

Best wishes, ✓

Jon

Colour patterns of Syrphidae. III. Sexual dimorphism in *Eristalis arbustorum*

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ABSTRACT. 1. The hoverfly *Eristalis arbustorum* L. (Diptera, Syrphidae) is a sexually dimorphic Batesian mimic of bees and wasps.

2. This dual mimicry entails good mimicry of several small, dark bees (mainly mining bees) by female *E. arbustorum*, and less specific mimicry of wasps and other yellow and black Hymenoptera by males.

3. There is also variability of colour pattern within both sexes of *E. arbustorum*.

4. Seasonal fluctuations in the pattern frequencies of males occur because the temperature during pupal development influences the coloration of the adult.

5. Temporal changes in the pattern frequencies of females are attributable to developmental darkening of the abdomen.

6. These effects can be explained by the fact that the phenotypic requirements for thermoregulation and protection against predation will be different for males and females, and will also vary with time.

7. Behavioural differences between males and females are a component of the sexual dimorphism in this species.

Introduction

In addition to their morphological differences, males and females of any bisexual species will differ in behaviour. If behaviour affects the relative advantages of alternative colour patterns, this may lead to sexual dimorphism in appearance. Batesian mimicry, the resemblance of an edible mimic to a protected model, occurs in many day-flying species of insect. Mimetic patterns are restricted to females in some butterflies, e.g. *Papilio dardanus* Brown and *P. glaucus* (L.). The non-mimetic male patterns may be maintained because of their significance in courtship (Sheppard, 1961). In two hoverflies that mimic bees (*Merodon equestris* Fab. (Conn, 1972), *Eristalis tenax* L. (Heal, 1979a)) the frequencies of certain colour patterns differ

between the sexes, owing to differential expression of certain alleles. However, genetic polymorphisms in these two species ensure much variability within wild British populations.

Another common Syrphid, *Eristalis arbustorum* L., has a sexual dimorphism, but there is some variation in coloration in both sexes. The females are darker, but they have pale pubescence over the body and unpigmented bands at the rear edges of the abdominal tergites. This creates a resemblance to several solitary bees. Many smaller mining bees of the genera *Colletes*, *Andrena* and *Halictus* are pale-haired and also have white bands on a black abdomen, but the bands are formed by rows of short appressed hairs rather than by unpigmented cuticle. All of these insects look broadly similar to very small workers of the darker varieties of honeybee (*Apis mellifera* L.).

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Male *E. arbustorum* usually have extensive yellowish areas at the sides of an otherwise black abdomen, and light yellow thoracic hair. In flight, this coloration can produce some resemblance to a worker wasp, particularly when the male is flying around a patch of flowers in search of females. A visual form of yellow patches on either side of a black body also occurs when a mining bee is carrying a load of pollen on each hind-leg; the bee would be female, and owing to its sting it could serve as a model for male *E. arbustorum*. If the fly is at rest on a yellow flower, the lateral yellow markings may merge into the background, so that one sees an apparently constricted body, with a generalized resemblance to aculeate Hymenoptera. *Eristalis arbustorum*, and other *Eristalis* species, were shown to be quite acceptable as food when given to captive passerines (Heal, 1977, 1979b) and so any mimicry involved is Batesian rather than Müllerian.

E. arbustorum is common in many habitats, both urban and rural, but is perhaps most frequent in moderately open areas of disturbed ground, e.g. derelict land in cities, gardens and hedgerows. The adults feed at a wide range of flowers, but especially at Compositae such as *Achillea*, *Tripleurospermum*, *Cirsium* and *Senecio*. These flowers also attract several species of solitary bees, which are excluded from flowers where pollen and nectar are less accessible because they have relatively short probosces.

