Dimorphism of wings, wing-folding and wing-toiletry devices in the ladybird, *Rhyzobius litura* (F.) (Coleoptera: Coccinellidae), with a discussion of inter-population variation in this and other wing-dimorphic beetle species

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Dimorphism of tergal wing-folding spicule patches and wing-toiletry fringes accompanies wing dimorphism in the ladybird, *Rhyzobius litura*. Such dimorphism of 'ancillary' structures is of rare occurrence in the Coleoptera; other instances are discussed. Data are presented concerning the incidence of long and short winged individuals of *R. litura* in samples from six populations in southern England. Factors likely to influence the relative proportions of the morphs in small populations, and in samples of different kinds, are discussed. Evidence that inter-population variation in the incidence of macropterous individuals has a 'geographical' component in *R. litura* is inconclusive.

KEY WORDS:—Coleoptera – Coccinellidae – *Rhyzobius litura* – polymorphism – wing-folding – geographical variation.

CONTENTS

INTRODUCTION

In the context of the present paper the term 'polymorphism' is used in its extended sense, including strict dimorphism as a special case, and without any imputation as to how the phenomenon is controlled or maintained. However, in practice wing polymorphism in beetles appears to be most often expressed as a strict dimorphism (Lindroth, 1949: 339–341). Also it seems to be most

frequently under at least partial genetic control (see below, p. 29), and is less frequently a polyphenism (see Vespälainen, 1978) involving environmental cues, and the switching on or off of alleles which are common to all members of the population.

Regrettably, coleopterists often fail to look beneath the wing-cases of the beetles which they study. For most families and most regions of the world the phenomenon of wing polymorphism remains little documented. Even in many British species of beetle the condition of the flight wings receives no mention in the literature. In several cases wing polymorphic species have been reported, incorrectly, to be either constantly macropterous or constantly brachypterous. Despite this lack of reliable information it is, nevertheless, reasonable to assume that wing polymorphism is of wide and frequent occurrence in the Coleoptera. In fact, the number of wing-polymorphic beetle species to be found in the British Isles alone exceeds 200 (various sources, including unpublished observations), and includes representatives of at least 15 families. Best known, perhaps, in the Carabidae (Darlington, 1936, etc.), wing polymorphism in species of Chrysomelidae, Curculionidae, Dytiscidae and Ptiliidae also figures fairly prominently in the literature. Its occurrence in other families is less well documented. For example, Brunsting (1981: 447) in discussing wing muscle dimorphism in Staphylinidae offered the view that dimorphism of the wings themselves probably does not occur in the family. However, in the British Isles alone some 50 staphylinid species have been found to exhibit this phenomenon (Hammond, unpubl. obs.)!

Although a number of species remain to be investigated wing polymorphism has already been found to occur in more than 5% of the beetle species recorded from the British Isles. Using Lindroth's (1949, 1963, etc.) and others' observations on Carabidae from Continental Europe and N America and my own on Staphylinidae as a guide, tentative extrapolations may be made. Wing polymorphism seems likely to be exhibited by at least 5% of beetle species in cool temperate areas of the world as a whole. Wing-polymorphic species of Staphylinidae occur in all major zoogeographical regions (pers. obs.), and some idea of the incidence of wing-polymorphism in Carabidae from various regions, including the tropics, may be obtained from the literature (e.g. Darlington, 1943, 1971, etc.). Nevertheless, the overall incidence of wing-polymorphism in the beetles of the wet tropics remains particularly difficult to gauge. In tropical rain forests, where the majority of beetle species undoubtedly occur, the incidence may be lower, possibly markedly lower, than in temperate regions. Even so, if the beetle fauna of the globe comprises some 2 to 5 million species (as my own unpublished estimates suggest), wing-polymorphic beetle species may be expected to number at least 20 000, and may exceed 100 000.

The scale of the phenomenon, as indicated in the previous paragraph, should suffice to emphasize the biological interest of investigations into wing-polymorphism in the Coleoptera. Apart from this interest the present paper is the outcome of finding, in the course of investigations of wing-folding mechanisms, that the ladybird *Rhyzobius litura* is unusual among wing-dimorphic species in exhibiting dimorphism of structures concerned with wing-folding. At the same time, an opportunity arose to study a population of the species in which, at least initially, the proportion of macropterous individuals was unusually high.

The first section of this paper deals with the dimorphism of wing-folding and toiletry devices in *R. litura,* along with some discussion of comparable dimorphism in other species. The second section details the relative incidence of the wing-morphs of *R. litura* in samples from various sites in southern England, emphasizing results from a site in London where the species was sampled over a period of about 1 year. These results, in conjunction with data from other sources, are then used to explore the likely basis of variation between sites. In conclusion, the origins of inter-population differences in a variety of wing-polymorphic beetle are discussed.

WING-FOLDING AND WING-TOILETRY DEVICES IN BEETLES

A variety of structures found on the dorsal surface of the abdomen and pterothorax, and on the ventral surface of the elytra of beetles are employed to fold or groom the flight wings. The surfaces of the flight wings themselves also bear outgrowths which play a significant role in the wing-folding process. The topic of flight-wing protection in beetles and of wing-folding mechanisms in particular has been reviewed by Hammond (1979) who concluded that wing-folding spicule patches located on the abdominal terga (Hammond, 1979: figs 16–27) have an especially important part to play. In many beetles the abdomen is used to push the more distal parts of the flight wings into a folded position so that the wings are fully protected by the elytra. Tergal spicules, which mesh with microtrichia present on the surface of the hind wings, enable the abdomen to grip the wings during wing-folding pushes. Although not used for wing-folding by all beetles (they are absent, for example, in all Cantharoidea), wing-folding spicule patches are found, generally on the terga of abdominal segments V and VI, in all winged ladybirds.

Characteristic of most winged beetles, including ladybirds, is a second type of structure: a fringe of spinules at or near the posterior margin of one or more abdominal terga. On the basis of interference experiments and observations of living beetles Hammond (1979: 134–135) concluded that these "palisade fringes" (Hammond, 1979: figs 30–38) are employed to manipulate unfolded or partially unfolded wings in various ways. Although sometimes used to *unfold* wings in cases of apparent difficulty, they do not play a significant role in wing-*folding,* and are best regarded as grooming or "toiletry" devices.

