recorded during the transect walks. ND : No data available on transect counts

	El Cortalet	El Remolar	Cal Tet	La Marquesa
Pieris rapae				16.VI (73)
Pontia daplidice	2.VI (4)			6.VII (44)
Colias crocea			27.V (10)	30.IV (12)
				16.VI (29)
Vanessa atalanta				22.IV (ND)
				16.VI (6)
Cynthia cardui	2.VI (26)	13.V (11)	27.V (124)	22.IV (ND)
				14.V (28)
				8.VI (47)
				16.VI (65)

migration that was observed at "el Remolar" on 28th September, when 34 *Pieris brassicae* and small numbers of *C. crocea* and *V. atalanta* were seen flying southward in a straight line above the beach for a period of one hour.

The EDNP was the only area where *Danaus chrysippus*, an African butterfly that periodically reaches the Iberian coast (e.g. Masó, 1992), was observed during the monitoring in 1995. That year, however, the migration was not as large as recorded in previous years, and almost all of the sightings were restricted to the area known as "Illa de Buda" a few kilometres from the monitored areas.

The first example was seen on 25th June, but it was not until 25th July that three more butterflies were recorded. On this latter occasion egg-laying was observed on *Cynanchum acutum*, one of the previously recorded feeding plants of the larvae in the northeast of the Iberian Peninsula (Masó, 1992). Afterwards, many eggs, larvae and pupae were found on *C. acutum*, and adults were seen regularly until the end of October. One adult was observed in "el Remolar" on 16th October, possibly a migrant from the Ebro Delta population. Another one was seen in "el Cortalet" on 30th October.

Discussion

The Mediterranean region is characterized by a high biodiversity in comparison with other areas in central and northern Europe (e.g., Mooney, 1988). This pattern of diversity is also very pronounced in the case of butterflies, as has recently been shown by Dennis & Williams (1995) and Munguira (1995). Within the Mediterranean region, the

Iberian Peninsula, with more than 200 species (Gómez-Bustillo & Fernández-Rubio, 1974 ; Fernández-Rubio, 1991), harbours one of the most diverse butterfly faunas. In this area, Martín & Gurrea (1990) locate the highest levels of species richness in the northeastern region, and explain this pattern as a consequence of a peninsular effect affecting the distribution of butterflies, as well as other organisms.

The sites surveyed in this study are within the richest region of the Iberian Peninsula (cf. Martín & Gurrea, 1990). However, they are characterized by a very poor butterfly fauna (Table 2), contrasting with that present in surrounding areas (Stefanescu, 1994). This low species richness can be explained, in part, by the location of the study sites at sea-level, taking into account that altitude has been suggested as the second most important factor affecting the distribution of Iberian butterflies, being positively correlated with the number of species found in an area (Martín & Gurrea, 1990).

Two other main reasons for this abnormally low species richness can also be advocated. First, the low observed butterfly diversity is a response to the reduced diversity of the vegetation communities of wetlands (reed beds and saltmarshes which still cover large parts of the areas), as has been previously noted in the case of moths (Stefanescu & Miralles, 1994). Moreover, the impoverishment of the butterfly fauna is highlighted by the fact that there are actually very few Iberian butterflies adapted to exploit true wetland plants.

Secondly, modern agricultural practices have resulted in the destruction of a great part of the formerly widespread and richest butterfly habitats (cf. Feber & Smith, 1995). A good example is provided by the events that have taken place in the EMNP (Vaqué *et al.*, 1989). Nearly all of the present protected area was occupied by extensive marshlands a few centuries ago. In the 17th and 18th Centuries an intensive process of drainage and desiccation of the wetlands began, and vast portions of the land were converted into grazing meadows and cultivated fields. The new conditions created suitable habitats for butterflies, in particular the locally named "closes" that is, highly diversified meadows enclosed by tracts of riverine forest (mainly ash, oaks, elms and, in saline environments, tamarisks) used for hay and cattle grazing. Not only are these meadows rich in both larval foodplants and abundant nectar sources (e.g., Gramineae, Leguminosae and Compositae) for typical grassland species, but they also provide a system of glades and rides that favour woodland butterflies.