The flight period of *E. arbustorum* extends from April to early November (in northern England); winter diapause occurs in larvae of late broods (Weise, 1938). In optimal conditions three generations per year would be possible; in the laboratory the time from laying of the egg to emergence of the adult can be less than a month. The larvae feed in rotting organic matter, usually of animal origin (Hartley, 1961). Data on diapause in laboratory broods suggested that the photoperiod experienced by the parent female is relevant to diapause induction (Heal, 1977), as is the case for the blowflies *Lucilia sericata* and *L. caesar* (Cragg & Cole, 1952; Ring, 1967).

Eristalis arbustorum has an extensive geographical distribution which includes all of Europe and parts of Asia and North America (Kanervo, 1938). This paper deals with English populations only, and shows that

different factors are responsible for the variability of abdominal pattern in males and in females. Hypotheses deduced from field results were shown to be applicable by laboratory experiments.

Materials and Methods

Sampling and breeding

The principal sampling sites were: (i) from 1972 to 1976, areas of waste ground in Liverpool on which there was much *Senecio squalidus* L. and *Tripleurospermum maritimum* (L.) Koch, and (ii) from 1976 to 1979, the campus of Keele University, comprising various habitats, with both cultivated and uncultivated patches of flowers. Besides regular collections of adult flies, further field observations were made throughout each year on the numbers of each phenotype and their behaviour.

The rearing techniques for *Eristalis arbustorum* are similar to those used successfully for *Eristalis tenax* and *E. intricarius* (Heal, 1979a, b). Adults were kept on a diet of pollen and honey, either in transparent plastic containers or in cages with wooden sides and netting covers. Captured females often laid eggs in tubes of rotting plant material or moist faeces, both of which were satisfactory as larval medium. The eggs were transferred to larger quantities of medium; they were 1.3 mm long and, if fertile, hatched after 2 days. Few laboratory crosses were done because *E. arbustorum* did not survive as well as *E. tenax*. For experiments on the effects of pupal temperature, pupae were removed daily and divided into equal groups for incubation at different temperatures.

Colour patterns: classification

The abdominal patterns of *E. arbustorum* vary considerably. Yellow areas at the sides of tergites 2–3 can be extensive or absent. This range of pigmentation is continuous but was divided into six arbitrary grades, defined as follows (see Fig. 1):

- vlt* (very light). Most of tergites 2–3 yellowish, with median black band.
- lt* (light). Yellow areas reduced such that black extends to both sides of tergite 3.
- mlt* (mid-light). Light areas on tergite 3

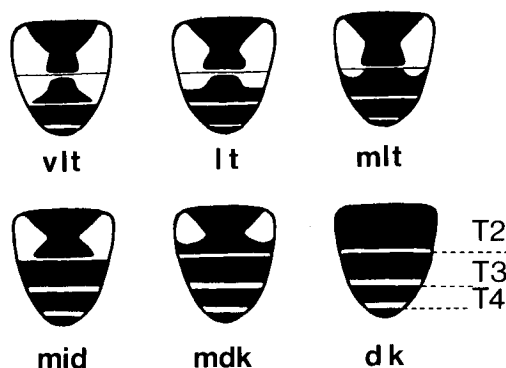


FIG. 1. Classification scheme for abdominal patterns of *Eristalis arbustorum*. Tergites 2–4 are indicated (T2, 3, 4); the first segment is small and lies beneath the scutellum. Shaded areas = black. Unshaded = yellowish or orange, except for bands at the rear of the tergites, which are usually white.

restricted to pair of small spots in anterior half.

mid. Yellow triangular markings on tergite 2, but no yellow on tergite 3.

mdk (mid-dark). Grey obliterating parts of the light markings, which do not reach the unpigmented band along the rear margin of tergite 2.

dk (dark). Abdomen extensively black, except for white bands at rear of tergites.

Generally, males are of the three lighter grades, and females are of the three darker grades. Amongst males, the paler areas tend to be light yellow when extensive, but more orange when smaller. For females as well, reduction in size of the markings is associated with a duller colour. On tergites 2–4 there are unpigmented strips of cuticle along the rear margins; these pale bands are broader in females and made more conspicuous by a layer of silvery dust over the unpigmented region.