POLYMORPHISM OF WINGS AND ANCILLARY STRUCTURES IN *RHYZOBIUS*

The general nature of wing-polymorphism in *Rhyzobius litura* (F.) and the related *R. chrysomeloides* (Herbst) has been described by Pope (1977: 59–61). A strict dimorphism, apparently with no bias to either sex, is found in both species. The brachypterous morph exhibits highly reduced strap-like wings of rather constant form (Fig. 1A, B). Hammond (1979) noted, in passing, that in *R. litura,* but not *R. chrysomeloides,* the wing-dimorphism is accompanied by a parallel dimorphism of two sets of ancillary structures: the tergal wing-folding spicule patches and the tergal palisade fringes. These findings are documented in more detail here.

In full-winged individuals of *R. litura* wing-folding spicule patches are present, as in most winged ladybirds, on the terga of the 5th and 6th abdominal
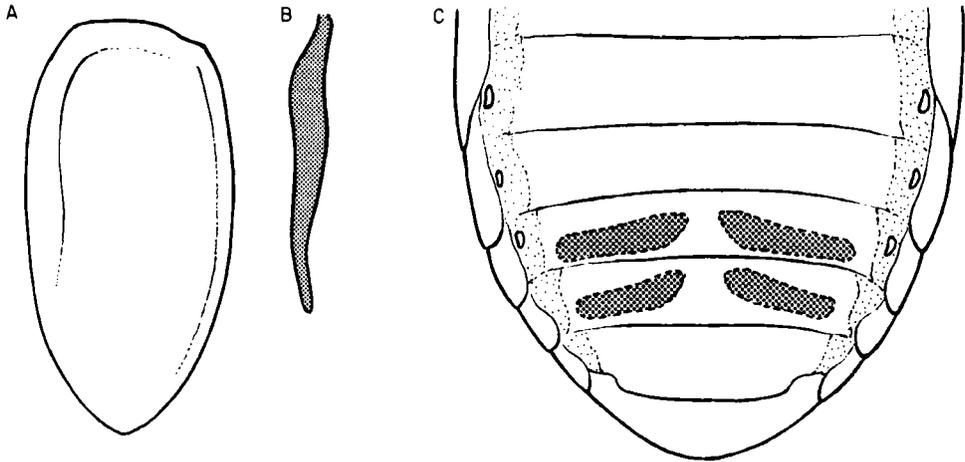
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Figure 1. *Rhyzobius litura*. A, right elytron in outline, ventral view; B, right wing from brachypterous individual (to same scale); C, dorsal surface of abdomen in full-winged individual, indicating position of tergal wing-folding spicule patches (shaded).

segments (Fig. 1C). These patches are relatively broad, and each consists of several hundred microtrichia directed away from the mid-line of the body (Fig. 2A). A palisade fringe occurs at the posterior margin of the tergum of the same (5th and 6th) segments (Fig. 2A). Individual spinules are spaced at intervals of about 3 μm (Fig. 2D). Very little variation in the size of wing-folding spicule patches or in the development of palisade fringes has been observed in the more than 100 full-winged individuals of *R. litura* examined.

In brachypterous individuals of *R. litura* (more than 200 examined), on the other hand, wing-folding spicule patches and palisade fringes (Fig. 2B, C) are both much reduced. This reduction is rather constant in extent, with the rudimentary wing-folding spicule patches consisting, at most, of some 50 short microtrichia, and the palisade fringes represented by scattered stumpy spinules (Fig. 2B).

In *R. chrysomeloides* wing dimorphism follows a similar pattern to that in *R. litura* but parallel dimorphism of ancillary structure does not occur. In brachypterous *R. chrysomeloides* (20 examined), as well as in the full-winged morph (10 individuals examined) the wing-folding spicule patches and palisade fringes resemble those of full-winged *R. litura* (Figs 1C, 2A, D).

POLYMORPHISM OF WINGS AND ANCILLARY STRUCTURES IN OTHER BEETLES

Leaving to one side certain instances of marked sexual dimorphism (e.g. the winged males and larviform females found in a number of species of Cantharoidea) and the apparently exceptional case of certain Ptiliidae (see below), wing polymorphism in beetles is generally accompanied by little in the way of genetically determined variation in other structures. A reduction in functional flight muscles is usual in beetles with much reduced wings, but is also by no means rare in constantly macropterous species (Den Boer, 1977), and occurs in at least some full-winged individuals of many wing-dimorphic species (Den Boer *et al.*, 1980: 131).
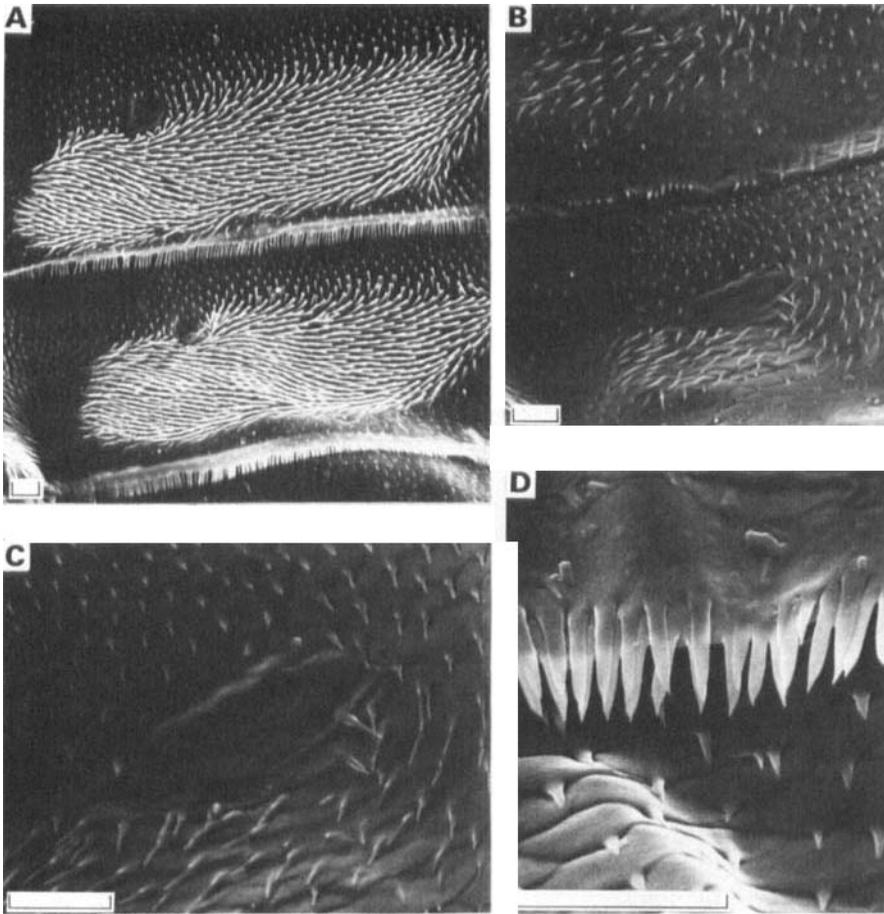
Figure 2. *Rhyzobius litura*. A, wing-folding spicule patches and palisade fringes on left side of abdomen in full-winged individual (neg. Ell/164); B, rudimentary wing-folding spicule patches on left side of abdomen in brachypterous individual (neg. SE2/505); C, rudimentary wing-folding spicule patch on left side of abdominal tergite VI in brachypterous individual (neg. SE2/716); D, palisade fringe at posterior margin of tergite VI in full-winged individual (neg. Ell/167). Scale bars = 20 μm.

