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COLOUR PATTERNS OF SYRPHIDAE: IV. MIMICRY AND VARIATION IN NATURAL POPULATIONS OF *ERISTALIS TENAX*

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SUMMARY

The dronefly, *Eristalis tenax* L., and the honeybee, *Apis mellifera* L., are similar in their general form, flight and coloration. Experiments with captive birds showed that *E. tenax* are very palatable, although they may be avoided if given after honeybees. Thus the mimicry is of the Batesian variety.

Both model and mimic vary in colour pattern. Although the phenotypic variation is continuous, in both species it is also bimodal owing to genetic polymorphisms which are modified by other factors. In north-west England the overall percentage of "light" patterns was roughly 50 per cent, both in the model and in the mimic. Pattern frequencies in *E. tenax* were fairly consistent between samples, as expected for a highly mobile species, but honeybees showed local fluctuations. In spring, *E. tenax* was less variable, and much less numerous, than it was in autumn.

Although similar in colour, the markings on the abdomens of the two species differ in shape. Possible reasons why *Eristalis tenax* has not evolved a more exact resemblance to *Apis mellifera* are that the modified patterns derive some added protection from a partial mimicry of wasps, and that they are more effective in temperature regulation.

1. INTRODUCTION

DIVERSITY is most easily understood when the benefits of alternative phenotypes can be visualised. For this reason, students of evolution have long been attracted to insect mimicry. In the case of a defenceless Batesian mimic, whose protection is dependent on the presence of a noxious model, the advantage of a particular pattern will decline as it becomes more numerous. Thus a polymorphism may evolve if there are several potential models. In some swallowtail butterflies distinct mimetic patterns are controlled by a series of supergenes, although the mimicry tends to be poorly developed or absent where models are scarce (see Sheppard, 1975; Turner, 1977). However, both theory and experiment indicate that mimicry can still occur when mimics outnumber their models, and also that imperfect resemblances can provide some protection against predation (Holling, 1965; Mostler, 1935; Brower, 1960; Duncan and Sheppard, 1965).

Worker honeybees (*Apis mellifera* L.) are protected by their stings against many predators, e.g., toads (Cott, 1936; Popham, 1948), and the venom is unpalatable even if the sting is not used (Liepelt, 1963). Bees are the models for several Dipteran mimics. Brower and Brower (1962, 1965) showed that an American hoverfly, *Eristalis vinetorum*, was acceptable to naive toads but was rejected by toads trained to avoid honeybees.

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Rejection of the flies was partly visual, but buzzing of the wings also contributed.

The dronefly *Eristalis tenax* L. mimics the honeybee in form, coloration and behaviour. The abdomen can be dark brown or extensively orange, but there is continuous variation between these extremes. Breeding studies (Heal, 1979) showed that an allele for light patterns (Ap^L) is dominant to the dark allele (Ap^d). The two morphs are not always discrete owing to variation within each morph attributable to secondary genes and environmental factors (e.g., rearing temperatures). There is also a sex difference in expression; males tend to have lighter patterns.

Apart from a difference in the shape of the light markings, the variability of *E. tenax* and of *Apis mellifera* in Britain is comparable. Golden-banded honeybees ("yellows"), principally "Italian bees" of the *ligustica* race, have been imported since 1859 and now, after over a century of hybridisation with the very dark brown varieties ("blacks"), British bees are quite variable in colour (Mace, 1976).

E. tenax are active during much of the year, from March to early December, and sometimes are far more numerous than foraging honeybees, especially at urban sites in autumn. There are at least three generations each year. Males are very scarce in spring when fertilised females emerge from hibernation. Males and females occur in roughly equal numbers in summer and autumn.

This paper describes the variation observed in natural populations of *Eristalis tenax* in north-west England, and relates the polymorphism in the fly to the colour variation in honeybees in the same areas. It is also shown that droneflies are palatable to birds, and so are Batesian mimics of Hymenopteran models.

2. MATERIALS AND METHODS

(i) Field work

The sites used for field work were as follows: (a) Several areas of derelict land in central Liverpool. At these urban sites *E. tenax* visited mainly yellow composite flowers such as *Tussilago farfara*, *Senecio squalidus*, *Leontodon autumnalis* and *Taraxacum officinale*. Honeybees also visited these sites, particularly from June to August when they foraged at Rosebay Willow-herb (*Chamaenerion angustifolium*). (b) Formby dunes (Merseyside). (c) The Wirral peninsula, including Liverpool University Botanic Gardens at Ness, where a wide variety of flowers was available during most of the year, and also along the Wirral Way footpaths. (d) Parts of north Cheshire around the Delamere Forest. (e) North Staffordshire, principally on the campus of Keele University, where there were garden flowers as well as wild composites.

In rural areas *E. tenax* were often on *Senecio jacobaea* or *Rubus fruticosus*, but they rarely occurred anywhere distant from human habitations, probably because human or animal sewage are the main sources of larval food (Lundbeck, 1916).

Colour pattern frequencies were assessed by two methods which gave similar results. Flies were collected when they were feeding on pollen or nectar at flowers, or resting on walls, bare ground or vegetation ("collec-

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tions"). Notes were also kept on study areas ("observations").

