Marginal range expansion in a host-limited butterfly species *Gonepteryx rhamni*

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Abstract. 1. The British distribution of the butterfly *Gonepteryx rhamni* (L.) follows closely the range of its natural host plants, *Rhamnus catharticus* L. and *Frangula alnus* Miller, suggesting that it is one of the few British butterflies that has a host-limited distribution. In North Wales, this species has its range margin, and it was recorded only occasionally in a 35-km^2 area prior to the 1980s. *Frangula alnus* bushes were planted in the area in about 1986, allowing the hypothesis that *G. rhamni* would expand its range following increased host plant availability to be tested.

2. From 1996 to 1998, the distribution of the butterfly and its host plants, *R. catharticus* (native), *Rhamnus alaternus* L. (introduced), and *F. alnus* (introduced to the area but native to Britain), was mapped in the study area. It was found that the butterfly was more widespread than any of its host plants. *Frangula alnus* was the most widespread of the host plants, and received most eggs, suggesting that the carrying capacity of the habitat would have increased substantially following the planting of this species. *Gonepteryx rhamni* was able to complete its lifecycle on both introduced species in the study area.

3. A mark–release–recapture study showed that adult *G. rhamni* moved an average of 512 m, and 50% of movements were further than 400 m; these values are underestimates. The relatively high mobility of this species suggests that it probably perceives host plants and nectar sources as resource patches (patchy population) in this fragmented landscape, and this population now represents a satellite population of the butterfly's main distribution in Britain.

4. The results presented here confirm empirically the host-limited distribution of *G. rhamni*, which expanded following the planting of extra host plants.

Key words. Butterfly, climate change, geographical range, *Gonepteryx rhamni*, North Wales, range expansion, range margins.

Introduction

Determinants of the positions of range margins are of considerable interest in ecology and conservation (Brown *et al.*, 1996). In butterflies, the range margins of localised and declining species are influenced strongly by habitat loss and fragmentation (Thomas, 1991; Pullin, 1995; Thomas & Hanski, 1997). The range margins of more widespread species are still poorly understood, although Bryant *et al.* (1997) suggested that differences in the ranges of four widespread nettle-feeding butterflies could be explained partly by

differences in developmental temperature requirements and thermoregulation behaviour of their larvae.

British butterfly species frequently have range sizes much smaller than those of their host plants, suggesting that their range margins are caused by factors other than host plant availability. Ecophysiological responses to climate variation have been suggested as the most plausible hypothesis to explain the fact that most species reside well to the south of the range margins of their host plants (Turner *et al.*, 1987; Bryant *et al.*, 1997). Only a minority of butterfly species has ranges that appear to be constrained by those of their host plants (Dennis & Shreeve, 1991; Quinn *et al.*, 1998). One of these species is the brimstone butterfly *Gonepteryx rhamni* (L.), the distribution of which follows closely the range of its native host plants in Britain, *Rhamnus catharticus* L. and *Frangula*