Flight muscle reduction is frequently accompanied by a change in size and/or form of various parts of the body. Where flight muscle development correlates with that of wings, differences between the morphs of wing-dimorphic species may be marked. For example, in some Staphylinidae differences between morphs involve the shape of the entire pterothoracic region, including in such species as *Platystethus nitens* (Sahlberg) a great reduction in elytral size and a narrowing of the base of the abdomen in the brachypterous morph.

If variation in gross form of the body sometimes parallels that of wing development in wing-polymorphic species, a similar variation might be expected to occur in the small cuticular outgrowths concerned with the manipulation of the flight wings. However, such variation appears to be rare (Hammond, 1979: 164–165). Shute (1980) discovered no differences in form of wing-folding spicule patches between wing-morphs in any of 25 wing-polymorphic species of *Longitarsus*, investigated.

The condition of wing-folding spicule patches in different wing-morphs of more than 300 wing-dimorphic species (mostly in the families Carabidae, Chrysomelidae, Cryptophagidae, Dytiscidae and Staphylinidae) has now been recorded (Hammond, unpubl. obs.). Putting to one side the special case of certain feather-winged beetles (Ptiliidae), dimorphism affecting these spicule patches has been found to occur in only one species—the ladybird, *Rhyzobius litura*. The exceptional nature of this dimorphism in *R. litura* is highlighted by the lack of variation in development of wing-folding spicule patches in other wing-dimorphic Coccinellidae, including *R. chrysomeloides,* a particularly close relative.

Similarly, the condition of palisade fringes has been investigated in more than 300 wing-dimorphic beetle species (Hammond, unpubl. obs.). Dimorphism of the fringes, paralleling that of the wings, has been found to occur in only a few species: Staphylinidae belonging to the genera *Othius* and *Mycetoporus,* and in the ladybird *Rhyzobius litura.*

Rhyzobius litura thus appears to be exceptional in exhibiting dimorphism of both wing-folding and toiletry structures. However, wing-dimorphism in certain species of Ptiliidae is accompanied by parallel dimorphism of various parts of the body which is of an even more extensive type. The incidence of wing-dimorphism in Ptiliidae had been reviewed by Dybas (1978) who recorded its occurrence in species of *Astatopteryx, Bambara, Pteryx, Ptinella, Ptinellodes* and undescribed genera. Most of the Ptiliidae in question belong to one probably monophyletic group (the "pterycine group" of Dybas, 1977: 66), and many of them are associated, at all stages of their life-history, with dead wood. In most wing-dimorphic species of Ptiliidae the morphs differ in a number of ways. Compared to the alate morph the apterous morph exhibits a reduction or loss of eye pigment, a reduction in size (or lack) of eyes, and a general reduction in pigmentation of the body as a whole, as well as absence of wings. In many instances the apterous morph is also narrower, has shorter elytra and lacks or has much reduced wing-folding spicule patches (referred to by Dybas (1978, etc.) as "finger-print whorl" patches) on the abdominal terga. In some cases apterous individuals also exhibit a shortened metasternum and lack a palisade fringe on tergum VII. Many wing-dimorphic species of Ptiliidae reproduce, at least facultatively, by thelytoky. However, in those species which are bisexual, dimorphism of wings and other features is exhibited by both sexes in an apparently identical manner (Dybas, 1978).

It has been suggested that the various reductions accompanying the absence of wings in the apterous morph of various wing-dimorphic species of Ptiliidae simply represent a means of conserving energy, releasing for reproduction energy which would otherwise be squandered on superfluous structures and behaviour (Dybas, 1978). This thesis may not provide a complete explanation for the lack or vestigial nature of various structures in apterous individuals of wing-dimorphic Ptiliidae (Taylor, 1981: 96). However, there would seem little doubt that some saving of energy could be achieved by the reduction or loss of wing-folding and toiletry devices in brachypterous or apterous individuals, where they are presumably redundant, of wing-dimorphic beetle species in general. Indeed, the condition of, for example, tergal wing-folding spicule patches in a number of wing-dimorphic beetle species, especially those in which the incidence of full-winged individuals is low, suggests that the advantages of

possessing well-developed tergal spicule patches do not always match the necessary expense. In several wing-dimorphic species of Staphylinidae (e.g. *Olophrum fuscum* (Gravenhorst), *Arpedium brachypterum* (Gravenhorst) and *Acidota cruentata* Mannerheim (in all of which macropterous individuals are relatively rare) tergal spicule patches are very small compared to those found in constantly full-winged species which are close relatives (Hammond, unpubl. obs.). The patches are, nevertheless, similarly developed in both morphs of all such wing-dimorphic species examined.