(ii) Classification

The colour patterns of *E. tenax* (UL, L, ML, M, MD, D). The males are smaller and darker through areas on tergites 2 and 3; ML, M on tergite 2 only; grade D is en and diagrams were given in a pre

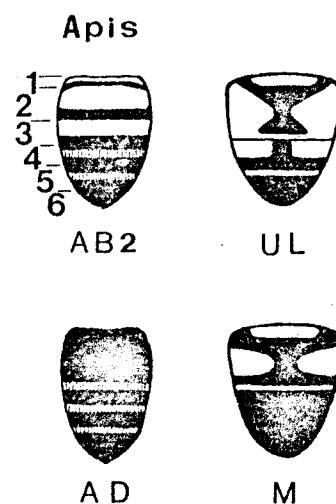


FIG. 1.—Diagrams of the abdomens of *Apis mellifera*. The two commonest forms are shown. Six principal grades of colour pattern in spring samples. Tergites of abdomen and the scutellum. Heavy shading = black; light brown, orange or golden. Very dark cuticle.

Breeding experiments show that the dark allele ($Ap^d Ap^d$) fell within MD or D only, if female overlap between dark homozygous allele, for practical purposes the

Light Phenotype (L. ph.)

Dark Phenotype (D. ph.)

The different demarcation for females are not included because they were not studied.

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(ii) Classification of patterns: *Eristalis tenax*

The colour patterns of *E. tenax* were classified into six arbitrary grades (UL, L, ML, M, MD, D). The markings on the abdomen become progressively smaller and darker through this series. Grades UL and L have orange areas on tergites 2 and 3; ML, M and MD have orange or brown markings on tergite 2 only; grade D is entirely dark (see fig. 1). Fuller definitions and diagrams were given in a previous paper (Heal, 1979).

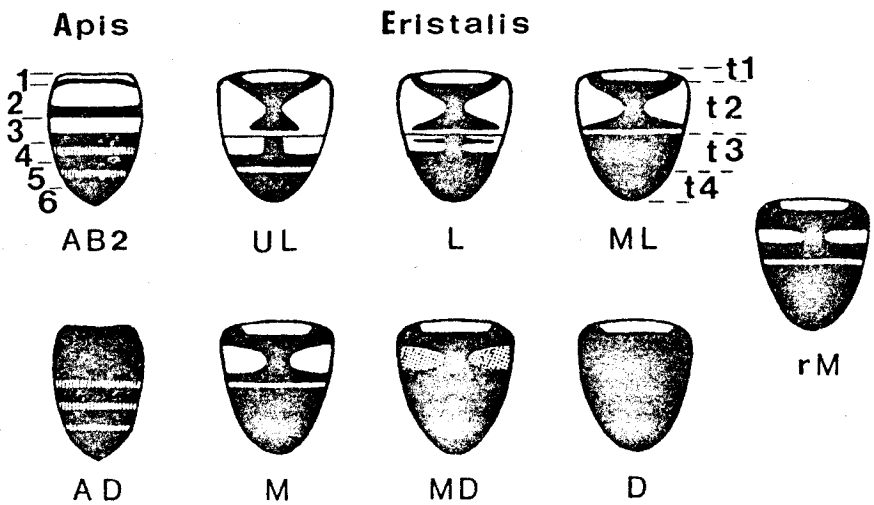


FIG. 1.—Diagrams of the abdomens of honeybees (*Apis*) and droneflies (*Eristalis*). *Apis*: The two commonest forms are shown. Segments of abdomen are numbered. *Eristalis*: Six principal grades of colour pattern are represented, and also the "rM" pattern found in spring samples. Tergites of abdomen (t1-4) indicated. Tergite 1 is dark but lies under the scutellum. Heavy shading = black or dark brown. Stippled = dull brown. Unshaded = light brown, orange or golden. Vertical hatching (*Apis* only) = bands of pale hairs on dark cuticle.

Breeding experiments showed that, in general, flies homozygous for the dark allele (Ap^dAp^d) fell within the grades M, MD or D, if male; but within MD or D only, if female. Although there was a slight phenotypic overlap between dark homozygotes and flies carrying the dominant light allele, for practical purposes the following division was made:

Light Phenotype (L. ph.)	♂	UL, L, ML
	♀	L, ML, M
Dark Phenotype (D. ph.)	♂	M, MD, D
	♀	MD, D

The different demarcation for males and females should be noted. UL females are not included because they did not occur in the populations studied.

One pattern that did not fit neatly into the classification scheme is termed "rM" (reduced Medium); the light brown markings are narrower than in standard M, but brighter than in MD. This "rM" pattern was frequent in spring samples of females, but was otherwise uncommon, suggesting that some modification can occur prior to or during hibernation.

(iii) Classification of patterns: honeybees

A different scheme was used to assess pattern variation in foraging honeybees. This was done because the light markings on the abdomen of *Apis* workers tend to occur as broad transverse bands across the tergites, whereas in *Eristalis* the markings comprise pairs of semi-oval spots separated by a median black area, with narrow pale bands along the rear margins of some tergites.

In 1977-1979 the following scheme was used for honeybees (see fig. 1): AD Tergites of abdomen entirely black. AC Some lighter areas on tergite 2, but these are obscured or restricted to the corners. AB1 One clear orange or light brown band on tergite 2. AB2 Two clear bands on tergites 2 and 3; rarely, a further band on tergite 4. In the brightest specimens the bands are golden. The first tergite is small and not easily seen from above, but it is usually dark in AD and AC, and lightly pigmented in AB1 and AB2.

Banded bees in north-west England are not as brightly coloured as the extreme type of *ligustica*, for the rearmost tergites are usually dark. The bands on tergites 2-4 vary in extent and tone, but were classified principally by their extent, except that a very dull band could be overlooked during field observation. *Apis* workers also have rows of pale hairs across the middle of tergites 3, 4 and 5. These bands of hairs are not present on *Eristalis tenax*.

Although the abdomens of model and mimic differ as described here, these differences are not obvious when the insects are active. The similar form and general colour still create a strong resemblance.

