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Population differentiation and conservation of endemic races: the butterfly, *Plebejus argus*

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Abstract

Five races of the Eurasian silver-studded blue butterfly, *Plebejus argus*, are restricted to different habitats in north Wales and north-west England. One of these races is extinct, and others are threatened. The four extant forms differ in morphology, habitat, host plant choice, performance on different host plant species and species of associated ant. Some of these differences are maintained in captivity, suggesting evolutionary divergence. Different races with different habitat requirements require different practical conservation management to maintain existing populations and metapopulations. Between-population, or racial, variation is an important consideration in the development of conservation programmes for this and other threatened species. Racial differentiation in *P. argus* suggests relatively long periods of isolation in particular habitats; the same areas contain other rare species and races. Many countries support the principle of conserving genetic variation within species, but practical methods do not exist for recognizing key areas to prioritize. We suggest that the existence of local races of well-known taxa may be used to indicate biodiversity hotspots, at a taxonomic level below that of full species. These may represent key locations for the conservation of genetic biodiversity.

INTRODUCTION

The British butterfly fauna consists largely of widespread species, under no threat of global extinction. In this respect, butterflies are similar to most other groups of animals and plants in Britain. Thus, the UK Biodiversity Action Plan has recently, and appropriately, assigned high priorities to the conservation of species that are threatened throughout Europe, or that are more numerous in Britain than elsewhere. In the absence of endemic *species*, it could also be argued that ecologically and evolutionarily distinctive *populations*, *races* and *subspecies* (hereafter ‘races’) that are endemic to Britain should be given a high priority within this region. Approximately 20% of named, endemic races of British butterflies have been recorded as becoming extinct in the past 150 years (Emmet & Heath, 1990). However, racial variation within species is not explicitly recognized under UK conservation legislation, and endemic forms have received rather little attention from conservation bodies unless, coincidentally, the entire species is threatened in the UK.

The silver-studded blue butterfly, *Plebejus argus*, is widely, if patchily, distributed across Europe and Asia (Higgins & Riley, 1980; Tolman & Lewington, 1997), but has three named endemic races in Britain (de Worms, 1949), one or two of which are extinct (C. D. Thomas, 1993; Ravenscroft & Warren, 1996). In this paper, we summarize information on ecological and evolutionary divergence among populations of *P. argus* near the margins of its geographic distribution, in north Wales and north-west England, and present new data on female colour patterns and on the performance of larvae from different races on different host plants. The results suggest that evolutionary differences among populations are sufficient to require separate conservation actions for different races.

Plebejus argus races

de Worms (1949) recognized several races of *P. argus* in Britain, and drew attention to additional

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interpopulation variation within each named race. Endemic *Plebejus argus masseyi* occurred on mosslands (wet heathland, on peat soils) of north-west England (Fig. 1), becoming extinct in about 1942 (Institute of Terrestrial Ecology/Environmental Information Centre (ITE/EIC) records). One mossland population survives at Llyn Hafod-y-llyn in north Wales, but is probably not especially closely related to the extinct *masseyi* (C. D. Thomas, 1985*a*,*b*). *Plebejus argus cretaceus* occurred on the chalk hills of southern England, but was extinct by the mid 1970s (ITE/EIC records); surviving populations on the limestone of Portland Bill, Dorset (Warren, 1986; Ravenscroft & Warren 1996) may not strictly belong to *cretaceus*. The endemic race *caernensis* still thrives on limestone in north Wales (C. D. Thomas, 1985*b*; C. D. Thomas & Harrison, 1992). All remaining populations were assigned by de Worms to non-endemic *P. argus argus*, occurring predominantly on heathlands in England. However, de Worms (1949) would probably have formally described other races, had he studied material from all British populations (e.g. Portland Bill, north Wales mossland, north Wales heathland, sand dune populations in south-west England).