Why then is reduction or loss of wing-folding and wing-toiletry devices apparently so rarely dimorphic in expression within wing-dimorphic species? Even in the exceptional case of the Ptiliidae these ancillary structures sometimes differ little in the two morphs of a wing-dimorphic species. In *Ptinella errabunda* Johnson, for example, the individuals of one morph lack wings and eyes and are of narrower form and less well pigmented than macropterous individuals but, although apterous, still bear rather well-developed wing-folding spicule patches and palisade fringes on the abdominal terga (Hammond, pers. obs.). Wing polymorphism in most beetle families is likely to be genetically based (Lindroth, 1949; Den Boer *et al.*, 1980; Furth, 1980, etc.), and even in the Ptiliidae there is likely to be an inherited component in its control (Taylor, 1981). Dimorphism of wing-folding and wing-toiletry apparatus is also likely to be under similar genetic control. The apparent rarity of such dimorphism seems likely to stem from the ways in which the growth of flight wings and the development of tergal cuticular outgrowths are controlled genetically. An investigation of the genetical basis of wing polymorphism in *Rhyzobius litura* and *R. chrysomeloides*, accompanied in the first but not the second by dimorphism of ancillary tergal structures, might lead to some understanding of this phenomenon.

THE RELATIVE INCIDENCE OF THE WING-MORPHS OF *RHYZOBIUS LITURA* IN SOUTHERN ENGLAND

The wing-dimorphic ladybird *Rhyzobius litura* occurs virtually throughout the British Isles. Both adults and larvae may be found at the roots of and on a great variety of herbaceous plants, and are regularly to be seen in the company of aphids on which they are assumed to feed. Adults overwinter in grass tussocks, at the roots of plants and in litter (pers. obs. and records). Although found in a variety of situations *R. litura* appears to be distinctly "culture-favoured" and able to exploit the agricultural and horticultural activities of man (Bielawski, 1955). The species is often common in and around hayfields, arable land and weedy gardens.

Pope (1977) reported on the frequency of the two wing-morphs of *R. litura* in material of this species from museum collections. Of 333 British specimens examined 23 (7%) proved to be full-winged, while 31 of 104 specimens (30%) from other contries were macropterous. In the same paper Pope (1977) noted that land use, as well as climate and flora, is likely to play a role in determining local incidence of wing-morphs in the ladybird *Subcoccinella 24-punctata* (L.); he nevertheless concluded that the relative incidence of wing-morphs varies geographically in both *R. litura* and *S. 24-punctata*.

However, variation in the incidence of wing-morphs recorded for different populations of wing-dimorphic species may reflect differences in sampling
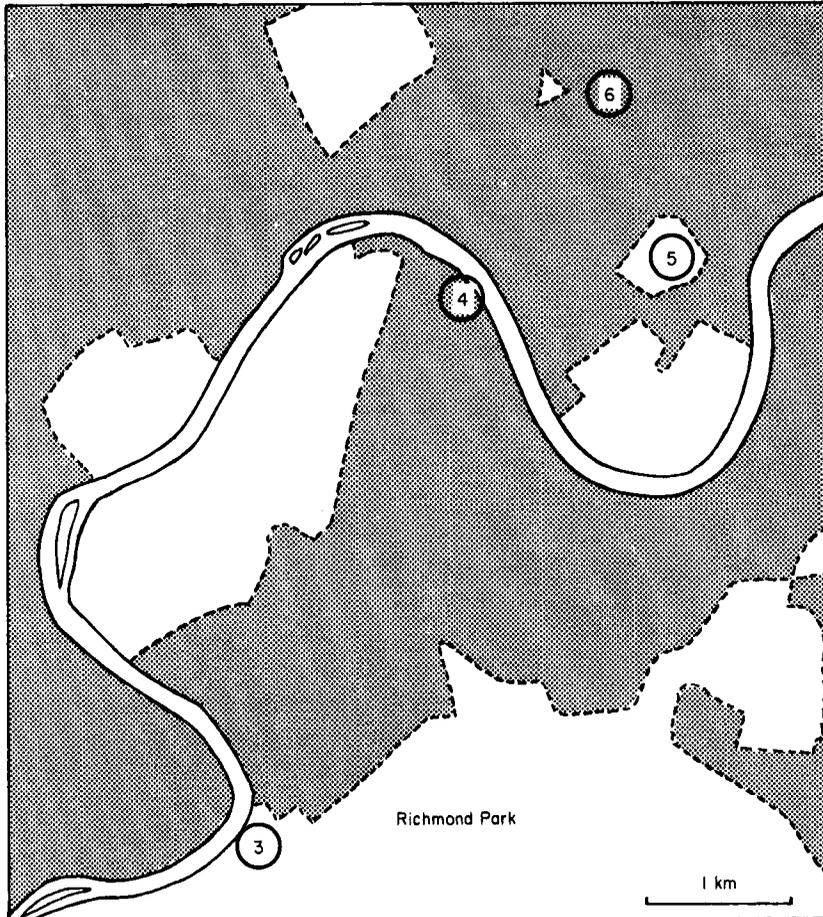
Figure 3. Sampling sites for *Rhyzobius litura* in SW London, England. Numbers (3 to 6) correspond to those given for localities listed in the text. Largely 'built-up' areas are indicated by shading.

methods, rather than real differences between the populations themselves. Particularly in the case of a culture-favoured species such as *R. litura* differences between populations may be more closely linked to the characteristics of the habitat occupied than to broad geographical location. Except for one series of samples taken at Kew, information concerning sampling methods and habitat sampled was not generally available for the museum material studied by Pope (1977). Evidence concerning the likely basis of local variation in the incidence of the two wing-morphs of *R. litura* was therefore sought in samples for which the precise provenance and method of collection were known.

Samples from six sites were studied, all of them from localities in southern England, at altitudes near to sea-level. The location of four of the sites is indicated by a map (Fig. 3), and the results of sampling at the six sites are summarized in Table 1.

The principal characteristics of each site and the methods by which samples were taken are given below.

Table 1. Samples of *Rhyzobius litura* from localities in southern England

Locality		No. of specimens	Full-winged	Brachypterous	Percentage full-winged
Site 1.	Studland Heath, Dorset	10	8	2	80
Site 2.	Burnham Beeches, Buckinghamshire	101†	36	65	36
Site 3.	Richmond, Surrey	23	1	22	4
Site 4.	Kew, Surrey	123†	0	123	0
Site 5.	Chiswick House, London W4	17†	2	15	12
Site 6.	Fishers Lane, London W4	201†	65	136	32
	Totals	475	112	363	24

*For details concerning sites see text.
†Sum of samples taken on various dates.