There is little variability in the appearance of the thorax. It is grey-brown and has a moderate covering of hairs, which are light yellow on males and rather pale on females; the hair colour is most easily seen at the sides of the thorax.

Field results

In Liverpool, *Eristalis arbustorum* was recorded from 4 April to 7 November, but

the maximum abundance at the urban sites was attained between mid-July and late September. The population in the more rural area at Keele declined earlier; the flight period recorded there was only 28 April to 14 October.

E. arbustorum was very susceptible to cold draughts when kept in the laboratory, and so one factor limiting its survival could be low temperatures at night. The urban habitat offers warm sheltering-places in late autumn. Also, the Liverpool sites provided flowers attractive to the flies from March to December, whereas the availability of food sources in rural areas fluctuates greatly during the year. At Keele, there were only a few suitable patches of flowers remaining by October. It is not known whether there is any specific migration into towns at this time of year, but *Eristalis* are highly mobile Syrphids and thus would be expected to move away from areas of low profitability.

The sample sizes in Tables 1–3 are not intended to be an accurate indication of population density in each month; apart from differences in the time spent sampling, the number of active flies is greatly influenced by the weather. Mean pattern scores for males (\bar{m}) and females (\bar{f}) have been calculated by putting $dk = 1 \dots vlt = 6$, and taking average values.

(i) Colour patterns of males

Table 1 summarizes the samples of *Eristalis arbustorum* collected in Liverpool during 1975–76. Most males were of the *lt* grade. Males with *vlt* patterns were found only in the middle of the flight period, i.e. July–September, but the darker grades (*mlt* and *mid*) were frequent in spring and late autumn. This suggests some relationship between male pattern and temperature, with duller flies occurring in cooler months. Similar results were obtained at Keele in 1978 (field observations only) and 1979 (samples collected), see Tables 2 and 3. The predominance of lighter patterns in the period of abundance was clearest in the exceptionally warm summers of 1975 and 1976; the scarcity of *vlt* males in 1979 may have been due to the cool weather of that summer.

The presence of these steady changes in pattern frequencies implies that flies are

TABLE 1. *Eristalis arbustorum* collected from sites in central Liverpool. Sampling ceased in August 1976. Sample sizes in each month are not an accurate indication of population density.

	Males				Females			Mean values*	
	<i>vlt</i>	<i>lt</i>	<i>mlt</i>	<i>mid</i>	<i>mid</i>	<i>mdk</i>	<i>dk</i>	\bar{m}	\bar{f}
1975									
April	0	0	2	0	0	2	0	4.00	2.00
May	0	4	5	2	3	6	0	4.17	2.33
June	0	0	1	0	0	0	0		
July	1	9	2	0	4	1	2	4.92	2.29
August	5	30	1	0	12	2	3	5.11	2.53
September	10	31	0	0	6	4	15	5.24	1.64
October	0	13	11	0	0	1	7	4.54	1.13
November	0	5	4	0	0	0	3	4.55	1.00
1976									
April	0	0	1	1	0	1	1	3.50	1.50
May	0	2	9	2	0	4	1	4.13	1.80
June	0	2	0	0	0	0	0		
July	3	14	0	0	3	1	0	5.18	2.75
August	3	5	0	0	5	2	2	5.38	2.33

* Mean pattern values for male (\bar{m}) and female (\bar{f}) samples are calculated from scores of: $dk = 1 \dots vlt = 6$.

TABLE 2. Comprehensive data from field observations of *Eristalis arbustorum* at Keele University campus, 28 April 1978 to 10 October 1978.