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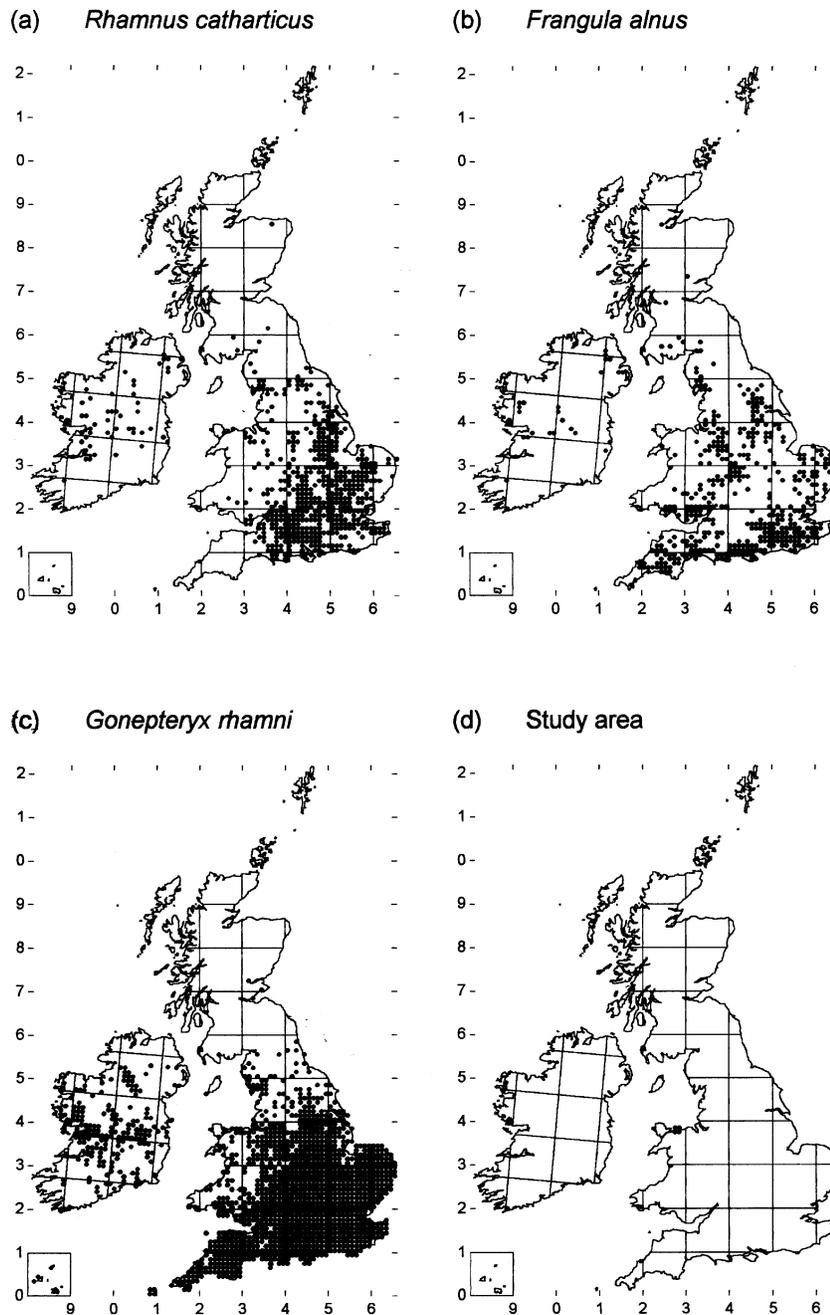
(a)   *Rhamnus catharticus*

(b)   *Frangula alnus*

(c)   *Gonepteryx rhamni*

(d)   Study area

Fig. 1. The British and Irish distribution of (a) *Rhamnus catharticus*, (b) *Frangula alnus*, and (c) *Gonepteryx rhamni*, plotted by 10-km grid squares (from data in Perring & Walters, 1962; Emmet & Heath, 1990), and (d) the location of the Creuddyn peninsula.

alnus Miller (Fig. 1). Although there are no direct estimates of dispersal for this species, it is thought to be a relatively mobile butterfly, able to find suitable plants even in quite isolated locations (Pollard & Hall, 1980; Dempster *et al.*, 1986; Emmet & Heath, 1990). Thus, it has been hypothesised that *G. rhamni* could have a host-limited distribution in Britain (Dennis & Shreeve, 1991; Dennis, 1993). This hypothesis could be tested by introducing the host plants outside their natural range and

examining whether *G. rhamni* is able to colonise and persist in the newly created habitat.