Sampling sites

Site 1. Studland Heath, Dorset (SZ/038862), 21 May 1977

Sample taken from shore debris on Shell Bay beach, during warm weather, with a strong wind from the neighbouring heath towards the beach. Two individuals (both brachypterous) taken on vegetation nearby (SZ/035860).

Site 2. Burnham Beeches, Buckinghamshire (SU/942866), 30 January 1977, 25 February 1977 and 18 November 1978

Samples taken from debris at the base of a haystack, flanked on two sides by a farmyard, and on the others by cow pasture and a 'stubble-field', with woodland beyond. Each sample contained a similar proportion of full-winged individuals: 16 out of 45 in the first, and 16 out of 42 and 4 out of 14 in subsequent samples.

Site 3. Richmond, Surrey (TQ/181736), 11 January 1978

Sample taken near the River Thames on a cold day from flood debris which had been deposited some two days previously. The coleopterous contents of the flood debris sample were analysed, indicating that the debris derived very largely from the surrounding area of meadows, used as pasture for cattle.

Site 4. Kew, Surrey (TQ/197772), 1965–1979

Samples taken on many dates by V. F. Eastop, swept from grass and low herbage beside a footpath. This site is relatively undisturbed and underwent few obvious changes during the sampling period (V. F. Eastop, pers. comm.).

Site 5. Chiswick House grounds, London W4 (TQ/208776), 1976–1980

This site was intensively sampled for Coleoptera during a 5 year period, but of some hundreds of litter, grass tussock and sweep samples taken only 12 contained *R. litura,* mostly as single individuals.

Site 6. Fishers Lane, Chiswick, London W4 (TQ/208786), August 1977–November 1978

Samples taken on 11 dates (see Table 2). From 1976 to mid-1978 this site (approximately square and with sides of about 80 m) was one of the few

Table 2. Samples of *Rhyzobius litura* from Fishers Lane, London W4

Date	How collected	No. of specimens	Full-winged	Brachypterous	Percentage full-winged
28.viii.1977	On plants	5	5	0	100
30.viii.1977	Swept from plants	9	6	3	67
3.ix.1977	Swept from plants	18	8	10	44
10.ix.1977	Swept from plants	13	6	7	46
18.ix.1977	Swept from plants	7	4	3	57
22.x.1977	Tussocks	2	1	1	50
13.xi.1977	Tussocks and litter	57	17	40	30
31.xii.1977	Tussocks	5	1	4	20
11.iii.1978	Tussocks	17	8	9	47
7.v.1978	Tussocks and on plants	41	8	33	20
20.v.1978	Swept from plants	27	1	26	4
Totals		201	65	136	32

relatively undisturbed areas of 'waste ground' in the built-up area of Central Chiswick (see Fig. 3). The site had formerly been occupied by houses, workshops, etc.; demolition of these had began in the early 1970s, but the major part of the site had not been cleared until 1976. While awaiting re-development the area consisted in part of open ground but, by 1977, had acquired a varied weed flora to add to the garden plants, such as *Syringa vulgaris* L. (lilac), which had survived in places amongst the rubble. Conspicuous among the weed species were Gramineae, *Chenopodium bonus-henricus* L., *Matricaria matricarioides* (Less.) Porter, *Tussilago farfara* L., *Chamaerion angustifolium* (L.) Scop., *Malva sylvestris* L., *Urtica dioica* L., *Cirsium* sp., *Solanum dulcamara* L. and various Cruciferae. From 1976 to mid-1978 much of the site remained undisturbed.

Some casual collecting of insects prior to August 1977 produced no *Rhyzobius litura*, the first being found, on aphid-infested plants of *Malva sylvestris*, on 28 August 1977. As all five of the individuals collected on this date proved to be full-winged the site was revisited periodically to take further samples (for results see Table 2). In June 1978 the site was cleared of rubble and weeds and, by October 1978, most of its area was covered by the foundations of new buildings, effectively terminating investigation of the *R. litura* population. However, a further visit to the site on 18 November 1978 produced two *R. litura* (both brachypterous), from a small isolated grass tussock left at one corner of the site.

Discussion of samples

For each of the sites from which *R. litura* samples were obtained some inferences concerning population characteristics may be drawn.

Site 1

Comment on the sample from Site 1 is included here principally because of its cautionary value. Assuming that this sample derived (as the prevailing weather conditions would suggest) from nearby, it demonstrates that the local population contains *some* full-winged individuals but provides little evidence

concerning the incidence of macroptery. The sample is small and the majority of individuals were collected *because* their ability to fly had brought them to the beach where part of the sample was taken. However, if appearing as a series of specimens in a museum collection, without precise information on the provenance of individual specimens and how the sample was taken, the series might be considered (unjustifiably) to provide evidence of a high local incidence of macroptery.

Site 2

The series of samples from Site 2 provides more reliable evidence concerning the population of *R. litura* found there, but is not without uncertainties of interpretation. The proportion of full-winged individuals was uniformly high in samples taken at Site 2 despite the fact that the dates on which samples were taken spanned almost 2 years (36% and 38% macropterous individuals on two dates in early 1977, and 29% in late 1978). A fairly high incidence of macroptery in the population from which the samples were drawn would seem to be indicated. However, it is by no means certain that the overwintering individuals collected at Site 2 represented a cross-section of the population (presumably from the surrounding fields and hedgerows) from which they came. It is possible that a favoured overwintering site recruits a larger proportion of winged than flightless individuals.

Site 3

An analysis of the beetle species collected with *R. litura* in the sample from Site 3 indicated that the sample was representative of the fauna of the immediately surrounding area. Because of the very cold conditions it is likely that few, if any, insects had left the debris from which the sample at Site 3 was taken by flying. A relatively low incidence of macroptery at this site may reasonably be inferred.

Site 4

The length of the sampling period, method of sampling and size of the overall sample taken at Site 4 would suggest that the results obtained there are representative. Macroptery is extremely rare, possibly absent, in this population.

Site 5

No obvious bias is likely to have affected the results of sampling at Site 5 and, as at Site 3, a relatively low incidence of macroptery at this site is indicated.