(iv) Experiments on mimicry

Some experiments were carried out in an indoor aviary (size: 1.50 × 1.10 × 0.90 m). Insect prey were immobilised by removal of legs and wings, and placed on a tray in the corner of the cage. The birds could examine the shape and colour of the insects, but behavioural components of the mimicry were unimportant. Most of the work was done with a robin (*Erithacus rubecula*); some preliminary tests involved two house sparrows (*Passer domesticus*). Insects were also fed to wild birds, principally great tits (*Parus major*).

3. RESULTS

(i) Batesian mimicry

Eristalis tenax are very palatable to birds. In February 1976 a pair of great tits took 22 *E. tenax* from a window ledge, although the flies were left untouched by blue tits and house sparrows. Two captive house sparrows were presented with tethered *E. tenax*; none of the first ten were taken,

but after one had been tried, all of 63 were taken by the sparrows (*Eristalis arbustorum* L., *Metasyrphus*). Initial avoidance could have been, possibly the sparrows were just not

A captive robin ate the first *E. tenax* regularly preferred to other Diptera on a surface, but were not as palatable as *mellifera* workers. The bees had been removed before the experiment; these inactive ones were treated and eaten but they were always picked up, broken into pieces and refused. Flies were usually picked up

Experiments on the selection of insects by a species of each species were offered, and was not given. The "preference rankings" from the sum of their places in the order, smallest sum was ranked first. Honeybees

	Period		
Trial number	1	2	3
Days after trial 1:	0	3	15
Preference rankings:			
<i>E. tenax</i> (T)	=1	=1	1
<i>E. arbustorum</i> (A)	=1	=1	2
<i>Calliphora</i> (C)	3	3	3
First fly taken	T	T	T
Honeybees eaten	—	—	—

	Period		
Trial number	11	12	13
Days after trial 1:	46	48	49
Preference rankings:			
<i>E. tenax</i> (T)	2	=2	3
<i>E. arbustorum</i> (A)	1	1	1
<i>Calliphora</i> (C)	3	=2	2
First fly taken	A	A	A
Honeybees eaten	1	2	2

Table 1 summarises the results of the robin's response to the model and poor mimic (*E. arbustorum*) and *Calliphora* (Period I). Eleven other Syrphids (e.g., *Syrphus*, *Helophilus*) than bluebottles. After the robin's experience with bees, the *Calliphora* (Period II), then *E. arbustorum* (in Period II) readily. Thus there was a period

but after one had been tried, all others were eaten. In the next five weeks, 63 were taken by the sparrows and other Syrphids given subsequently (*Eristalis arbustorum* L., *Metasyrphus luniger* (Meig.)) were also eaten. The initial avoidance could have been due to the flies' bee-like appearance, but possibly the sparrows were just not used to taking insect prey.

A captive robin ate the first *E. tenax* that it was given. Hoverflies were regularly preferred to other Diptera, possibly because of their less bristly surface, but were not as palatable as mealworms (larvae of *Tenebrio molitor*). After two months of palatable insects, the robin was offered some *Apis mellifera* workers. The bees had been kept in a freezer and their stings were removed before the experiment. Although no live bees were used, these inactive ones were treated very cautiously by the robin; some were eaten but they were always picked up and rejected several times, then pecked, broken into pieces and rubbed on the ground before being swallowed. Flies were usually picked up once and swallowed whole.

TABLE 1

Experiments on the selection of insects by a robin. Unless indicated otherwise, two immobilised specimens of each species were offered, and eaten, in each trial; a dash means that the species was not given. The "preference rankings" were worked out—for the two flies of each species—from the sum of their places in the order in which the flies were eaten; the species with the smallest sum was ranked first. Honeybees were given to the robin for the first time between trials 5 and 6

	Period I						Period II			
Trial number	1	2	3	4	5	6	7	8	9	10
Days after trial 1:	0	3	15	17	22	34	35	36	37	45
Preference rankings:										
<i>E. tenax</i> (T)	=1	=1	1	—	—	3	3	=1	3	3
<i>E. arbustorum</i> (A)	=1	=1	2	1	1	2	2	=1	2	1
<i>Calliphora</i> (C)	3	3	3	2	2	1	1	=1	1	2
First fly taken	T	T	T	A	A	C	C	C	C	C
Honeybees eaten	—	—	—	—	—	2	1	—	—	—
	Period III						Period IV			
Trial number	11	12	13	14	15	16	17	18	19	20
Days after trial 1:	46	48	49	50	51	55	56	58	63	67
Preference rankings:										
<i>E. tenax</i> (T)	2	=2	3	2	1	2	1	1	2	1
<i>E. arbustorum</i> (A)	1	1	1	1	2	3	2	2	1	2
<i>Calliphora</i> (C)	3	=2	2	3	3	1	3	3	3	3
First fly taken	A	A	A	A	T	C	T	T	A	T
Honeybees eaten	1	2	1	2	2	0	0	—	—	—

Table 1 summarises the results of a series of experiments and compares the robin's response to the model (*Apis mellifera*), good mimic (*E. tenax*), poor mimic (*E. arbustorum*) and non-mimic (bluebottle, *Calliphora* spp.). Prior to experience with bees, the robin preferred both *Eristalis* species to *Calliphora* (Period I). Eleven other trials during this period showed that other Syrphids (e.g., *Syrphus*, *Helophilus* species) were also more acceptable than bluebottles. After the robin had been given some honeybees on four occasions (days 30–33), *Calliphora* was preferred for a few trials (period II), then *E. arbustorum* (in Period III), and finally *E. tenax* was taken most readily. Thus there was a period of mimetic protection before the robin

learnt to discriminate, firstly between model and poor mimic, and then between model and good mimic. The changes in behaviour were significant (table 2). The final choice of *E. tenax* over *E. arbustorum* may have been due to larger size. Bees were never touched until all flies had been taken except once in trial 12, when the robin picked up and rejected a bee immediately after eating an *E. tenax*.