In North Wales, *G. rhamni* is rarely recorded, and there are only a few records of its host plants (Whalley, 1997; Fig. 1). No *G. rhamni* individuals were seen on the Creuddyn peninsula (Fig. 1) in the period 1968–73 (R. L. H. Dennis, pers. comm.) or another period of intensive work in 1983 (C. D. Thomas, pers. obs.). Only two records, from 1950 and

1973, are available from the Creuddyn peninsula (Whalley, 1997; Environmental Information Centre, unpublished). Although occasional breeding in the past cannot be ruled out, these records are most likely to represent stray individuals of this conspicuous and mobile butterfly. *Gonepteryx rhamni* has also been recorded further west in Wales, but most of those records are likely to be vagrants: the host plants are virtually absent, hence no breeding could take place in that area (Fig. 1). *Frangula alnus* bushes were planted along three main roads in the Creuddyn peninsula in about 1986 (Highways Division of the County Council for Conwy, pers. comm.), allowing testing of the hypothesis that *G. rhamni* would expand its range in North Wales in response to increased host plant availability.

Materials and methods

The study was carried out from 1996 to 1998 in the Creuddyn peninsula, North Wales, U.K. (53°18′N, 3°50′W). The landscape is highly fragmented, consisting mostly of urban habitats and improved grasslands. Semi-natural habitats include limestone grassland, wet meadows, coastal dunes, woodland, hedgerows, ditches, scrub, and bracken.

In 1996, 1997, and 1998, 100-m grid square records for the butterfly (adults, eggs, and larvae) and its three host plants (*R. catharticus*, *Rhamnus alaternus* L., and *F. alnus*) were collected throughout the study area, and their distributions were represented at 500-m grid resolution. In addition to native *R. catharticus* and recently planted *F. alnus*, another host plant reported for *G. rhamni* occurs in the study area: *R. alaternus* (Frohawk, 1940; Ellis, 1983). This species is indigenous to the Mediterranean but is sometimes planted in gardens and can be used for oviposition by *G. rhamni* (Frohawk, 1940). Although the earliest records available for *R. alaternus* in the study area are from 1960 (Ellis, 1983), this plant species was probably introduced during Victorian times, becoming naturalised in warm sites that resembled its habitat in southern Europe.

In spring and early summer 1997, host plant use was investigated by searching intensively for eggs and larvae in each 100-m grid square containing host plants. Because of the high numbers of host plants in the landscape, a grid square approach rather than an individual plant approach was used as the basis for assessing host plant use. Eggs are frequently laid beneath the young shoots on the tips of prominent branches growing in sheltered and sunny sites (Bibby, 1983; McKay, 1991; Thomas, 1992). The recording was confined to the presence/absence of eggs and larvae in each 100-m grid square. Checking for *G. rhamni* eggs (including egg shells) and larvae was started on branches apparently growing in the ideal situation described above, up to a height of ≈2.5–3 m (≈10% of bushes had foliage above this height). If no egg or larva was found, other branches were searched until an egg or larva was found or until all accessible and prominent branches were checked within the grid square. The larvae are easy to spot and when fully grown they sit conspicuously exposed along the midrib of a leaf. They also leave characteristic and obvious feeding damage on the leaves (e.g. Thomas, 1992), which makes them easier to locate.

The green pupae of *G. rhamni* are difficult to find in the wild (Thomas, 1992), so to test whether the butterfly was able to complete its lifecycle on each host, mostly fifth- and a few fourth-instar larvae were collected from the host plants. The larvae were reared in plastic jars indoors and provided with fresh leaves of the same host plants until pupation. Emerging butterflies were released within 1 or 2 days.