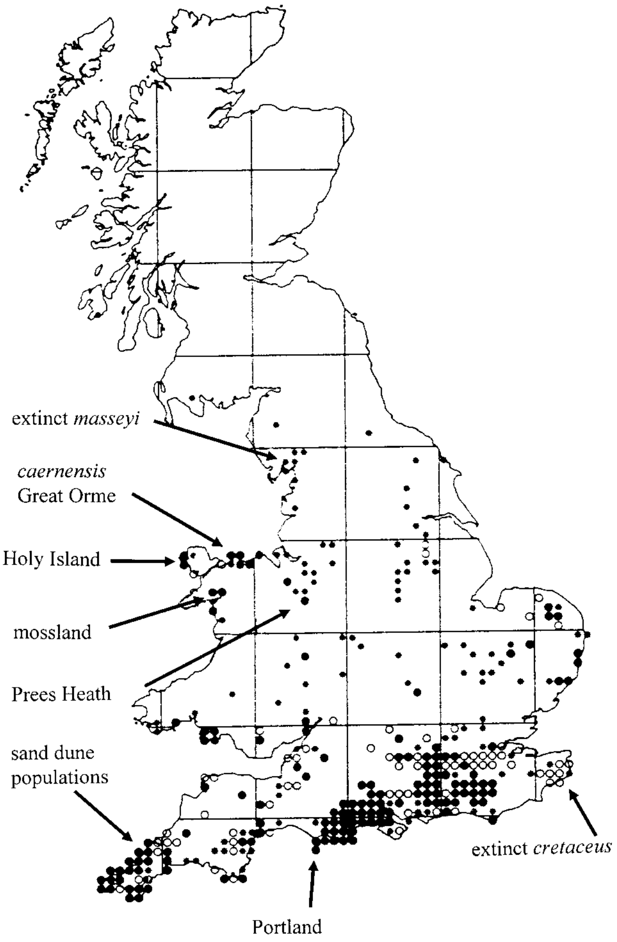

Fig. 1. Map of the distribution of *Plebejus argus* in Britain. •, 1970–1988 records; ○, 1940–1959; *, pre-1940. Map modified from Emmet & Heath (1990).

Genetic results (allozymes, mtDNA and microsatellites) show that races and populations do differ significantly from one another, and Llyn Hafod-y-llyn samples appeared to be particularly distinctive for allozyme loci; but the differences were generally slight and were mainly changes in allele frequencies (Brookes *et al.*, 1997; O. C. Rose & J. L. B. Mallet, pers. comm.). However, a lack of major divergence among *large* populations that have only been separated for 10^3 to 10^4 years (generations) is not unexpected for *neutral* loci, and is perfectly consistent with major divergence having taken place at adaptive loci over the same period. Strategies for conserving patterns of neutral and adaptive variation are likely to be quite different from one another.

Overall, at least one (two if we include *cretaceus*) endemic race has become extinct, other unnamed races are threatened, and yet other races have probably become extinct unnoticed. We do not advocate separate naming of every distinctive population, but intraspecific variation clearly impinges on conservation planning for this species.

MORPHOLOGY

Our focal area in north Wales and north-west England used to support the extinct race *masseyi*, and still contains four distinctive extant forms, which we refer to as races in this paper. The extant races are *P. argus caernensis* on limestone, and three other forms, all formally regarded as belonging to *P. argus argus* (Holy Island (off Anglesey), Prees Heath and Llyn Hafod-y-llyn mossland: see Fig. 1 and Table 1). The race *caernensis* and the Holy Island butterflies are amongst the smallest in the UK, whereas the Prees Heath and Llyn Hafod-y-llyn butterflies are about the largest (Dennis, 1977; C. D. Thomas, 1985*a*; C. D. Thomas, Hill & Lewis, 1998; and see below).

Females from northern populations have varying amounts of blue on the uppersides of their wings, the blue colour being most extensive in the extinct race *masseyi* (de Worms, 1949; Dennis, 1977; Table 1). *Plebejus argus* from several races were reared under controlled conditions in 1994 and 1996 (see below). Females were placed in six intensity categories, according to the percentage of blue scales in a band on the upper hindwing (Table 2). Females with no blue scales, and most of those with 1–5% blue scales, do not appear blue to the human eye, so we report the percentages of females with >5% blue scales (those that do appear blue). Samples from the Great Orme and Dulas Valley (both race *caernensis*) had 61% and 63%, respectively, of females with >5% blue scales, whereas the values were 19% of females for Llyn Hafod-y-llyn, 9% for Prees Heath, and 2% for the race *argus* populations in south and east England (pooling three populations: Table 2). Populations with relatively high percentages of females with >5% blue scales also tended to have more bright blue females (>25% blue scales: Table 2).