TABLE 2

Selection of insects by a robin, showing the changes of preference as a result of experience. Figures are for the total numbers of each species of fly amongst the first three flies eaten in each trial. Data are as in table 1

Period	Trials	<i>E. tenax</i>	<i>E. arbustorum</i>	<i>Calliphora</i>	Fisher exact probability
		(a) Before honeybees were given:			
I	1-3	3	5	1	0.02
		(b) After honeybees given:			
II	6-10	1	6	8	0.01
III	11-15	5	8	2	
IV	16-20	8	5	2	0.62

A case of Batesian mimicry was indicated by these experiments, but the effect did not last long, probably because the bees had no stings and the robin had time to inspect all the insects. It was not clear what led to the initial rejection of the bees, unless some taste or texture on the surface elicited an innate response or recalled some previous experience in the wild. The behaviour of captive juvenile reed warblers, *Acrocephalus scirpaceus*, towards their first wasps showed an innate avoidance, probably on the basis of colour, shape and texture (Davies and Green, 1976), although juvenile birds of some species made more attacks on bees and wasps than older birds did (Mostler, 1935).

(ii) Natural populations of *E. tenax*—summer and autumn generations

Eristalis tenax is a Syrphid that becomes common late in the year, and so most estimates of phenotype frequencies were done then. In Liverpool there seemed to be, from late May onwards, a small summer generation derived from overwintered females, followed by an abundant autumn generation, individuals of which either produced a further generation or went into hibernation.

The autumn generation started to appear in August, but the very large increase in the central Liverpool populations that took place in mid-August of four consecutive years may have been helped by some migration into the city from surrounding areas. A recapture rate of under 2 per cent for marked specimens released in Liverpool and at Keele suggested high mobility. Migrations of *E. tenax* have been noted previously by Aubert *et al.* (1976), Jones (1955) and Williams (1958).

In woodlands or open agricultural areas, the frequency of *E. tenax* is always low. However, in late autumn patches of flowers at Ness Gardens, *Eristalis* species, especially *E. peritrichus*, but *E. tenax* was still abundant. *E. tenax* and *E. peritrichus* tended to be often present in parks and gardens, and wasteground favoured by *E. tenax*.

Data on colour patterns in a sample of 100 males and 100 females (Heal, 1979), and more extensive data for 1977 and 1978. Most sets of figures show a bimodal distribution of phenotypes at L and MD or D for males. The female mode coincides with the male mode and is not just an artefact of the sampling process, but is genuine and not just an artefact of the sampling process, with males lighter on average, a result of the sampling process. The difference in phenotype in the two sexes is justifiable. It also provides good evidence for the existence of a bimodal distribution in females for most sets of figures.

Data for different months in the tables because the D. ph. from the annual flight period. The only time there was an excess of darker phenotypes was in November. In some, but not all, years the cause of this. Pupal temperature in 1977 and in preparation of the data (Heal, 1981).

For field observations (table 1) the frequency of the Dark phenotype was 69 per cent for Liverpool in 1973 and 63 per cent. The combined D. ph. in all 13 sets of data was 48.4 ($P < 0.001$), but if the high values are excluded ($\chi^2 = 8.55$, $P > 0.05$) heterogeneity between years. However, for 1974-1976 only, the frequency of variation in the figures is a high value from Liverpool. This may reflect the earliest field estimates are high.

The frequency of the Dark phenotype was higher than on the Wirral in 1973-1974 ($\chi^2 = 9.59$, $P < 0.01$) and for 1975-1976 ($\chi^2 = 0.75$, $P > 0.3$). Looking at a tendency for the D. ph. frequency from collections (table 1) the Dark Phenotype was 50 per cent in the Wirral and 55 per cent in the Wirral. Different years were not significantly different between the sexes.

The figures in tables 3-4 show that the frequency of the Dark phenotype is between 0.7 and 0.8 in north

a model and poor mimic, and then changes in behaviour were significant over *E. arbustorum* may have been touched until all flies had been taken when picked up and rejected a bee

Fig. 2. Ranges of preference as a result of experience of fly amongst the first three flies eaten in each of the sets in table 1

	<i>Calliphora</i>	Fisher exact probability
flies were given:		
flies given:	1	0.02
	8	0.01
	2	0.62
	2	

indicated by these experiments, but because the bees had no stings and effects. It was not clear what led to the taste or texture on the surface of some previous experience in the reed warblers, *Acrocephalus scirpaceus* (innate avoidance, probably on avian and Green, 1976), although the attacks on bees and wasps than

Summer and autumn generations

flies common late in the year, and flies were done then. In Liverpool Warrington, a small summer generation followed by an abundant autumn generation produced a further generation or

near in August, but the very large numbers that took place in mid-August helped by some migration into the rate of under 2 per cent for 1973 and at Keele suggested high (noted previously by Aubert *et al.* 1978).

In woodlands or open agricultural areas, population densities were always low. However, in late autumn large numbers were recorded on patches of flowers at Ness Gardens and Keele University. Some other *Eristalis* species, especially *E. pertinax* Scopoli, were at the same flowers, but *E. tenax* was still abundant later in the autumn. In urban areas *E. tenax* and *E. pertinax* tended to use different food sources; *E. pertinax* was often present in parks and gardens but rarely visited the nearby areas of wasteland favoured by *E. tenax*.