The present century (and especially over recent decades) has resulted in a further transformation of the landscape, leading to important

changes in land-use and the loss of major butterfly habitats. An increasing number of "closes" have been ploughed and transformed into cultivated fields of corn, lucerne and sunflower, while others have been abandoned. Consequently only a few good butterfly habitats remain today inside the park, and these sites are becoming more and more isolated. Most of the best conserved "closes" have become virtual islands within vast extensions of arable land, intensively "improved" with the use of herbicides and fertilizers.

In the EDNP and LLDNR the situation is similar to that described above for the EMNP, and historical events have also led to a significant impoverishment in the butterfly fauna. In both areas, however, the present situation is even worse and is the consequence of extreme habitat loss. No riverine woodland remains in either area and the intensification of agriculture has been more severe (employing very high levels of herbicides, insecticides and fertilizers).

Many authors have recently argued that habitat fragmentation and isolation is acting as one of the major causes of the decline of European butterflies in the second half of the century (e.g., Kudrna, 1986 ; Thomas, 1984, 1991 ; Warren, 1992). Moreover, the way in which this process is taking place has been satisfactorily explained on theoretical grounds for an increasing number of species following the development of metapopulation dynamics theory (Thomas *et al.*, 1992 ; Hanski & Thomas, 1994).

It is to be expected in degraded areas and in areas with good but highly fragmented habitats that butterfly communities consist principally of very mobile species, and that the proportion of sedentary species with closed populations is increasingly smaller. This is the current situation in the remaining three wetlands in the northeastern Iberian Peninsula, where there has been a recent and relatively rapid decline in several species with closed populations (Fig. 3). The more extreme example is provided by the EDNP, where the loss of habitats has been so severe that it has led to the disappearance of almost all the sedentary species with closed populations (Fig. 2). The few which still resist hang on in small numbers, in no way comparable to the numbers of species with open populations (Table 3).

Moreover, it is important to note that the majority of resident species with closed populations (Table 2) are capable of exploiting resources available in disturbed and early seral habitats. This is the case of ubiquitous species such as *Polyommatus icarus, Lycaena phlaeas, Pararge aegeria, Lasiommata megera* and *Carcharodus alceae* (the last mainly

restricted to the Mediterranean region), which can breed in almost all habitat types (Dennis, 1992) and in the area have a multivoltine strategy with at least three complete broods per year. Although a closed population structure is currently accepted for these species, there is no doubt that they have good dispersal abilities, which enable them to colonize other areas easily (e.g., Shreeve, 1995).

In fact, the distinction of open and closed populations is an oversimplification of the reality, as noted by Thomas (1995) who argues that these two categories could be replaced with a continuum of mobility. For instance, the "closed" category may represent those species showing a Levin's type metapopulation structure (Hanski & Kuussaari, 1995), while the "open" category would be applicable to those species with large "patchy population" structures. Even the placement of a species within one of these two groups may be viewed as something variable in time, as factors affecting mobility (e.g., those associated with the habitat, with population parameters and with environmental factors which influence individual activity) are in permanent change (Shreeve, 1995). However, the dichotomy of open *vs.* closed populations can still be useful as it exemplifies two contrasting structures in the populations of most butterflies (Thomas, 1995) : those species in which local abundance is mainly determined by immigration and emigration, and those species in which local birth and death processes are the major determinants of the population dynamics.

The butterfly communities today of the three last wetlands remaining in the northeastern Iberian Peninsula are composed, thus, of a few number of species characterized by their great adaptability in a changing environment that has lost many of its former suitable habitats for these insects. Although different ecological characteristics (e.g., whether populations are "closed" or "open"/migratory, the stage at which hibernation occurs, the type of larval food plants, etc.) can be found in these most successful species, all of them conform to the concept of "butterflies of the future" expressed by Bink (1992). As observed in other European countries, the distribution of these species has not declined in the second half of this century and some have even expanded their ranges and become more abundant (van Swaay, 1990 ; Pollard *et al.*, 1995).

In spite of the absence of almost any rare butterfly in these areas, continuous monitoring will provide abundant and interesting information on different aspects of the ecology of many species (e.g., phenology, migration, population trends, etc.), an important achievement given the lack of reliable data being collected in the Mediterranean region.