	Males				Females			Mean values*	
	<i>vlt</i>	<i>lt</i>	<i>mlt</i>	<i>mid</i>	<i>mid</i>	<i>mdk</i>	<i>dk</i>	\bar{m}	\bar{f}
April	0	0	0	0	0	1	0	—	2.00
May	0	7	12	1	3	3	7	4.30	1.69
June	0	6	6	1	0	1	6	4.38	1.14
July	5	53	12	0	28	20	14	4.90	2.23
August	6	19	6	0	12	6	15	5.00	1.91
September	1	15	2	0	22	11	11	4.94	2.25
October	0	2	1	0	2	3	5	4.67	1.70

* Calculated as in Table 1.

TABLE 3. Samples of male *Eristalis arbustorum* collected at Keele between 9 May and 4 October 1979.

	<i>vlt</i>	<i>lt</i>	<i>mlt</i>	<i>mid</i>	Mean values \bar{m}	Comparisons between months*
May	0	0	5	0	4.00	$P < 0.06$
June	0	15	13	2	4.43	
July	0	18	2	0	4.90	n.s.
August	1	28	1	0	5.00	
September	0	10	4	0	4.67	$P < 0.05$
October	0	0	1	0		

* Comparisons made between numbers of (*vlt* + *lt*) and (*mlt* + *mid*) in successive monthly samples, using χ^2 or Fisher's exact probability. n.s. = not significant.

emerging throughout the flight period, without any discrete generations. Reproduction occurs rapidly while favourable conditions persist.

(ii) Colour pattern of females

Examination of female pattern frequencies in Tables 1 and 2 does not reveal the same simple seasonal trends as for males. During most of the flight period females of the three darkest grades (*mid*, *mdk*, *dk*) were present. However, in the first week of August 1975 there was a marked increase in the numbers of *E. arbustorum* at the Liverpool sites. Judging by the fresh condition of their wings, these were mainly recently emerged flies rather than migrants, although some migration to better habitats soon after emergence is quite likely to occur as well. At that time the majority of females had *mid* patterns, but the frequency of *mid* steadily declined and by late October nearly all females were of the darkest grade (see Table 4). Most flies caught in October or November showed signs of age; their wings were ragged and heavily infuscated with brown. The data recorded at these urban sites in the autumns of 1973 and 1974 showed a similar trend.

If lower temperatures produced darker abdomens (in newly emerged females), *dk* patterns should be more frequent in spring. The correct interpretation of the variation seems to be that at emergence most females are *mid*, but the abdomen subsequently

darkens and the yellow markings are obscured (see below). A temporal change in frequencies is not so obvious in the first generation of the year as in late autumn, because females from diapaused larvae are emerging in small numbers over several weeks. However, the 1978 field observations at Keele (Table 2) suggest that overwintering female larvae emerged as adults in May, had darkened in June and were being succeeded by their offspring in July.

Experimental results

Studies of wild populations of *E. arbustorum* suggested that: (i) male patterns vary with rearing temperature, and (ii) female patterns vary with age. These two hypotheses were tested experimentally.

Several broods were raised from eggs laid by captured females. When reared on ample larval medium in the laboratory, the sex ratio was usually close to unity and there was no tendency for one sex to emerge earlier than the other, except in a few broods containing many diapausing larvae, where there was a substantial excess of females in the larvae which did not diapause. At temperatures around 18°C female progeny had *mid* patterns and most males were of the *lt* grade.

(i) The effect of pupal temperature

The larvae of each brood were reared together, but shortly after pupation the

TABLE 4. Estimates of female pattern frequencies from field observations in Liverpool, August to October 1975. Data for the Crown Street site are given as totals for groups of four consecutive visits, following an increase in abundance of *E. arbustorum* in early August.