Data on colour patterns in autumn collections from three areas (table 3), and more extensive data for all field observations (table 4) are shown. Most sets of figures show a bimodal distribution. In general, the two modes are at L and MD or D for males, but at M or D for females. As the lighter female mode coincides with the male antimode, the bimodality is seen to be genuine and not just an artefact of scaling. This differential bimodality, with males lighter on average, agrees with the results of breeding experiments (Heal, 1979). The different demarcation between Light and Dark Phenotype in the two sexes (see Classification of Patterns) is therefore justifiable. It also provides good agreement for D. ph. frequencies in males and in females for most sets of figures in tables 3 and 4.

Data for different months in any one locality have been combined in the tables because the D. ph. frequency did not vary significantly through the annual flight period. The only exception was at Keele in 1977 when there was an excess of darker flies active at the end of the season, in November. In some, but not all, years the position of the modes changed slightly from month to month. Environmental changes might have been the cause of this. Pupal temperature can modify the adult pattern (Heal, 1977 and in preparation) as has already been shown for *Eristalis arbustorum* (Heal, 1981).

For field observations (table 4), the highest Dark Phenotype estimate is 69 per cent for Liverpool in 1973, but other values fell between 48 per cent and 63 per cent. The contingency table for numbers of L. ph. and D. ph. in all 13 sets of data has a highly significant heterogeneity χ^2_{12} of 48.4 ($P < 0.001$), but if the high D. ph. figures from Liverpool in 1973-1974 are excluded $\chi^2_{10} = 8.58$ ($P > 0.50$). Liverpool was the only area with heterogeneity between years, $\chi^2_3 = 20.5$, $P < 0.0001$, for 1973-1976. However, for 1974-1976 only, $\chi^2_2 = 2.14$ ($P > 0.30$). Thus the major source of variation in the figures is a higher proportion of dark flies in earlier data from Liverpool. This may reflect a genuine frequency change; however, the earliest field estimates are likely to have been the least accurate.

The frequency of the Dark Phenotype was slightly higher in Liverpool than on the Wirral in 1973-1975; the difference is significant for 1973 ($\chi^2_1 = 9.59$, $P < 0.01$) and for 1974 ($\chi^2_1 = 4.98$, $P < 0.05$), but not for 1975 ($\chi^2_1 = 0.78$, $P > 0.3$). Looking at all five areas in table 4, there is a slight tendency for the D. ph. frequency to decrease southwards. However, data from collections (table 3) do not show a cline. Overall, the percentage of Dark Phenotype was 52 per cent in Liverpool, 51 per cent on the Wirral peninsula, and 55 per cent in north Staffordshire. In each area, data from different years were not significantly different and there was no heterogeneity between the sexes in any year sample.

The figures in tables 3-4 suggest that the frequency of the Ap^d allele is between 0.7 and 0.8 in north-west England.

TABLE 3

Colour patterns in samples of *E. tenax* collected in August–November (autumn generations). Note that Dark Phenotype comprises M, MD and D males, but only MD and D females. Estimates of q , the frequency of Ap^d , assume that all D.ph. flies are recessive homozygotes

Area	δ						η						Totals*		Gene frequency $q \pm s.e.$
	UL	L	ML	M	MD	D	L	ML	M	MD	D	L.ph.	D.ph.		
Liverpool	3	42	23	13	36	28	4	18	34	12	47	124	136	0.72 ± 0.02	
Wirral	2	19	3	8	6	8	2	4	10	5	14	40	41	0.71 ± 0.04	
North Staffs.	10	49	14	11	20	50	6	10	50	12	74	139	167	0.74 ± 0.02	

* (i) Heterogeneity amongst areas total = 2.05 (D.F. = 2, $P < 0.05$).

* (i) Heterogeneity amongst area totals, $\chi^2 = 0.53$ ($P > 0.7$). (ii) Heterogeneity amongst totals for each year, Liverpool (1972, 73, 75): $\chi^2 = 1.29$ ($P > 0.5$); Wirral (1973, 75): $\chi^2 = 0.60$ ($P > 0.3$); North Staffs (1976–79): $\chi^2 = 1.87$ ($P > 0.3$).

TABLE 4

Field observations on frequencies of colour patterns in summer and autumn generations of *Eristalis tenax*. These figures include the captured flies given in table 3. Note that the Dark Phenotype comprises M, MD and D males, but only MD and D females

Year	UL	♂						♀						Totals*		% D.ph.
		L	ML	M	MD	D	L	ML	M	MD	D	L.ph.	D.ph.			
(a) Liverpool†																
1973	2	33	32	36	42	74	0	16	44	33	95	127	280		68.8	
1974	4	121	99	69	120	110	9	55	157	79	253	445	631		58.6	
1975	8	76	31	12	62	60	4	29	45	19	85	193	238		55.2	
1976	8	49	20	3	39	39	4	16	32	20	57	129	158		55.1	
(b) Formby																
1974	0	11	7	7	11	13	0	2	4	1	8	24	40		62.5	
1975	1	5	2	2	8	0	0	3	2	1	9	13	20		60.0	

10 49 14 11 20 50 6 10 50 12 74 139 167 $\chi^2_1 = 0.53$ ($P > 0.7$); (iii) Heterogeneity amongst totals for each year, Liverpool (1972, 73, 75): $\chi^2_2 = 1.29$ ($P > 0.5$); Wirral (1973, 75): $\chi^2_1 = 0.60$ ($P > 0.3$); North Staffs (1976-79): $\chi^2_2 = 1.87$ ($P > 0.3$).