Site 6

The population sampled at Site 6 requires comment in a little more detail. No obvious biases were present in the sampling methods. On occasions when more than one method of sampling was employed the different methods produced similar proportions of the two wing-morphs. The results obtained at Site 6 thus provide clear evidence of a dramatic fall in the incidence of full-winged individuals there over a period of less than one year. The results summarized in Table 2 chart a decline in the proportion of full-winged individuals from 58% in August-September 1977 to 13% in May 1978. The most obvious explanation for such a rapid change in population characteristics is to be found in the

'island' nature of the site and the fact that the population, although a substantial one by August 1977 was, nevertheless, relatively newly founded. At that time the population is likely to have been composed in large part of the progeny of immigrant individuals which had flown to the site not long before, perhaps in 1976 and/or early 1977.

Assuming that wing-development in *R. litura* is under genetic control (see below), and that genes for both long and short wings were present in the population at Site 6, a relatively high level of macroptery is likely to have been maintained while the population was still expanding rapidly. Once fully established, however (i.e. by late 1977), a fall in the proportion of full-winged individuals is to be expected, as a direct consequence of a disproportionate number of flying (as opposed to flightless) individuals leaving the site. Had the site been left undisturbed a further fall in the incidence of full-winged individuals is likely to have occurred. Changes of this type in the incidence of wing-morphs are well documented for populations of wing-dimorphic ground-beetles. For example, a fall of some 20% in the proportion of full-winged individuals in a population of *Calathus mollis erythroderus* Gautier, over a 5-year period, has been reported by Den Boer (1979) for a site in Holland. The rapidity with which the relative numbers of macropterous individuals of *R. litura* fell at Site 6 indicates a high vagility on the part of winged individuals of this species, which left the site. Other contributory factors are likely to have been the relatively small size of the population, and the small size and distinctly circumscribed nature of the site occupied.

Although populations of *R. litura* are not restricted to the sites sampled (Sites 4 to 6), it is clear that the species is not at all evenly distributed through southwest London. *Rhyzobius litura* is to be found regularly in grassy hedgerows to the south and in a grassy churchyard to the east of Site 5, but has not been encountered at other sites which have been intensively collected in the area. In particular, none have been found in small gardens or amenity areas (mostly areas of mown grass) which comprise the greater proportion of 'open' land in this largely 'built-up' district. Populations of *R. litura* occupying well-defined 'islands' of suitable habitat (e.g. Site 6) may thus be expected to exhibit quite independent population characteristics.

Although unaccompanied by any breeding or experimental work the results obtained from the few samples discussed above are sufficient to demonstrate that considerable variation in the incidence of long and short winged individuals of *R. litura* occurs in the London area. Furthermore, large differences may be observed between populations which are separated by no more than 1 km. Habitat stability is likely to be the principal factor determining the relative incidence of wing-morphs at any site. A high level of macroptery may be maintained where the habitat is subject to regular disturbance (e.g. arable land at Site 2). New habitats created by changes in land use may be promptly exploited by *R. litura*. A rapid change in the incidence of wing-morphs may occur in newly-founded populations (e.g. as at Site 6); the rate and extent of such change is likely to be influenced by many factors, including population size and evenness, isolation and habitat stability.

DOES THE INCIDENCE OF WING-MORPHS VARY GEOGRAPHICALLY IN
RHYZOBIUS LITURA?

As may be seen from Table 1 the overall proportion of full-winged individuals of *R. litura* in the British samples discussed above is 24%. This differs considerably from the figure (7%) reported by Pope (1977) for British material from museum collections, and approaches that (30%) reported by the same author for other countries in Europe, N Africa, etc. What then can be deduced concerning the pattern of variation from the available evidence? Does it have a geographical basis? Populations composed entirely of brachypterous individuals seem likely to occur (e.g. at Site 4—Kew, England), but it is by no means clear that these are restricted to any one part of the species' range. A sample (of 16 individuals) from the Canaries examined by Pope (1977: 61) containing no full-winged individuals may prove to be representative of populations occurring in these islands. In southern England populations separated by no more than a few kilometres differ widely in terms of the proportion of full-winged individuals which they contain. *Rhyzobius litura* is a culture-favoured species able to exploit a range of habitats which are subject to regular disturbance by man. Wherever the species occupies a variety of habitat types, including those which are relatively stable as well as those which are much disturbed, considerable inter-population variation in levels of macroptery may be expected. Such conditions are likely to prevail through much of the species' geographical range. In order to identify any broad geographical pattern to variation in the incidence of *R. litura* wing-morphs samples from a very large number of sites would need to be examined. Evidence gathered to date, such as it is, provides no indication that the incidence of long and short winged individuals varies on a broad geographical scale throughout the species' range.

Variation in the incidence of the wing-morphs of a second wing-dimorphic species of ladybird—*Subcoccinella 24-punctata* (L.)—has been reported on by Pope (1977). Evidence that variation in this species has a geographical component seems more compelling. Only 26 (6.5%) of 400 British specimens of *S. 24-punctata* examined by Pope (1977) were full-winged, the proportion being even lower (less than 3%) if material collected before 1835 is excluded from consideration. Contrasting markedly with these figures was the incidence of macroptery in samples from the south-eastern part of the species' range; 475 (95%) of 500 specimens from Czechoslovakia, Hungary, Jugoslavia and countries further to the southeast proved to be full-winged. The incidence of macropterous individuals in samples from the Iberian peninsula and Morocco (35 specimens) was also rather high at 43%, and was somewhat variable elsewhere (208 specimens), averaging 24% for the remaining areas of Europe.

Nevertheless, large-scale geographical variation in incidence of macroptery in *S. 24-punctata* may be less convincingly demonstrated by these results than would appear to be the case at first sight. *Subcoccinella 24-punctata,* in at least part of its range, is distinctly culture-favoured, and it ranks as a pest of Lucerne in southeastern Europe. The great majority of 'southeastern' specimens reported by Pope (1977: 62), including a very large sample from Jugoslavia (424 full-winged out of 428), were collected from crop-fields or their vicinity (R. D. Pope, pers. comm.). In contrast, the majority of specimens of British origin were obtained, mostly in ones and two's by amateur coleopterists building their

collections. How representative of the *S. 24-punctata* populations of the two geographical areas in question are these samples likely to be?

That varying sampling methods and differences, from region to region, in the type of habitat sampled may have been responsible for many of the differences between samples is further indicated by the results for other countries. The proportion of full-winged individuals in Swedish samples (91 specimens) was 32%, while samples from Switzerland and Italy (30 specimens), far to the south, included only the brachypterous morph. The few specimens (5) from Syria and Iran, in the extreme southeast, also all exhibited reduced wings. If representative of populations to be found throughout the respective countries these samples would suggest a rather complex pattern of geographical variation in incidence of macroptery.