To evaluate the dispersal ability of *G. rhamni*, a mark–release–recapture study was carried out on sunny days between 18 April and 18 May 1998, which is the spring peak flight period in North Wales. Butterflies were given a unique mark and released immediately at their position of capture. The date, time, location, sex, wing condition (perfect = 4, fine = 3, poor = 2, well worn = 1), and behaviour were recorded at each capture. Marks consisted of a unique number applied to the ventral surface of both hindwings using permanent pens. A mark consisting of an ≈25 × 5 mm strip was also applied to the dorsal wing surface of both forewings, allowing marked butterflies to be spotted in flight. The entire study area was far too large to be searched thoroughly during the mark–release–recapture study, and *G. rhamni* is an active butterfly that occurs at relatively low densities in the Creuddyn peninsula, so capture rates would have been too low if the whole area had been covered. Thus, marking of individuals was confined to the area occupied by the host plants, where the butterfly was most abundant. Four other colleagues working on butterflies in the Creuddyn peninsula also recorded marked individuals of *G. rhamni*, in order to record butterfly movements outside the host plant distribution. Dispersal ability was estimated as distance between successive recaptures. Recaptures on the day of marking were excluded from analyses to avoid underestimating dispersal (Gall, 1984).

Results

Rhamnus catharticus was very rare in the study area. It was recorded in only two 500-m grid squares (Fig. 2). All records were in woodland clearings or scrub on rocky limestone outcrops with southerly or westerly aspects. *Rhamnus alaternus* was also very localised, being recorded in three 500-m grid squares (Fig. 2). It also occupied steep southerly or west-facing limestone rocky outcrops, occurring in woodland clearings as well as more open situations. *Frangula alnus* was the most widely distributed host plant; eleven 500-m grid squares were occupied by this species (Fig. 2). Most bushes were planted along hedges and woodland edges next to three main roads in the study area.

A total of 347 *G. rhamni* records was collected throughout the study area during 1996–98. The butterfly distribution was fairly solid around the host plant distributions, and much more localised elsewhere (Fig. 2). *Gonepteryx rhamni* was recorded from all 500-m squares that contained host plants. Outside the host plant distribution, *G. rhamni* may have been slightly closer than average to the nearest grid square containing host plants but the difference was not significant (Mann–Whitney
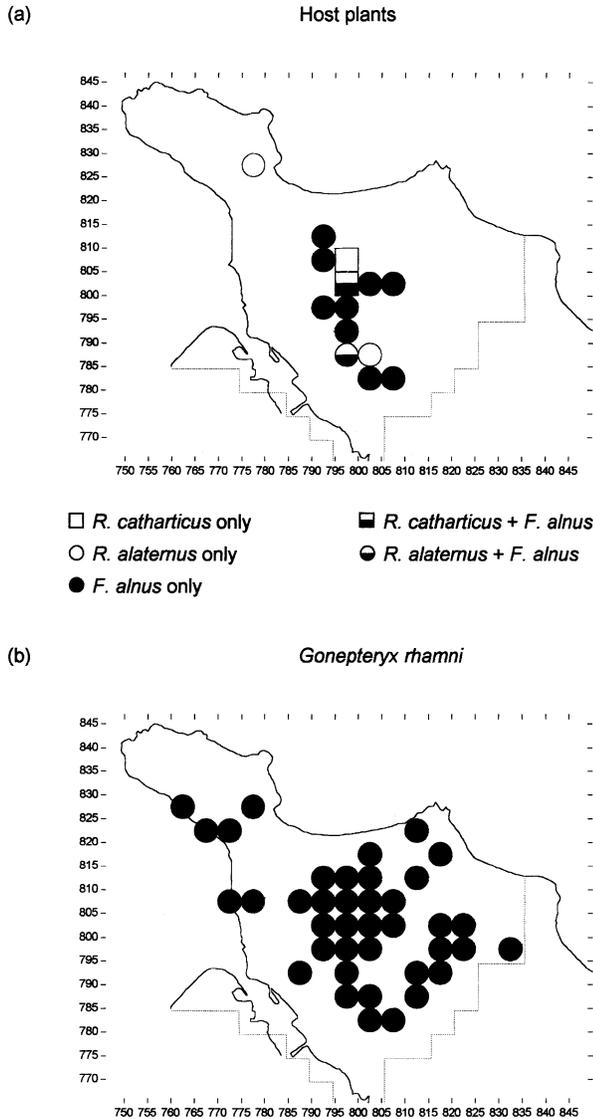
(a)