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References

Baker, R. R., 1969. The evolution of the migratory habit in butterflies. *J. Anim. Ecol.* 38 : 703-746.

Bink, F. A., 1992. The butterflies of the future, their strategy. *In* Pavlicek-van Beek, T., Ovaa, A. H. & van der Made, J. G. (Eds) : Future of butterflies in Europe : strategies for survival, pp. 134-138. Department of Nature Conservation, Agricultural University Wageningen, Wageningen.

Dennis, R. L. H., 1992. The ecology of butterflies in Britain. 354 pp. Oxford Science Publications, Oxford.

Dennis, R. L. H. & Williams, W. R., 1995. Implications of biogeographical structures for the conservation of European butterflies. *In* Pullin, A. S. (Ed.) : Ecology and conservation of butterflies, pp. 213-229. Chapman & Hall, London.

Feber, R. E. & Smith, H., 1995. Butterfly conservation on arable farmland. *In* Pullin, A. S. (Ed.) : Ecology and conservation of butterflies, pp. 84-95. Chapman & Hall, London.

Fernández-Rubio, F., 1991. Guía de mariposas diurnas de la Península ibérica, Baleares, Canarias, Azores y Madeira. 1 (1) : 418 pp., 1 (2) : 408 pp. Pirámide, Madrid.

Folch I Guillèn, R. (Ed.), 1976. Natura, ús o abús ? Llibre blanc de la gestió de la natura als Països Catalans. 575 pp. Ed. Barcino, Barcelona.

Gómez-Bustillo, M. R. & Fernández-Rubio, F., 1974. Mariposas de la Península Ibérica. Ropalóceros II. 258 pp. ICONA, Madrid.

Hall, M. L., 1981. Butterfly Monitoring Scheme. Instructions for independent recorders. 14 pp. Institute of Terrestrial Ecology, Huntingdon.

Hanski, I. & Kuussaari, M., 1995. Buttefly population dynamics. *In* Cappuccino, N. & Price, P. (Eds) : Population dynamics. New approaches and synthesis, pp. 149-171. Academic Press, London.

Hanski, I. & Thomas, C. D., 1994. Metapopulation dynamics and conservation : a spatially explicit model applied to butterflies. *Biol. Conserv.* 68 : 167-180.

Higgins, L. G. & Riley, N. D., 1980. Guía de campo de las mariposas de España y de Europa. 452 pp. Omega, Barcelona.

Kudrna, O., 1986. Aspects of the conservation of butterflies in Europe. *In* Kudrna, O. (Ed.) : Butterflies of Europe. Vol. 8, 323 pp. AULA-Verlag, Wiesbaden.

Lack, D. & Lack, E., 1951. Migration of insects and birds through a Pyrenean pass. *J. Anim. Ecol.* 20 : 63-67.

Martín, J. & Gurrea, P., 1990. The peninsular effect in Iberian butterflies (Lepidoptera : Papilionoidea and Hesperioidea). *J. Biogeogr.* 17 : 85-96.

Masó, A., 1992. *Danaus chrysippus* (L.) en Méditerranée occidentale. Migrations dès 1979 jusqu'à 1985. *Nota lepid.*, Suppl. 3 : 53-60.

Miralles, M. & Stefanescu, C., 1994. Population structure and ecological assessment of the butterfly community in "El Cortalet" (Aiguamolls de l'Empordà Natural Park, NE Iberian Peninsula). *In* Studies on terrestrial Arthropod biocoenoses of wetlands, 1. *Quad. Staz. Ecol. civ. Mus. St. nat., Ferrara* 6 : 103-116.

Mooney, H. A., 1988. Lessons from Mediterranean-climate regions. *In* Wilson, E. O. (Ed.) : Biodiversity, pp. 157-165. National Academy Press, Washington.

Munguira, M. L., 1995. Conservation of butterfly habitats and diversity in European Mediterranean countries. *In* Pullin, A. S. (Ed.) : Ecology and conservation of butterflies, pp. 277-289. Chapman & Hall, London.

Orta, J. *et al.*, 1992. Espais naturals. *In* Folch, R. (Ed.) : Història natural dels països catalans, 483 pp. Enciclopèdia Catalana, Barcelona.