When sampling methods and type of habitat sampled are not fully documented the conclusions that may be drawn from samples of wing-dimorphic beetle species are strictly limited. Indeed, this is axiomatic if the principal factors determining local levels of macroptery are characteristics of the habitats occupied, particularly their stability. Such is likely to be the case for relatively vagile species (e.g. *Rhyzobius litura*) which are able to exploit habitats much perturbed by man. Evidence that other factors influence the incidence of long and short winged individuals of *R. litura* in most parts of its range is slight. However, if the availability of suitable but unstable habitats or the ability to exploit such habitats should vary on a broad geographical scale, variation in the incidence of macroptery may acquire a geographical dimension. This is possibly the case in *Subcoccinella 24-punctata*. If variation in the incidence of its wing-morphs does have a large-scale geographical component, regional differences in land use may be largely responsible. The strongest indication that variation in the incidence of macroptery in *S. 24-punctata* has a geographical basis, at least in part of its range, is provided by the extremely low proportion of full-winged individuals among specimens collected since 1835 in Britain. As yet no British populations exhibiting a high level of macroptery have been reported. In addition to the samples reported by Pope (1977), Crowson (1981: 425) notes that he has seen no full-winged *S. 24-punctata* in collections from southern Scotland. If a uniformly low incidence of macroptery is found to be characteristic of British populations, endogenous and climatic factors, as well as questions of land use, may be involved. Finally, it may be noted that, except in phases of population growth and expansion, populations towards the periphery of a wing-dimorphic species' range may be less uniformly distributed than in many parts of its range. In such circumstances brachyptery may be at an increased selective advantage. The same may be true of populations inhabiting certain islands. However, unusually low incidence of macropterous individuals in such circumstances may be a temporary phenomenon and may have little bearing on levels of macroptery through the major part of the species' range.

Whatever the pattern of variation in the incidence of macroptery is finally shown to be in the two ladybird species discussed above, this is unlikely to be at all faithfully mirrored by material to be found in museum collections. Such collections are frequently of use in enabling wing-dimorphic species to be identified as such. If material from many localities is present they may provide a general indication of overall levels of macroptery. If the collections include long enough series of specimens they may also indicate certain areas where

macropterous individuals are likely to be rare or absent. However, they will rarely serve to distinguish local inter-population variation from that which has a broader geographical basis. Particular caution is needed in interpreting the significance of samples containing a high proportion of macropterous individuals. If not the result of sampling methods favouring the capture of winged individuals they may still be relatively uninformative with regard to the general incidence of macroptery in the areas from which they derive.

GENERAL DISCUSSION

The assumption that wing-polymorphism in *Rhyzobius litura* (and certain other beetle species) is under genetic control has formed the basis of the greater part of the discussion above. Although this has not been investigated directly it is supported by the observed variation in incidence of the wing-morphs in space and time. However, it has been argued that assumptions concerning an inherited component in the expression of wing-polymorphism are made too readily, and that the available data for many insect species can be interpreted in terms of individual variation in threshold responses. Harrison (1980) not only adheres to this view but concludes that, "it appears that insects are not, in general, programmed to produce a particular morph but are able to respond to environmental cues". This generalization *may* prove to be applicable to certain insect groups (e.g. Orthoptera, Homoptera, Heteroptera), but seems to receive little support from evidence available concerning the Coleoptera. The breeding experiments reported by Jackson (1928), Lindroth (1946), Den Boer *et al.* (1980) and Stein (1973) indicate that for the beetle species investigated (of Curculionidae, Carabidae and Apionidae, respectively) wing length is a simple Mendelian character, with the brachypterous condition dominant. That a similar form of genetic control is prevalent in many beetle families is suggested by observations concerning the incidence of wing-morphs in numerous wing-polymorphic species: Carabidae (Darlington, 1936; Lindroth, 1949, etc.; Thiele, 1977; Den Boer, 1970, etc.); Coccinellidae (Pope, 1977; this paper); Chrysomelidae (Furth, 1980; Shute, 1980); Staphylinidae, Pselaphidae, Cryptophagidae, Dytiscidae (Hammond, unpubl. obs.). It might reasonably be expected that other groups of holometabolous insects resemble the Coleoptera in this respect. For groups such as the Heteroptera, however, generalizations may be unwarranted, as control of wing-length seems to be particularly variable (Slater, 1977; Vespälainen, 1978). For example, in wing-polymorphic species of the genus *Gerris* brachyptery is the expression of a single dominant allele (as in *Sitona*—Jackson, 1928) in some cases, while variation in wing development is polyphenic in others (Vespälainen, 1978).

In one family of beetles—the Ptiliidae or featherwing beetles—wing polymorphism is exceptional in that it is commonly accompanied by polymorphism affecting the development of the eyes, of pigmentation and other features (Dybas, 1978, and see above). Dybas (1978) considered it likely that production of alate and apterous individuals in species of this family is environmentally cued. This view is lent some support by the observation that in populations inhabiting decaying wood (the habitat of many wing-polymorphic ptiliid species) winged individuals appear to be relatively *less* frequent *early* in a

succession. However, an inherited component in species of *Ptinella* is suggested by breeding experiments conducted by Taylor (1981), who found that alate parents produce a significantly higher percentage of alate progeny than do apterous parents under the same conditions. Taylor (1981) also demonstrated seasonal variation in the incidence of morphs in field collections of *Ptinella* species (increasing in abundance in the summer), and found that the incidence of macropterous individuals varied with temperature in laboratory cultures of *P. aptera* (Guérin-Meneville). She concluded that these latter results implied the involvement of a physiological switch in morph determination. However, not all eggs of *P. aptera* in laboratory culture are viable, and mortality of eggs (and/or larvae) might vary independently, with temperature and other environmental factors, between genetically determined morphs, thus simulating a purely environmental effect.