TABLE 4

Field observations on frequencies of colour patterns in summer and autumn generations of *Eristalis tenax*. These figures include the captured flies given in table 3. Note that the Dark Phenotype comprises M, MD and D males, but only MD and D females

MIMICRY AND VARIATION IN *ERISTALIS*

Year	UL	♂										♀		Totals*		% D.ph.
		L	ML	M	MD	D	L	ML	M	MD	D	L.ph.	D.ph.			
(a) Liverpool†																
1973	2	33	32	36	42	74	0	16	44	33	95	127	280		68.8	
1974	4	121	99	69	120	110	9	55	157	79	253	445	631		58.6	
1975	8	76	31	12	62	60	4	29	45	19	85	193	238		55.2	
1976	8	49	20	3	39	39	4	16	32	20	57	129	158		55.1	
(b) Formby																
1974	0	11	7	7	11	13	0	2	4	1	8	24	40		62.5	
1975	1	5	2	2	8	0	0	3	2	1	9	13	20		60.6	
(c) Wirral†																
1973	2	31	14	16	24	12	1	3	23	4	25	74	91		55.2	
1974	4	25	16	8	13	17	3	11	24	9	34	83	81		49.4	
1975	13	59	12	14	46	25	4	21	23	11	46	132	142		51.8	
(d) North Cheshire																
1974	3	5	1	2	4	7	1	2	6	2	6	18	21		53.8	
(e) North Staffordshire†																
1977	5	33	8	4	17	35	7	10	30	4	52	93	112		54.6	
1978	6	31	8	5	10	30	5	11	35	11	34	96	90		48.4	
1979	17	126	43	31	65	97	29	42	117	34	165	374	392		51.2	

* Comparing all sets of data for L.ph. and D.ph. totals, heterogeneity $\chi^2_{12} = 48.4$ ($P < 0.001$).
† Heterogeneity amongst year totals for each site: (a) Liverpool $\chi^2_3 = 20.52$ ($P < 0.001$); (c) Wirral $\chi^2_2 = 1.11$ ($P > 0.5$); (e) North Staffs. $\chi^2_2 = 1.55$ ($P > 0.3$).

73 605 293 209 461 519 67 221 542 228 809 1801 2296

4097
%L = 44.0

TABLE 5
Colour patterns of *Eristalis tenax* collected in spring. The samples were entirely female

Area	Years	Range of capture dates	Patterns of ♀♀*				Totals		% D.ph.
			L	ML	M	MD	D	L.ph.	
Liverpool	1973-76	25/2-25/4	0	9	27	22	15	36	37
Ness (Wirral)	1973-74	22/3-10/4	0	0	2	2	1	2	3
North Staffs.	1977-80	19/3-16/4	0	0	7	4	5	7	9
Total			0	9	36	28	21	45	49

* Grade M includes nine "rM" females (Liverpool-6, Ness-1, North Staffs.-2).

MIMICRY AND

(iii) Natural populations

Eristalis tenax is one of the first of the females whose ovarian development lengths (Kendall and Stradling, 1977) in March or April of any year. Females in stocks; the majority were from a unimodal distribution of patterns, and morphs could not be made reliably from most numerous, but there were some of those scored "rM"). These two females were patterns during the winter.

Unfortunately, in spring the numbers in northern England were smaller than in 1955; Dr D. A. Kendall, pers. comm. on migrations, as described for several years (Williams, 1958).

(iv) Surveys

Detailed surveys of honeybees in the north indicated a bimodal distribution of patterns, most workers were quite numerous, most workers were banded (table 6).

Field observations of *Apis mellifera* workers around Keele, north Staffordshire. See text for details. Note that banded bees are compared with the Light

Year	Banded <i>Apis</i>	
	AB2	AB1
1977	260	88
1978	90	40
1979	22	7
Total	372	135
<i>Apis</i> , %:	32.9	11.9
compared with		
<i>E. tenax</i> , %:	29.1	19.9
	(UL-ML)	(M)

* Figures in end-column are from "0"

† Figures in bottom row are from "0"

From a subjective assessment of the four *Apis* classes have been defined: (i) AD = D; (ii) AC = MD; (iii) All defined light zones are present in the first two. Although measurements of the markings usually occupy 5-10% of the surface in AB1 bees and M *Eristalis*

(iii) *Natural populations—spring females*

Eristalis tenax is one of the first British Syrphids to appear in the spring. The earliest ones are adults coming out of hibernation, principally fertilised females whose ovarian development has been suppressed by short day-lengths (Kendall and Stradling, 1972; Heal, 1977). No males were seen in March or April of any year. Females were collected to initiate breeding stocks; the majority were from urban sites. In each year there was a unimodal distribution of patterns, and consequently the division into two morphs could not be made reliably (table 5). Grades M and MD were the most numerous, but there were some flies with unusual markings (e.g., those scored "rM"). These two facts suggest that changes occur in the patterns during the winter.

Unfortunately, in spring the numbers obtainable from these towns in northern England were smaller than at sites in southern England (Jones, 1955; Dr D. A. Kendall, pers. comm.). This could be due to seasonal migrations, as described for several British butterflies (Baker, 1978; Williams, 1958).

(iv) *Surveys of honeybees*

Detailed surveys of honeybees at Keele University campus (1977–1979) indicated a bimodal distribution of colour patterns. Although other types were quite numerous, most workers were either completely dark, or two-banded (table 6).

TABLE 6

Field observations of *Apis mellifera* workers and comparisons with *E. tenax*. Data from sites around Keele, north Staffordshire. See text for classification and explanation of the comparisons made. Note that banded bees are compared with the four lightest grades of fly pattern, not with the Light Phenotype category

Year	Banded <i>Apis</i>		Dark <i>Apis</i>		<i>Apis</i> % banded	<i>E. tenax</i> * % UL-M
	AB2	AB1	AC	AD		
1977	260	88	83	210	54.3	47.3
1978	90	40	58	175	35.8	53.8
1979	22	7	32	65	23.0	52.9
Total	372	135	173	450	44.9	52.1
<i>Apis</i> , %:	32.9	11.9	15.3	39.8		
compared with						
<i>E. tenax</i> , %:	29.1	19.9	10.5	40.5†		
	(UL-ML)	(M)	(MD)	(D)		

* Figures in end-column are from "observations" in table 4.