Table 1. Key features of the morphology, ecology, and conservation of *Plebejus argus* races in north Wales and north-west England

Site/race	Females with blue[a]	Adult size	Habitat	Main host plants	Main ant partner	Habitat dynamics	Conservation management	Status
Great Orme/ *caernensis*	Many	Small	Limestone grassland	*Helianthemum* spp.; *L. corniculatus*; other Leguminosae	*L. alienus*	Relatively stable	Grazing	Good
Prees Heath/ *argus*	Few	Large	Dry heathland	*C. vulgaris*; *E. cinerea*; *L. corniculatus*; shrubby Leguminosae	*L. niger*	Dynamic/ successional	Create new successions/ introductions (and see the text)	Threatened
Holy Island/ *argus*	Some/many	Small	Coastal heathland	*C. vulgaris*; *E. cinerea*; *E. tetralix*; *Ulex* spp.; (rarely other Leguminosae)	*L. niger*	Dynamic/ successional	Create new successions	Vulnerable
Llyn Hafod-y-llyn/ *argus*	Some	Large	Mossland/ dry mounds	*C. vulgaris*; *E. cinerea*; *E. tetralix*; (occasional Leguminosae)	*L. niger*	Dynamic	Grazing/ create new mounds/ introductions	Threatened
Cumbria/ *masseyi*	Almost all	Large	Mossland	presumably Ericaceae	presumably *L. niger*	Dynamic	–	Extinct

Plant names. Ericaceae: *Calluna vulgaris, Erica cinerea, Erica tetralix*; Cistaceae: *Helianthemum chamaecistus, Helianthemum canum;* Leguminosae: *Lotus corniculatus, Ulex europaeus, Ulex gallii.*
Ant names. *Lasius alienus, Lasius niger.*
[a] From Dennis (1977) and Table 2; on upper surface.

Table 2. Colour patterns of female *Plebejus argus*, reared in captivity

	Intensity					
	0	1–5%	6–25%	26–50%	51–75%	>75%
caernensis						
Great Orme	0	42	33	19	11	3
Dulas Valley	10	101	115	53	16	4
Northern *argus*						
Llyn Hafod-y-llyn	6	23	3	3	0	1
Prees Heath	6	35	3	1	0	0
South-eastern *argus*						
New Forest	14	14	1	0	0	0
Hollesley	13	5	0	0	0	0
Silchester	6	0	0	0	0	0

The intensity of blue colouration is the percentage of blue scales on the hindwing upperside, in the area bounded by Veins 4 and 6 (which normally forms a band); blue scales have a distinct morphology and were scored using a binocular microscope. The numbers of females examined are given in the Table.
Taking *caernensis* as one group, and considering Llyn Hafod-y-llyn and Prees Heath to be separate groups, with south-east *argus* as another group, and 0–5% as one category and ⩾6% as another; X^2=103.7, d.f.=3, P<0.001.

HABITAT AND CONSERVATION MANAGEMENT

Races differ in their ecology and habitat (Table 1). The race *caernensis* inhabits southerly-facing limestone hillsides in coastal north Wales, where eggs are laid in warm, sparse vegetation, dominated by *Lasius alienus* ants, with which *P. argus* larvae and pupae enter into mutualistic relationships (C. D. Thomas, 1985*a*,*b*; Jordano, Rodríguez *et al*, 1992; Jordano & Thomas, 1992; Glen, 1997: see Fig. 1). The larvae feed on *Helianthemum* species (Cistaceae), *Lotus corniculatus* and other low-growing legumes. Limestone habitats are potentially relatively stable, being maintained by grazing; the conservation of large, extant populations is the main priority (C. D. Thomas, 1985*a*,*b*; C. D. Thomas & Harrison, 1992).