Other objections to the view that wing-polymorphism is at all frequently under genetic control stem from a belief that dispersal by flight occurs *prior* to reproduction in most insects. Behaviour of this type (reproduction following flight) implies some difficulty, where inheritance is of a simple Mendelian kind with short wings dominant, in dispersing genes for brachyptery. Newly founded populations (of winged individuals) would need to "acquire the allele for short-wings either through mutation or through gene flow dependent on dispersal mechanisms other than flight" (Harrison, 1980: 103), seemingly unreliable if not unlikely ways of maintaining a genetic polymorphism. However, the view that dispersal generally precedes reproduction receives little support from the available evidence as it relates to the Coleoptera. For example, Den Boer *et al.* (1980) report the capture in flight of fertilized females of a number of species of Carabidae, both wing-polymorphic and constantly macropterous. Of 26 monomorphic macropterous species studied, only one—*Amara plebeja* (Gyll.)—conformed completely to the oogenesis flight syndrome (i.e. only unfertilized females fly; with the onset of reproduction flight ceases, to be resumed only when reproduction is completed). Furthermore, *A. plebeja* appears to be something of a special case, the pre-reproduction flight in this species being connected with dispersal from overwintering sites to those where reproduction regularly takes place. Indeed, where flight is important for the dispersal of bisexual species, fertilization of females prior to dispersal flights might be expected to be the norm.

The relatively low incidence of full-winged individuals in many populations of wing-dimorphic beetle species (see below) implies a greater likelihood of a resident winged female mating with a male lacking genes for macroptery than one lacking genes for brachyptery. Fertilization of females before dispersal will thus ensure that most newly founded populations contain genes for brachyptery as well as macroptery from the outset.

Den Boer *et al.* (1980) have discussed the circumstances in which the development of wing-polymorphism in ground-beetles will be favoured by natural selection, and have shown how selection will tend to produce a strict dimorphism in many species with time. As a consequence of the same processes macroptery is likely to become a recessive character in the long run in most, if not all, wing-dimorphic species. Nevertheless, the frequency of full-winged individuals may be maintained at a relatively high level in at least some parts of the range of species whose populations inhabiting unstable habitats are of

sufficient number and size. *Rhyzobius litura* appears to be a species of this type. However, without the intervention of man, whose activities may be responsible for disturbances to stable habitats and the creation of many suitable but unstable habitats, a high frequency of macropterous individuals is rarely observed in wing-polymorphic beetle species. For example, only nine of 30 wing-dimorphic species of Carabidae studied by Den Boer (1977) exhibited levels of macroptery exceeding 20%, whereas the frequency of macropterous individuals was below 3% in 16 species. This study was conducted in Holland where the contribution of unstable man-made habitats to high frequencies of macroptery in some species may be expected to be considerable.

If the great majority of suitable habitats in a geographical area are stable the frequency of macropterous individuals in wing-dimorphic species will generally be driven towards very low levels. However, a low but continuous production of recessives may prevent the frequency from becoming zero. A good example of this phenomenon seems to be provided by the staphylinid *Arpedium brachypterum* (Grav.). In the British Isles this species is more or less restricted to moorland and mountain-sides where it is found in moss and ground-litter. I have examined some 1500 British specimens of *A. brachypterum*, from more than 100 different sites; only one specimen—a female taken in flight at Arnfield, Cheshire in July 1933—proved to be full-winged! In species of this type genes for macroptery may be lacking in large parts of its range.

Geographical variation in the incidence of macroptery in wing-dimorphic species is possible on a variety of scales. In some instances variation may be seen to reflect significant aspects of a species' recent history, such as extensions or retractions of range (lindroth, 1963). In other instances the pattern of geographical variation is complex and its origins less readily understood. Observed variation in the staphylinid *Anthobium unicolor* (Marsham) provides an example. This species is common in ground-litter in most parts of the British Isles; it is to be found in both wooded and open country over a wide altitude range, but tends to avoid habitats much perturbed by man. It exhibits a generally modest level of macroptery, often in the region of 10%. Available data are inadequate to reveal any variation on a broad geographical scale, but extensive sampling of moorland sites in northern England has shown that the incidence of macroptery there varies greatly from area to area (Hammond, unpubl. obs). Pitfall trap samples from three localities in the northern Pennines (north of Weardale) exhibited a high incidence of full-winged individuals, averaging 47% (out of 400 individuals). Similar samples from eight localities in the North York Moors (some 60 km to the east) exhibited even higher levels of macroptery, with 74% (out of 265 individuals) full-winged. However, samples from six sites some 50 kms to the south (between Swaledale and Wensleydale) contained few full-winged specimens, averaging only 2% (out of 568 individuals). In each of these three areas between-site variation was relatively small, and at each site the incidence of macroptery remained more or less steady over a 3-year study period (1976–1978). One may conclude from these results that the recent history of populations in the three areas has differed and that gene flow between the areas (but not between sites within an area) is likely to be small. No obvious correlations between environmental factors and the relative incidence of macroptery at the various study sites has been noted. The differences in levels of macroptery in this case appear to have a genuinely

geographical basis, although on a relatively small scale, but may prove to be of a (relatively) temporary nature. Their origin is quite likely to remain obscure.

It has been widely recognized (Southwood, 1962; Stein, 1977; Vespälainen, 1978, etc.) that flight polymorphism in insects is likely to arise as an adaptation to environments which vary in stability. Less frequently stressed is that, if under genetic control, such polymorphism is unlikely to be advantageous, where habitats occupied are particularly unstable. Insect species which utilize ephemeral and patchy resources (e.g. carrion, dung, many types of flowers or fruits) rarely exhibit wing polymorphism. It is in habitats which remain suitable for occupation for longer periods and which are less patchy (with a greater average patch size), but nevertheless prone to become rather abruptly unsuitable, that wing-polymorphic species seem to be most evident. In particular, wing polymorphism caters well for the needs of species in which dispersal by flight is relatively infrequently required for a population's genes to be saved from extinction. Genetically based wing polymorphism not only serves variable dispersal needs in the short-term but enables a species' dispersal power to be adjusted in accordance with longer term changes in the types of habitat which are occupied.

Little information concerning the incidence of wing-polymorphism in beetles has as yet been collated, and even less is known of how the proportion of full-winged individuals varies between populations, geographically, and with time. However, where flight ability is under genetic control, the essential characteristics of wing-dimorphic populations will vary little. Genes associated with the ability to fly will be removed from a population by flying individuals and, frequently, will not be replaced by new arrivals. New populations will mostly be founded by flying individuals. How these population characteristics affect a species' future will depend on its vagility and the nature of habitats occupied: their stability, patchiness and patch size.

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