† Figures in bottom row are from "collections" in table 3.

From a subjective assessment of the general brightness of the abdomen, the four *Apis* classes have been equated to *Eristalis* grades as follows: (i) AD = D; (ii) AC = MD; (iii) AB1 = M; (iv) AB2 = ML, L, UL. Clearly defined light zones are present in the last two groupings, but not in the first two. Although measurements were never made for routine scoring, the markings usually occupy 5–9 mm² of the exposed dorsal abdominal surface in AB1 bees and M *Eristalis*, but over 9 mm² in AB2 and ML–UL

specimens. *E. tenax* are slightly larger, and thus their markings take up a smaller proportion of the total dorsal surface, but this is balanced by slightly brighter colours.

Using this method of comparison, it is seen that there is a similar bimodality in honeybees at Keele and in samples of *Eristalis tenax* (males and females combined) collected in the same period. However the percentage of banded bees observed did vary between years (heterogeneity $\chi^2_2 = 59.4$, $P < 0.001$), and is not matched very closely by the percentage of lighter grades of *E. tenax* (UL-M) in each year.

TABLE 7

Field observations of *Apis mellifera* workers (simpler classification, 1973-76) and comparison with sympatric populations of *E. tenax*

Area/Year	<i>Apis mellifera</i> workers			<i>E. tenax</i> * % UL, L, ML, M
	Banded	Dark	% banded	
(a) Liverpool				
1973	52	145	26.4	40.0
1974	7	68	9.3	47.8
1975	21	59	26.3	47.6
1976	15	16	48.4	46.0
Total†	95	288	24.8	46.1
(b) Formby				
1973-75	36	51	41.4	47.4
(c) Wirral				
1973	84	70	54.5	54.5
1974	320	306	51.1	55.5
1975	87	106	45.1	53.3
Total†	491	482	50.5	54.2
(d) North Cheshire				
1973-74	34	10	77.3	51.3
All sites combined				
	656	831	44.1	47.9

* Figures from "observations" of *E. tenax* in table 4.

† *Apis*—heterogeneity amongst data from different years, Liverpool: $\chi^2_3 = 19.2$ ($P < 0.001$), Wirral: $\chi^2_2 = 3.37$ ($P > 0.1$).

Earlier field observations in Merseyside and Cheshire (1973-1976) used a simpler scoring scheme (see table 7). For both *Apis* and *E. tenax*, lighter forms were less frequent at sites north of the Mersey than south of it. However individual estimates varied far more for *Apis* (9-77 per cent) than for *E. tenax* (40-56). One explanation is that the social life of bees limits their movements; at one site counts could be dominated by bees from a single hive. Hoverflies are not social and so can move more widely. When making comparisons, large numbers of honeybees from a wide area are needed. In fact, from tables 6 and 7, the overall proportion of banded *Apis* (44 per cent) is quite close to the 49 per cent of *E. tenax* with light brown or orange markings, and the correspondence between model and mimic was best where the sample size of bees was largest.

In the dronefly, *Eristalis tenax*, a polygenic and environmental factor in its variation it can be seen only as a bimodal distribution. Experiments with birds have shown that mimics are sometimes rejected on sight because they are not like honeybees.

Mimicry of honeybees is quite common because neither *Bombus* nor *Vespa* are abundant until summer. British birds include the larger *Eristalis* species (*E. tenax* and *E. pertinax* Scopoli) and a single generation in spring (e.g. *Syrphus*) *eligans* Harris). Of these

Much of the variation in *E. tenax* is genetic polymorphism in the model. of honeybees show that the factors as in *E. tenax*. Crosses between genotypes of dominance of the light bands, although (Kulincevic, 1967; Laidlaw and others) suggested that further variability is caused (see Roberts and Mackensen, 1954) (1954) showed that the extent of variation is temperature and so varies seasonally.

The honeybees of north-west Merseyside show patterns, from completely dark to completely light. The surface is orange. Sympatric populations of honeybees in the range, and both model and mimicry are present. There were roughly 50 per cent of dark forms in the north of the river Mersey. The variation is only a gradual one. Unless the mobility of the flies would limit the spread of mimics. On the other hand, honeybees live in colonies so local fluctuations in morph frequency are derived from a few colonies only. The frequency of mimics for models and for mimics do not always match.

In spring, samples of female *E. tenax* show patterns, not bimodal as in summer. The model receives greatest protection if it has patterns that are not greatly dissimilar from mimics remain scarce (see Holling and others).

In autumn, *E. tenax* outnumber birds, earlier experiences with sufficient bee-like mimics. However, other factors between *Eristalis* and *Apis* (as in creating a selection pressure for mimics are abundant).

However, a "perfect" resemblance between model and mimic explanations can be put forward for

4. DISCUSSION

In the dronefly, *Eristalis tenax*, a genetic polymorphism is obscured by polygenic and environmental factors (Heal, 1979), and in natural populations it can be seen only as a bimodal distribution of patterns in each sex. Experiments with birds have shown that *E. tenax* are very palatable, but are sometimes rejected on sight because they are Batesian mimics of worker honeybees.