Llyn Hafod-y-llyn (mossland) is flat, poorly drained, and dominated by grasses, sedges and heathers (Ericaceae) growing on acid peat. Females lay almost all of their eggs on short vegetation associated with slightly raised peat mounds (and rocky areas), where the larvae feed mainly on young shoots of heathers (Ericaceae: Table 1). Peat mounds provide relatively warm and dry nesting locations for *Lasius niger* ants, with which the larvae and pupae are associated (Jordano, Rodríguez *et al.*,1992; Jordano & Thomas, 1992). Suitable mounds can be long-lived, but conditions are highly sensitive to grazing levels, and the spatial distribution of *P. argus* is dynamic (C. D. Thomas & Harrison, 1992). Conservation measures need to manage the spatial dynamics, maintaining grazing and creating new peat mounds (with possible introduction to the former range of *masseyi*).

On Holy Island, *P. argus* inhabits early successional coastal heathland, especially on southerly-facing slopes (C. D. Thomas, 1985*b*), where eggs are laid in short, warm vegetation (C. D. Thomas, 1983; J. A. Thomas *et al.*, in press). The larvae feed on Ericaceae and gorse (*Ulex* spp., Leguminosae), and larvae and pupae are tended by *Lasius niger* ants (C. D. Thomas 1985*a*,*b*;

Jordano, Rodríguez *et al.*, 1992; Jordano & Thomas, 1992: Table 1). Physical disturbances (e.g. cutting, fire, grazing, or salt spray) generate new successions, but these conditions are generally transient, and so the butterfly's distribution is dynamic (C. D. Thomas & Harrison, 1992). Conservation measures must generate new successional conditions for ants and butterflies to colonize (C. D. Thomas, 1985*b*).

At Prees Heath, *P. argus* inhabits early and mid stages of succession on dry heathland, where *Lasius niger* ants are abundant. Eggs are laid on, and larvae consume, *Calluna vulgaris*, *Erica cinerea* and various Leguminosae, especially *Ulex europaeus*, *Lotus corniculatus* and *Sarothamnus scoparius* (C. D. Thomas, 1985*a*; Jordano, Rodríguez *et al.*, 1992; C. D. T. unpublished results). As on other heathlands, these conditions are successional and transient, and the butterfly distribution is dynamic (C. D. Thomas & Harrison, 1992). Recent anthropogenic changes to the site have reduced its natural acidity and increased its nutrient status (low-nutrient, acid conditions are required to maintain heathland vegetation), so the conservation imperative here is to decrease the pH and nutrient status of the vegetation, and to establish new heathland vegetation successions.

Because these four different races interact with different ants, host plants, vegetation types and landscapes, quite different conservation actions are required at each location.

RACIAL DIVERGENCE

Three lines of evidence suggest that *P. argus* possesses ecologically significant local adaptations that are likely to be important to the conservation of these races.

First, experimental releases of *P. argus* into unoccupied habitats were only successful when butterflies were released in the same general vegetation type as the one from which they originated. Four experimental releases of *P. argus* were carried out in north Wales in 1983 (C. D. Thomas, 1983). Heathland (Holy Island) and limestone butterflies (*caernensis*) were released into both unoccupied limestone and heathland habitats. Thus, two releases took place in the 'correct' habitat (limestone butterflies on limestone; heathland butterflies on heathland) and two releases took place in the 'wrong' habitat (limestone butterflies on heathland; heathland butterflies on limestone). The two releases of races into the 'correct' habitat were successful (the limestone population has become large, and although the heathland population died out after a few years, it probably would have survived with adequate habitat management), whereas the two releases in the 'wrong' habitat failed completely (C. D. Thomas & Harrison, 1992). This suggests that local adaptations are sufficient to make transfer to other habitat types difficult.