Pérez De-Gregorio, J. J., 1990. Els macroheteròcers dels Aiguamolls de l'Empordà (Lepidoptera : Macroheterocera). *Treb. Soc. cat. Lepid.* 10 (1989) : 7-25.

Pollard, E., 1977. A method for assessing changes in the abundance of butterflies. *Biol. Conserv.* 12 : 115-134.

Pollard, E., Moss, D. & Yates, T. J., 1995. Population trends of common British butterflies at monitored sites. *J. Appl. Ecol.* 32 : 9-16.

Pollard, E. & Yates, T., 1992. The extinction and foundation of local butterfly populations in relation to population variability and other factors. *Ecol. Ent.* 17 : 249-254.

Pollard, E. & Yates, T., 1993. Monitoring butterflies for ecology and conservation. 256 pp. Chapman & Hall, London.

Riba, O., Bolòs, O. De, Panareda, J. M., Nuet, J. & Gosalbez, J., 1980. Geografia física dels països catalans. 226 pp. Ketres Editora, Barcelona.

Shreeve, T. G., 1992. Monitoring butterfly movements. *In* Dennis, R. L. H. (Ed.) : The ecology of butterflies in Britain, pp. 120-138. Oxford University Press, Oxford.

Shreeve, T. G., 1995. Butterfly mobility. *In* Pullin, A. S. (Ed.) : Ecology and conservation of butterflies, pp. 37-45. Chapman & Hall, London.

Stefanescu, C., 1994. Butterfly Monitoring Scheme (Pla de Seguiment de Ropalòcers). Primer any d'aplicació a Catalunya. 94 pp. Departament de Medi Ambient, Generalitat de Catalunya, Barcelona.

Stefanescu, C. & Miralles, M., 1994. Macroheterocera assemblages and indicator species in relation to plant associations in a Spanish wetland area. *In* Studies on terrestrial Arthropod biocoenoses of wetlands, 1. *Quad. Staz. Ecol. civ. Mus. St. nat., Ferrara* 6 : 81-102.

Swaay, C. A. M. van, 1990. An assessment of the changes in butterfly abundance in the Netherlands during the 20th century. *Biol. Conserv.* 52 : 287-302.

Templado, J., 1977. Una migración otoñal de *Colias crocea* Geof. en Mandayona, Guadalajara (Lep. Pieridae). *Graellsia* 32 : 167-169.

Thomas, C. D., 1995. Ecology and conservation of butterfly metapopulations in the fragmented British landscape. *In* Pullin, A. S. (Ed.) : Ecology and conservation of butterflies, pp. 46-63. Chapman & Hall, London.

Thomas, C. D., Thomas, J. A. & Warren, M. S., 1992. Distributions of occupied and vacant habitats in fragmented landscapes. *Oecologia*, 92 : 563-567.

Thomas, J. A., 1983. A quick method of assessing butterfly numbers during surveys. *Biol. Conserv.* 27 : 195-211.

Thomas, J. A., 1984. The conservation of butterflies in temperate countries : past efforts and lessons for the future. *In* Vane-Wright, R. I. & Ackery, P. R. (Eds) : The biology of butterflies, pp. 333-353. Academic Press, London.

Thomas, J. A., 1991. Rare species conservation : case studies of European butterflies. *In* Spellerberg, I. F., Goldsmith, F. B. & Morris, M. G. (Eds) : The scientific management of temperate communities for conservation, pp. 149-197. Blackwell, Oxford.

Vaqué, E., Roca, A. & Ribera, E., 1989. El Poblament Humà Actual. *In* Sargatal, J. & Fèlix, J. (Eds) : Els Aiguamolls de l'Empordà. Aspectes ecològics, històrics i socials, pp. 119-146. Editorial ART-3, Figueres.

Warren, M. S., 1992. Butterfly populations. *In* Dennis, R. L. H. (Ed.) : The ecology of butterflies in Britain, pp. 73-92. Oxford University Press, Oxford.

Williams, C. B., 1951. Seasonal changes in flight direction of migrant butterflies in the British Isles. *J. Anim. Ecol.* 20 : 180-190.