Mimicry of honeybees is quite common amongst flies active in spring because neither *Bombus* nor *Vespula* workers—other potential models—are abundant until summer. British Syrphids which resemble honeybees include the larger *Eristalis* species active during most of the year (e.g., *E. tenax* and *E. pertinax* Scopoli) and some medium-sized species that have a single generation in spring (e.g., *Cheilosia grossa* Fallen, *Epistrophe* (*Syrphus*) *eligans* Harris). Of these species, *E. tenax* is the most variable.

Much of the variation in *E. tenax* is attributable to the corresponding genetic polymorphism in the model, *Apis mellifera*. Reports on the genetics of honeybees show that the factors controlling the coloration are the same as in *E. tenax*. Crosses between golden-banded and dark strains showed dominance of the light bands, although dominance was not complete (Kulincevic, 1967; Laidlaw and el-Banby, 1962). Some workers have suggested that further variability is due to several other genes being involved (see Roberts and Mackensen, 1951; Rothenbuhler *et al.*, 1968). Soose (1954) showed that the extent of the abdominal bands is sensitive to temperature and so varies seasonally.

The honeybees of north-west England have a range of abdominal patterns, from completely dark to forms in which about half of the dorsal surface is orange. Sympatric populations of *Eristalis tenax* have a similar range, and both model and mimic have a bimodal distribution. In this study there were roughly 50 per cent with light markings in both species. The percentage of dark forms in the models and mimics observed was a little higher north of the river Mersey. However if a cline exists in *E. tenax* it is only a gradual one. Unless the two morphs differed in choice of habitat, the mobility of the flies would limit any local variation in gene frequency. On the other hand, honeybees live in large colonies of related insects and so local fluctuations in morph frequencies could occur if samples were derived from a few colonies only. Consequently, at a single site the data for models and for mimics do not always correspond closely with each other.

In spring, samples of female *E. tenax* were unimodal for intermediate patterns, not bimodal as in summer and autumn. An intermediate pattern receives greatest protection if predators generalise between two model patterns that are not greatly dissimilar. Generalisation is favoured while mimics remain scarce (see Holling, 1965; Heal, 1977).

In autumn, *E. tenax* outnumbered their models at many sites. For some birds, earlier experiences with sufficient bees would lead to aversion of all bee-like mimics. However, other birds will learn to discriminate visually between *Eristalis* and *Apis* (as in the experiments reported above), thus creating a selection pressure for close mimicry, and also variation, whilst mimics are abundant.

However, a "perfect" resemblance to bees has not evolved yet. Two explanations can be put forward for the light pattern of *E. tenax* consisting

er, and thus their markings take up a surface, but this is balanced by slight

n, it is seen that there is a similar d in samples of *Eristalis tenax* (males ie same period. However the percent y between years (heterogeneity $\chi^2 =$ d very closely by the percentage of each year.

7
simpler classification, 1973-76) and com-
putations of *E. tenax*

workers	<i>E. tenax</i> *
dark	% UL, L, ML, M
% banded	
45	26.4
68	9.3
59	26.3
16	48.4
18	24.8
1	41.4
0	54.5
6	51.1
5	45.1
2	50.5
	77.3
	44.1
	47.4
	47.8
	47.6
	46.0
	46.1
	51.3
	47.9

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different years, Liverpool: $\chi^2 =$

and Cheshire (1973-1976) used both *Apis* and *E. tenax*, lighter of the Mersey than south of it. more for *Apis* (9-77 per cent) on is that the social life of bees s could be dominated by bees l and so can move more widely. of honeybees from a wide area ie overall proportion of banded per cent of *E. tenax* with light pondence between model and es was largest.

of paired spots rather than continuous bands as in *Apis*—firstly, partial wasp-mimicry, and secondly, thermoregulation.

Mostler's (1935) classic experiments showed that captive birds sometimes confused *E. tenax* with wasps. After being stung by a wasp, a flycatcher avoided many insects that were only crudely mimetic (Steiniger, 1937). Similarly, in my experiments, *E. arbustorum* got some protection from its moderate resemblance to a honeybee.

To improve the wasp-mimicry there seems to be an epistatic influence of the *Ap* gene on the hair colour genes (Heal, 1977). Dark Phenotype flies have hair colours varying from white to dark brown. However, on most Light Phenotype *E. tenax* the pubescence is light yellow, and seen most clearly as yellow bands along the sides of the thorax, where a wasp has stripes of yellow pigment. These lighter patterns would get less benefit from wasp-mimicry early in the year, before wasps are numerous. This could explain why L and UL grades were absent from spring samples. It may also explain why males, which appear later, tend to have brighter patterns than females, although differences in flight and behaviour may make wasp-mimicry more appropriate for males, as is the case in the sexually dimorphic *Eristalis arbustorum* (Heal, 1981).

Pigmentation can also have an important role in the control of body temperature. In the laboratory, pupal temperature influences the adult pattern, to give darker patterns at lower temperatures, both in *E. tenax* and *E. arbustorum* (Heal, 1977, 1981 and in preparation). The black areas down the centre of the abdomen of *E. tenax* (see fig. 1) may serve to absorb solar radiation and so warm the dorsal blood vessel that lies directly beneath. The usual basking position of *Eristalis* species, and also of many other large Diptera, is with the wings spread slightly so as to expose the middle of the abdomen. A black central stripe is a common feature in hoverflies. Honeybees lack this stripe and do not bask in sunshine.

On a global scale, geographical associations between brighter markings and hot climates are known for *Apis mellifera* (Rothenbuhler *et al.*, 1968; Mace, 1976). Thus clines are to be expected in *E. tenax*, as a result of selection for both mimicry and thermoregulation. The mobility of adult flies limits the differentiation between populations in north-west England. Nevertheless the main factor in preserving phenotypic variation within populations is clearly Batesian mimicry of Hymenoptera.

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