Second, the ant associations differ. The main ant-associate is *Lasius alienus* on the limestone, and *L. niger* on the mossland and heathland (Jordano, Rodríguez *et al.*, 1992). Although *P. argus* can be reared from egg to adult without ants in captivity, larvae and pupae are apparently always associated with *Lasius* ants in the wild (for a review, see Jordano, Rodríguez *et al.*, 1992). Jordano & Thomas (1992) showed racial differences in larval attractiveness to different *Lasius* species, using larvae reared in a common environment. Mossland (Llyn Hafod-y-llyn) larvae were more attractive to *Lasius niger* that they were to *L. alienus* (these caterpillars are naturally associated with *L. niger*), whereas limestone (*caernensis*) larvae were equally attractive to both species of *Lasius* (these caterpillars are naturally associated with *L. alienus*). The implications for conservation are that introduction or re-introduction programmes should ensure that the same *Lasius* species that are associated with *P. argus* in donor populations are also abundant in receptor habitats.

LARVAL HOST PLANT ADAPTATIONS

The third line of evidence of racial divergence is that larvae from different populations prefer different host plants. C. D. Thomas (1985*a*) provided larvae of different races with a choice of host plants and showed that limestone larvae (*caernensis*: that naturally feed on *Helianthemum*) preferred *Helianthemum* species to heathers, whereas heathland larvae (Holy Island: that naturally feed on heathers) preferred heathers to *Helianthemum* (C. D. Thomas, 1985*a*).

In the light of these different preferences, and because different natural host plant species are used by larvae in different populations (see above), we investigated differences in larval performance on different host plant species. In 1993 and 1995, wild eggs were collected from limestone (Great Orme) and heathland (Prees Heath), and also from the mossland (Llyn Hafod-y-llyn) in 1993. Larvae were reared in a common environment the following Spring, on *Lotus corniculatus*, *Helianthemum chamaecistus* or *Calluna vulgaris*. In both years, adults were frozen on emergence and subsequently thawed, dried to constant weight at 60 °C, and weighed on a Cahn Electrobalance (sensitivity 0.1 μg). In 1994, larvae were reared in an incubator (20 °C, 16L:8D), in small plastic boxes (5 cm × 10 cm) and provided daily with fresh-cut host plant. In 1996, larvae were reared in a common environment, in small 'clip cages' (of foam and netting) attached to growing plants in screened-houses. Unfortunately, in both years, the *Calluna* plants grew poorly, resulting in high larval mortality, so we have excluded these results from subsequent analysis.

Mean adult dry weights (± standard error, SE) are shown in Table 3. GLM analysis of Log_{10} total adult dry weight revealed significant differences among populations in both years. In 1994, mossland butterflies were the heaviest, Prees Heath intermediate, and Great Orme butterflies were lightest ($F_{2,109} = 122.8$, $P < 0.001$). In 1996, Prees Heath butterflies were again significantly heavier than Great Orme butterflies ($F_{1,88} = 40.7$, $P < 0.001$). Females were heavier than males in both years (1994, $F_{1,109} = 142.9$, $P < 0.001$; 1996, $F_{1,88} = 31.1$, $P < 0.001$).

Table 3. Log_{10} dry adult weight (mg) for *Plebejus argus* from different populations, reared on different host plants

Population	Host plant	Sex	mean	SE	*n*
(a) 1994					
Great Orme	*L. corniculatus*	M	0.907	0.012	14
	L. corniculatus	F	1.010	0.013	13
	H. chamaecistus	M	0.807	0.013	13
	H. chamaecistus	F	0.915	0.012	14
Prees Heath	*L. corniculatus*	M	1.007	0.019	6
	L. corniculatus	F	1.098	0.013	13
	H. chamaecistus	M	0.856	0.019	6
	H. chamaecistus	F	0.984	0.017	7
Llyn Hafod-y-llyn	*L. corniculatus*	M	1.073	0.017	7
	L. corniculatus	F	1.159	0.014	11
	H. chamaecistus	M	0.904	0.026	3
	H. chamaecistus	F	1.016	0.012	14
(b) 1996					
Great Orme	*L. corniculatus*	M	0.773	0.015	23
	L. corniculatus	F	0.869	0.020	13
	H. chamaecistus	M	0.624	0.021	12
	H. chamaecistus	F	0.700	0.023	10
Prees Heath	*L. corniculatus*	M	0.885	0.017	18
	L. corniculatus	F	0.986	0.019	14
	H. chamaecistus	M	0.697	0.041	3
	H. chamaecistus	F	0.707	0.041	3

Note that rearing conditions differed between years, resulting in different overall mean dry weight in the 2 years.
Plant names: *Lotus corniculatus*; *Helianthemum chamaecistus*.