Dates	<i>mid</i>	<i>mdk</i>	<i>dk</i>	% <i>mid</i>	\bar{f}
(a) Crown Street site					
8–21 August	40	14	16	57.1	2.34
23–30 August	31	25	27	37.3	2.05
1–8 September	35	30	36	34.7	1.99
12–18 September	17	19	49	20.0	1.62
23 September–4 October	1	7	48	1.8	1.16
15–27 October	0	0	26	0	1.00
(b) Other sites in Liverpool					
August	25	14	29	36.8	1.94
September	17	18	27	27.4	1.84
October	0	0	13	0	1.00

For (a), regression of \bar{f} on date, $b = -0.021 \pm 0.002$. Rank correlation between \bar{f} and date, exact $P = 0.003$.

TABLE 5. Summary of experiments on the effect of pupal temperature on adult coloration in *E. arbustorum*.

Temperature* (°C)	% survival of pupae	Patterns of adult flies							
		Males				Females			
		<i>vl</i>	<i>lt</i>	<i>mlt</i>	\bar{m}	<i>mid</i>	<i>mdk</i>	<i>dk</i>	\bar{f}
25	74	32	4	0	5.89	62	0	0	3.00
20–25	59	14	9	0	5.61	27	0	0	3.00
15–20	79	38	72	1	5.33	122	1	0	2.99
5–15	41†	7	30	16	4.83	53	5	6	2.73
Coefficient (<i>b</i>) for regression of mean value on temperature		0.068 ± 0.005				0.018 ± 0.006			
For deviation of <i>b</i> from 0, <i>t</i> =		13.9 (<i>P</i> < 0.01)				2.9 (<i>P</i> > 0.1)			

* When not constant, average incubation temperatures were taken.

† Survival was only 4% when the temperature was maintained below 8°C.

puparia were removed and divided between two or more incubation sites differing in mean temperature. Constant incubation temperatures were not always available, so data have been grouped according to whether the average temperature was 15°C or less 15–20°C, or over 20°C. The consistency of the trends allowed summation of results from various sources (Table 5).

The pigmentation of adult males was clearly influenced by the temperature experienced as a pupa. Low temperatures yielded darker patterns, high temperatures gave mainly males of the lightest grade. This accounts for the seasonal changes in pattern frequencies in samples of wild males. Nearly all newly emerged females were scored as *mid*,

but a few darker ones were obtained in cooler conditions. At around 5°C very few puparia gave rise to adults.

(ii) The effect of age

At a range of temperatures females had *mid* markings when their abdominal pigmentation developed a few hours after emerging from the puparium, but darker patterns were present in stocks that had been in the laboratory for a few weeks. In one brood, nine females that survived less than 37 days were still *mid*, whilst others surviving between 53 and 112 days were finally scored as four *mdk* and five *dk*. Therefore females can darken with age, the side-markings on tergite 2 changing

TABLE 6. Final patterns of female *Eristalis arbustorum* kept in cages on a diet of pollen and honey. All were initially of the *mid* grade. Only flies surviving over 30 days in the cages are included.

Temperature† (°C)	Males in cage	Final patterns*			Maximum periods (days)	
		<i>mid</i>	<i>mdk</i>	<i>dk</i>	No change of pattern	Survival
(a) Wild females, scored as <i>mid</i> at capture						
20–25	See note ‡	2	2	0	36	43
15–20	See note ‡	2	0	4	55	55
(b) Virgin females, bred in captivity						
20–25	Present	7	0	0	69	69
15–20	Present	0	0	4	29	62
15–20	None	0	3	1	30	57

* Comparing the proportion of females (both bred and captured) that darkened (i) above 20°, and (ii) below 20°, Fisher's exact *P* = 0.001.

† Average daytime temperatures (night-time temperatures may often have been lower).

‡ Captured females – most probably these would have mated in the wild.

from yellow to black. No comparable process was recorded amongst males, but similar darkening did occur in females of the related species *Eristalis nemorum* L.