Host plants

☐ *R. catharticus* only   ◧ *R. catharticus* + *F. alnus*
○ *R. alaternus* only   ◓ *R. alaternus* + *F. alnus*
● *F. alnus* only

(b)

Gonepteryx rhamni

Fig. 2. Distribution of (a) the host plants *Rhamnus catharticus*, *Rhamnus alaternus*, and *Frangula alnus* and (b) the butterfly *Gonepteryx rhamni* in the Creuddyn peninsula at 500-m resolution.

Table 1. Numbers of 100-m grid squares occupied by *Rhamnus catharticus*, *Rhamnus alaternus*, and *Frangula alnus*, and number and proportion of those squares that contained *Gonepteryx rhamni* eggs or larvae in 1997.

	No. of 100-m squares	No. of squares with eggs or larvae	Proportion of squares with eggs or larvae
R. catharticus	4	2	0.50
R. alaternus	13	7	0.54
F. alnus	53	48	0.91

76 larvae collected from *F. alnus*, 66 (87%) pupated and produced adults. Two pupae and one larva were killed by unidentified parasitoids.

A total of 47 individuals was marked during the mark–release–recapture study. Seventeen (36%) individuals (13 males and 4 females) were recaptured a total of 26 times, on different days. Adult brimstones moved a distance of 512 ± 467 m (mean $\pm$ SD, $n = 26$) between successive recaptures, 50% of movements being further than 400 m (Fig. 3). With only 26 recaptures, the maximum distance recorded was 2.03 km, and unmarked *G. rhamni* were recorded in eight 500-m grid squares further than 1 km from the nearest host plants (Fig. 2). No significant relationship between distance and time between successive captures was found, although the sample size was small (Spearman rank correlation coefficient, $r_s = 0.129$, $n = 26$, $P = $ NS).

Discussion

The distribution of the butterfly was wider than that of its host plants, probably due to the relatively high mobility of adults. Thus, the butterfly was able to move easily from breeding sites to relatively distant locations searching for other resources such as nectaring and overwintering sites (see Pollard & Hall, 1980). Within the study area, this species can probably be characterised as a patchy population (Harrison, 1991; Harrison & Taylor, 1997). It is worth bearing in mind that, given the difficulty of recapturing a low-density, mobile butterfly over large areas, and that the same *G. rhamni* individuals would also have been active in the previous summer/autumn (they overwinter as adults), the dispersal distances obtained represent underestimates of real per-generation rates of movement. A maximum distance moved of >2 km with a low sample size ($n = 26$ recaptures) indicates high mobility of the butterfly in the study area.

Gonepteryx rhamni was able to use all host plant species in the study area for oviposition. Differences in host use could arise from differences in habitats where bushes were located. Some *R. catharticus* and *R. alaternus* bushes were located along sheltered woodland edges that were probably highly suitable for oviposition (Bibby, 1983) but others were growing on windy crags. In contrast, the *F. alnus* bushes had been planted in small groups along hedges, generally in fairly
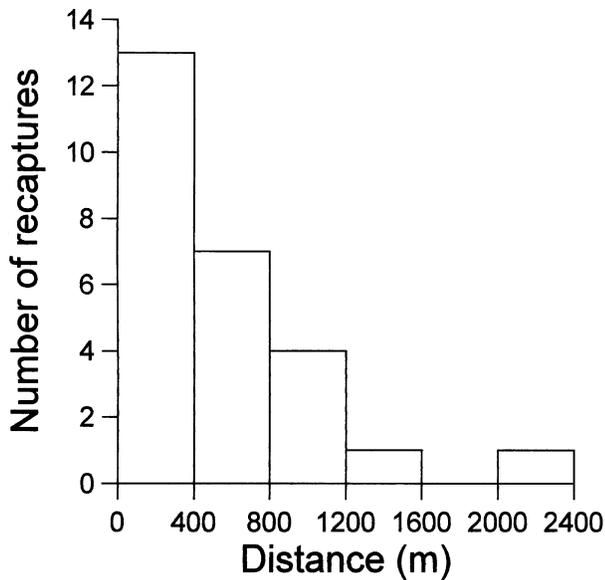
test, $Z = -1.367$, $P = $ NS); occupied grid squares $= 1133 \pm 574$ m (25); unoccupied grid squares $= 1378 \pm 721$ m (101) [mean $\pm$ SD (n); Fig. 2].