Butterflies were heavier if they were reared on *L. corniculatus* rather than on *H. chamaecistus*, in both 1994 ($F_{1,109} = 213.1$, $P < 0.001$) and 1996 ($F_{1,88} = 159.3$, $P < 0.001$). There was a significant host plant × population interaction in 1994 ($F_{2,109} = 3.86$, $P = 0.024$), and a marginal effect in 1996 ($F_{1,88} = 3.77$, $P = 0.055$). Examination of means indicated that the host plant × population interaction occurred in the same direction in both years. Since these are independent samples revealing the same (predicted) pattern, it is legitimate to regard the overall probability as the product of these two values (i.e. $P = 0.0013$). The interaction can be interpreted as follows. Adults from all populations were heavier if they had been reared on *L. corniculatus* rather than on *H. chamaecistus*, but limestone adults from the Great Orme were *relatively* heavy if they had been reared on *H. chamaecistus*. Prees Heath butterflies reared on *H. chamaecistus* attained about 66% of the weight they achieved on *L. corniculatus*, whereas Great Orme attained more like 75% of their *L. corniculatus* weight when reared on *H. chamaecistus*: an approximately 14% improvement in performance. Thus, the limestone butterflies from the Great Orme (which naturally feed on *H. chamaecistus*, as well as on *L. corniculatus*) are relatively good at developing on *H. chamaecistus*, even though this is not the best host species for *P. argus* in general.

These results indicate that larvae from different populations differ in relative performance on different host plants (see also Glen, 1997). Despite doing best on *L. corniculatus*, this plant occurs at quite low densities on most *P. argus* sites, and so larvae usually have to consume alternative host species. Larvae tend both to prefer and attain greater weights on the alternative host plant that they encounter naturally.

DISCUSSION

Racial differentiation

The results from this and previous studies point to local adaptations by different races of *Plebejus argus*. Data on adult weight (this paper, and C. D. Thomas *et al*., 1998), female colour pattern (this paper), performance when reared on different host plants (this paper), and interactions with different *Lasius* ant species (Jordano & Thomas, 1992), reveal racial differences that continue to be expressed when larvae are reared in a common environment. This implies probable genetic divergence, and suggests local adaptations of different races to local environments.

Despite clear evidence for local divergence and adaptation, each of the racial differences is quantitative, and not absolute. For example, mossland *P. argus* larvae are attractive to *L. alienus* ants (not the natural partner), although not quite as attractive as *P. argus* larvae from limestone (natural partners). Similarly, heathland *P. argus* larvae can develop to maturity on *Helianthemum chamaecistus*, even though it is not a particularly good host plant for them. C. D. Thomas (1985*a*) concluded that quantitative differences in morphology and ecology of different populations of *P. argus* in north Wales were probably not sufficient to warrant calling each a separate subspecies. Since definitions of taxonomic status below the level of species are poorly defined, such conclusions are always subjective, and we cannot resolve the issue, even though there is now clearer evidence of genetic divergence. More interesting is whether all of these quantitative differences in traits, between them, generate sufficient divergence among races that each has become both ecologically and evolutionarily restricted to its own environment (on the time scale of conservation planning). The success of release experiments in the ‘correct’ habitat, and failure of those in the ‘wrong’ habitats, suggest that this may often be the case. Thus, each race must be considered as a separate entity for conservation.