Darkening of the cuticle did not occur at the same rate in all female *E. arbustorum* (see Table 6). It was more rapid in cooler conditions, and inhibited at 25°C. Some pollen in the diet seemed necessary for the colour change, but survival was, in any case, poor when *E. arbustorum* were kept on a diet consisting of only honey. Normally the *mid* to *dk* transition took at least 4 weeks, by which time the ovaries should have matured, and in natural conditions oviposition might have begun. However, a single virgin *dk* female shows that mating is not essential for darkening. Another female laid several batches of eggs but was still *mid* after 10 weeks at 25°C. Nevertheless, it is still possible that in the wild the change of pattern is linked to some modification of behaviour when the *E. arbustorum* female is ready to oviposit.

The experimental data provide evidence that the increasing *dk* frequency in Liverpool during autumn results from developmental changes in ageing females, but generalizations must be made cautiously. The experiments described above were done with a Liverpool stock, but when repeated with a Keele stock the cuticular darkening was very much slower. An autumnal trend towards darker females was also less apparent in the Keele population (Table 2). Regrettably, the great mobility of *E. arbustorum*, and many other Syrphids, renders them unsuitable for mark-release-recapture experiments, so that field data on the longevity and the changes in pattern or behaviour of individual flies would be rather difficult to obtain.

Discussion

Monomorphism is common amongst Syrphidae that resemble wasps, but many bee-like hoverflies are polymorphic. Variation in both the abdominal patterns of the *Apis*-mimic *Eristalis tenax* and the thoracic pubescence of the *Bombus*-mimic *E. intricarius* are determined primarily by segregation of alleles at major gene loci, although in each case there is some environmental modification of expression (Heal, 1979a, b). Apart from the genetic-

ally determined sexual dimorphism, most of the phenotypic variation in *E. arbustorum* is attributable to environmental and developmental effects, which lead to seasonal changes in the frequencies of colour patterns in wild populations. The mimicry is also less specific, with some resemblances to both smaller bees and wasps.

Owing to the influence of temperature during the pupal stage, *E. arbustorum* males that emerge in the warmest months have brighter markings. The darker appearance of the earliest males each year is due to cooler spring temperatures rather than any direct effect of diapause. Dusek & Laska (1974) have shown a very similar effect of pupal temperature on the adult patterns of four yellow and black hoverflies: *Metasyrphus corollae* (Fabr.), *M. luniger* (Meig.), *Episyrphus balteatus* (De G.) and *Sphaerophoria scripta* (L.). Changing temperatures are also a secondary factor promoting variability in polymorphic populations of *E. tenax* (Heal, 1977).

As regards female *E. arbustorum*, there was only a slight trend to duller initial patterns at low temperatures (but note the high frequency of *mdk* in spring, see Tables 1 and 2). However, even when recently emerged from puparia, female *E. arbustorum* have more restricted areas of light cuticle than males, and these light areas may then darken during the next few weeks. Although the biochemical nature of the colour change was not investigated, it is probably a secondary melanization. Fuzeau-Braesch (1966) has shown that new melanin formation unassociated with ecdysis can be induced in *Locusta migratoria* by rearing them on a dark background.

The pigmentation of animals can influence: (i) their susceptibility to predation, (ii) thermoregulation, and (iii) courtship. Reduced predation on mimetic morphs is a tenet of Batesian mimicry, but this protection may be balanced by reduced mating success, sometimes giving rise to polymorphism with mimetic and non-mimetic morphs, e.g. the butterflies *Papilio glaucus* and *Hypolimnas misippus* (Turner, 1977). The mating behaviour of *Eristalis* species, in which a male finds and pursues a female, may render the male's coloration unimportant in courtship. The visual acuity of Syrphids may be inadequate to discriminate between the extremes of pattern amongst female

E. arbustorum. Males will sometimes chase insects of similar size and shape as a female; behavioural cues seem more important than pattern discrimination in subsequent attempts to mate whilst in flight.