The numbers of 100-m grid squares containing *G. rhamni* eggs or larvae during the 1997 survey are shown in Table 1. Approximately 50% of the squares with *R. catharticus* and *R. alaternus* contained eggs or larvae. In contrast, more than 90% of 100-m grid squares with *F. alnus* were used for oviposition. These differences were significant (log-likelihood ratio test, $G^2 = 10.58$, d.f. $= 2$, $P < 0.01$).

Although some *G. rhamni* feeding damage was noticed on the leaves of some *R. catharticus* bushes, no larvae were found during the spring 1997 survey. Two fifth-instar larvae were collected on *R. alaternus* and produced two adult females. Of

Fig. 3. Number of recaptures of *Gonepteryx rhamni* on different days at different distances, in 400-m distance categories (*n* = 26).

sheltered and sunny positions, which are known to be highly suitable for egg-laying (McKay, 1991).

Gonepteryx rhamni completed its lifecycle on at least the two introduced species, *R. alaternus* and *F. alnus*. The inability to find larvae on *R. catharticus* probably arose because the number of suitable sites for oviposition on this plant was very low in the study system, hence few eggs developed into fully grown larvae. Most of the *G. rhamni* population in the Creuddyn peninsula breeds on *F. alnus*, and it probably depends on this host plant species.

Before *F. alnus* was planted in the 1980s, it may be hypothesised that some vagrant *G. rhamni* individuals would occasionally have arrived in the Creuddyn peninsula and might have laid some eggs on both *Rhamnus* species. The nearest natural host plant populations were about 30 km away (Fig. 1). The carrying capacity of the habitat would be so low, and patches of host plants so far apart, however, that the population would almost certainly have been prone to rapid demographic extinction (Thomas & Hanski, 1997). Thus, most occasions on which the peninsula was colonised by *G. rhamni* would probably be followed by very rapid extinction, and the population would have been entirely dependent on migration from other populations. This would be consistent with the occasional early records of *G. rhamni* in the area. In contrast, following the planting of *F. alnus*, the carrying capacity of the habitat for *G. rhamni* would have increased, possibly about 40-fold (given the ratios of mature larvae found on each host). Based on the mark–release–recapture study, very roughly 100–150 adults were present in spring 1998, so it can be presumed that the pre-*Frangula* population could only have numbered a few individuals. Hence, the probability of survival of the population would have increased greatly with the planting of

F. alnus; this would make the population less dependent on immigration for persistence. The Creuddyn peninsula population of *G. rhamni* probably now represents a satellite or island population, some 30–40 km west of the butterfly's main distribution (cf. Jordano *et al.*, 1991).

Overall, the results presented here support empirically the host-limited distribution of *G. rhamni*. Nonetheless, it is worth indicating that the range of *G. rhamni* is likely not to be totally food limited, as the northern edge of its range in England has fluctuated, assuming that these retreats and advances occurred independently of the host plants (Rimington, 1992). In addition, it has been shown that *G. rhamni* has fluctuated markedly in abundance at the northern edge of its range in north-west England (Pollard & Yates, 1993).

Finally, in contrast to predictions made for other highly mobile butterflies (Bryant *et al.*, 1997), *G. rhamni* cannot be expected to expand its distribution in response to climatic warming unless its host plants colonise or are themselves introduced further north.

Acknowledgements

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