Origin of the races

The extent of racial differences implies probable separation for a considerable period (1 year = 1 generation). There are two probable scenarios for the origin of these populations, although there are additional possibilities, and we may never be able to distinguish between them with certainty. The first hypothesis, and the one that we favour, is that, when temperatures rose sharply at the beginning of the present interglacial, 9000–12 000 years ago, *Lasius* ants and *P. argus* would have spread rapidly and colonized the north European plain, spreading faster than, and in front of, the advancing forests (Dennis, 1977, 1993). *Plebejus argus* is generally a rather poor colonist, and does not spread easily across non-breeding habitat (C. D. Thomas & Harrison, 1992; Lewis *et al.*, 1997); this was the one time in the last 50 000 years when northern Europe was thermally suitable for *P. argus* and dominated by uninterrupted landscapes of open vegetation that contained at least some potential host plants for this species. Following range extension, most populations would have become extinct naturally, as closed forest subsequently came to dominate northern landscapes, and *P. argus* would have survived only in those few areas that retained open vegetation. This could explain why *P. argus* races in north Wales and north-western England are associated with naturally open vegetation (limestone crags and cliffs, mossland swamps and coastal heathland), and on sand dune systems elsewhere in England. Inland populations on heathlands probably have a more recent origin, spreading when humans began to clear the forest; in the case of Prees Heath, the butterflies may have originated from nearby mosslands.

The alternative hypothesis is that all racial divergence has arisen in the past 1000–5000 years. Humans progressively opened up northern European forests during this period, and *P. argus* might have spread at this time. However, the matrix of forest and early agricultural habitats would have provided a much less continuous landscape for *P. argus* than the landscapes of 10 000 years ago.

Conservation of genetic biodiversity

Regardless of when these racial differences originated, they are of considerable conservation interest, yet receive no formal recognition under current British conservation legislation. In *P. argus*, we see a species where much of the biodiversity exists at the level of races and populations within the species.

But, is the preservation of endemic races or subspecies a conservation detail that we cannot afford to consider (see Vane-Wright, Humphries & Williams, 1991)? On a world scale, the answer is clearly 'yes'. Conservation of population-level variation is simply an impossible task, given Hughes, Daily & Ehrlich's (1997) guestimate of about 6.6 billion populations globally, of which some 16 million might be becoming extinct annually (these estimates are probably too low). From a British perspective, however, we think that there is a case for prioritizing endemic races for three main reasons. First, under a broad definition of biodiversity that includes genetic variation, most of the genetic variation that is unique to Britain is likely to be contained within endemic races, although much more work is needed on this topic. Many governments are, in principle, committed to the conservation of all aspects of biodiversity, but often lack specific policies to achieve this for genetic variation; other than as a consequence of species and habitat conservation. Development of policies aiming to conserve racial variation may represent one practical step forward (it would be necessary to find a legislative alternative to the problem in the USA of actually *defining* races or subspecies as 'endangered species' in their own right).

Second, endemic races are typically associated with ancient habitats that also contain other endemic forms, and other rare species. For example, the Great Orme also supports the endemic grayling butterfly race *Hipparchia semele thyone* (Dennis, 1977), as well as many other rare invertebrates, while the mossland site contains a host of invertebrates that are rare or threatened in Britain (A. Fowles, pers. comm.). The conditions that have given rise to endemic variation in one insect group have almost certainly also given rise to comparable variation in some other invertebrate groups. We would argue that the locations of endemic races are likely to be highly aggregated, and that the *known* distributions of endemic races can probably be used to indicate the existence of biodiversity hotspots, in terms of genetic variation at a taxonomic level below that of full species. This is consistent with Avise's (1992) conclusion that the distributions of relatively deep evolutionary divisions within species (clades) are often spatially concordant with those from other species. Thus, effective conservation of the racial structure of some species is likely to go some way towards conserving the racial structures of some of the other species that occur in the same habitats and regions.

Third, by virtue of the fact that races have had sufficient time to develop local characteristics and adaptations, races *may* also pinpoint the existence of persistent biological systems that can be conserved relatively effectively. Given the 'agony' of conservation choices (Vane-Wright *et al.*, 1991), these areas should be close to the top of our priority lists.

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