Thermoregulation in insects can be achieved by appropriate changes in posture and position, as in *Colias* butterflies (Watt, 1968) and in the dragonfly, *Libellula saturata* (Heinrich & Casey, 1978). *E. arbustorum*, and other *Eristalis* species, spend much time basking on herbage, allowing their body temperature to be raised by radiant energy. Watt (1968) showed that darker *Colias* adults warm up more quickly than pale ones. Some comparable measurements are needed to determine whether darker hoverflies have an appreciable advantage where there is limited direct sunshine, but this is suggested by the seasonal changes in male pattern frequencies in *E. arbustorum*, with darker patterns present in cooler months (Tables 1–3). Duller flies are also less conspicuous and so less likely to attract the attention of a predator when perched on a leaf in an exposed position. The corollary of this is that some opposing factor favours brighter patterns in warmer months; this appears to be mimicry of aculeate Hymenoptera.

A male *E. arbustorum* with *vlt* or *lt* markings seems only a crude mimic of a wasp when at rest, but in flight the partial resemblance afforded by areas of yellow and black cuticle would be a deterrent to visual predators. In experiments involving captive passerine birds, even a partial mimicry of bees and wasps was effective (Mostler, 1935; Heal, 1977). The flight itself also improves the resemblance; a male *E. arbustorum* touring patches of flowers in search of receptive females can be mistaken for a wasp searching for prey.

One presumes that the advantage of the mimicry is greatest when large numbers of wasp workers are active (i.e. July–September). The lighter male patterns do predominate in this period. *Eristalis arbustorum* are also most abundant in these months.

When present at patches of flowers, females spend less time than males in flying about, and more time in feeding. Consequently, their mimetic resemblance is to the numerous smaller species of solitary bees which have a dark thorax bearing pale

pubescence, and an abdomen which is black apart from narrow white bands on each tergite. These bees can be found at many of the weedy flowers that *E. arbustorum* visit. Species of *Colletes* and *Megachile* occurred at the Liverpool sites, *Andrena* and *Halictus* at the Keele sites. Although the mimicry is very good, especially for a *dk* female, the protection is limited by the bees' unpredictable abundance, varying from year to year, and their relatively weak stings.

The change from *mid* to *dk* pattern may be associated with altered behaviour when the ovaries have matured, as suggested above. Some tendency for *dk* females to be in more sheltered areas was noted, and the more rapid development of darker pigmentation in cool conditions implies that an increased capacity for heat absorption is relevant. The particular value of the *mid* pattern has not been clarified but the following speculation is offered: if old and ragged *dk* females are taken more easily by predators, there would be some advantage to fresh females in not looking exactly the same, especially if models were scarce, or mimics abundant, and the mimetic protection reduced. In the populations studied, variability was, in fact, greatest when *E. arbustorum* were numerous, less when they were uncommon.

This paper has emphasized the relevance of behaviour to mimetic variation, especially to the sexual dimorphism. A case of mimicry limited to males is described by Hespeneide (1975); his explanation is that males of the beetle *Chrysobothris humilis* sit in exposed positions, whilst females are hidden in the vegetation. In butterflies, sex differences in behaviour and habitat choice may favour mimicry restricted to females, or dual mimicry of different models by male and female. However, sex-limited female mimicry may usually occur because reduced mating success of mimetic morphs is less serious for females than for males, if females only need to mate once (Turner, 1977).

A modified form of dual mimicry exists in *Eristalis arbustorum*. Perfect wasp-mimicry is not attained by males because its obvious advantage for active flies is counterbalanced by the benefits of inconspicuousness at rest and better thermoregulation when sunny spells are limited. The bee-like form of females reflects their bee-like behaviour – at flowers,

foraging only, and not chasing other insects — but the mimetic resemblance to solitary bees is improved during the life of the female. Since males, young females and old females have different requirements, they will behave differently, with the variation in pigmentation a further consequence. This raises the question of whether there may also be unnoticed behavioural differences between mimetic morphs of species with genetic polymorphisms, possibly with loci affecting behaviour associated with supergenes for colour pattern.

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