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# COLOUR PATTERNS OF SYRPHIDAE:

## I. GENETIC VARIATION IN THE DRONEFLY *ERISTALIS TENAX*

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SUMMARY

*Eristalis tenax* is a Batesian mimic of the honeybee *Apis mellifera* and resembles its model in general form, coloration and flower-visiting behaviour. The abdominal patterns of *E. tenax* vary from completely dark brown to those in which the abdomen is mainly orange. A major gene locus (termed *Ap* for abdominal pattern) has been identified with alleles for light and dark colour pattern. Light pattern is dominant, but there is a sex difference in expression such that males tend to have more extensive orange markings. Thus a different division into Light and Dark Phenotype classes is necessary in males and females. Besides the major gene, other sources of variability are important. Both environmental and polygenic factors produce a range of patterns within the two principal categories.

### 1. INTRODUCTION

COMING shortly after the publication of *The Origin of Species* in 1859, the paper by Bates (1862) dealing with similarities between some South American butterflies was one of the earliest to indicate how natural selection may influence the evolution of wild populations. Batesian mimicry, the resemblance of edible mimics to warningly-coloured and protected models, may lead to genetic polymorphism (see Clarke and Sheppard, 1960; Sheppard, 1964, 1975).

Neither mimicry itself nor polymorphism in colour pattern are restricted to the Lepidoptera. Female aculeate Hymenoptera are well protected against vertebrate predators by the possession of a sting. Resemblances to bees or wasps have evolved in many insect species, especially amongst Diptera (although striking examples can also be found within the Coleoptera and Lepidoptera). Nearly all the British species of hoverflies (Syrphidae) show some similarity in form, coloration or behaviour to bees or wasps, and several Syrphids are very fine mimics. Some of these are also polymorphic. Conn (1972) concluded that six separate loci were involved in producing the diverse colour patterns of the bumblebee mimic *Merodon equestris*. Although there was no evidence of a supergene, Conn suggested that there was some linkage disequilibrium between loosely linked loci. The results of Gabritchevsky (1924) indicate the presence of a major gene in *Volucella bombylans*. The two principal varieties resemble red-tailed and yellow-banded bumblebees respectively.

The genus *Eristalis* includes several large species which are mimics of different sorts of bees (*e.g. Apis, Bombus, Andrena, Colletes*). Genetic polymorphisms affecting colour patterns occur in both *E. tenax* L., a honeybee

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mimic, and *E. intricarius* L., which mimics bumblebees (Heal, 1977). This paper describes the genetics of *E. tenax*. The colour pattern variation observed in wild populations and the relationship between mimic and model will be dealt with subsequently.

## 2. Materials and methods

Most of the adult *Eristalis tenax* used in these studies were collected from areas of derelict ground in Liverpool, and were often taken whilst feeding at Composites such as *Tussilago farfara* L., *Senecio squalidus* L. and *Leontodon autumnalis* L. On a diet of pollen and honey, adult flies often survived for several weeks in the laboratory.

Initially, plastic boxes ($23 \times 14 \times 9$ cm) were tried as breeding cages, but these were unsuitable for *E. tenax*, probably because the boxes were too small and the air inside became very humid. Thereafter the breeding techniques used were based on those of Dolley, Hassett, Bowen and Phillies (1937). Breeding cages had wooden sides and floor, and the top was covered with a fine mesh plastic netting. A suitable size was $28 \times 23 \times 14$ cm, with wooden legs at each corner. Honey was smeared on the netting and fresh flowers (usually *Senecio squalidus*) were provided in a glass tube. Pollen appears to be necessary for the laying of fertile eggs. Another tube contained some rotting organic matter, in which eggs were usually laid. Cages were kept in a greenhouse. Extra illumination from fluorescent lamps was given in autumn and winter because short day lengths inhibit maturation of the ovaries.

Stocks for breeding experiments were derived from wild females captured in spring. These females had mated in the autumn prior to hibernation. Some broods were obtained from laboratory crosses between single pairs, but most crosses were set up with about three or four of each sex together in a cage in order to ensure that the majority yielded some data. Males with similar colour patterns would be chosen from one brood, and females would then be selected (from this or another brood) in like manner. Multiple crosses of this nature are considered valid in *E. tenax* because:

(i) Females oviposit in individual clusters (of about 100-200 eggs) which can be reared separately.

(ii) Females seem to use sperm from only one male. This has been concluded from the consistency of the breeding results, particularly in comparisons between consecutive broods from single females, and it is probable—from observations of behaviour—that female *E. tenax* only mate once.

Batches of eggs were transferred to larval medium of decomposing organic material, which was usually a mixture of water and rabbit faeces. The eggs hatched after 2 days, and in laboratory conditions pupation occurred at the surface of the medium about 3 weeks later. Pupae were removed to dry boxes. Adults emerged after 9-14 days, depending upon the temperature.

### (i) *The abdominal colour patterns*

In samples of wild *E. tenax* the most obviously variable character is the colour pattern on the dorsal surface of the abdomen, although there is also

variation in the coloration of the ventral surface, the hind femora and thoracic pubescence (Heal, 1977). *E. tenax* is primarily a mimic of the honeybee (*Apis mellifera* L.), which also shows variation in body and hair coloration. In *A. mellifera* most worker bees either have a dark brown or black abdomen, or bear transverse orange bands on the abdominal tergites—see Butler (1954).

The basic dorsal markings of most *Eristalis* species consist of a pair of semi-oval yellow or brown spots on tergite 2, sometimes extending to tergite 3. *E. tenax* exhibits a continuous range of patterns from very light forms in which most of tergites 2-3 are orange, to the opposite extreme which has an entirely dark brown abdomen. An arbitrary classification was devised, taking into account differences in both the extent of the markings and their colour. Size was more important in distinguishing the lighter grades (UL, L, ML) and shade for the darker grades (M, MD, D). The six grades are defined as follows (see fig. 1):

D (dark). Abdomen entirely dark brown.

MD (medium-dark). Abdomen dark except for a pair of semi-oval brown spots on tergite 2.

M (medium). Markings on tergite 2 as in MD but light brown in colour. Thin light brown line often present at rear of tergite 2.

ML (medium-light). Side markings extending to front of segment and frequently joining a distinct light brown band at rear edge.

L (light). Tergite 2 as in ML but a pair of narrow orange areas extend from the sides of tergite 3, not quite joining at the dorsal mid-line.

UL (ultra-light). Light areas enlarged; front half of tergite 3 orange except for median black band.

Most patterns could be fitted into this scheme. Occasionally, wild samples included females with light brown side markings (as for grade M) in which the size of the light areas was smaller than usual. These patterns were termed rM (reduced Medium), but were absent from nearly all laboratory broods.

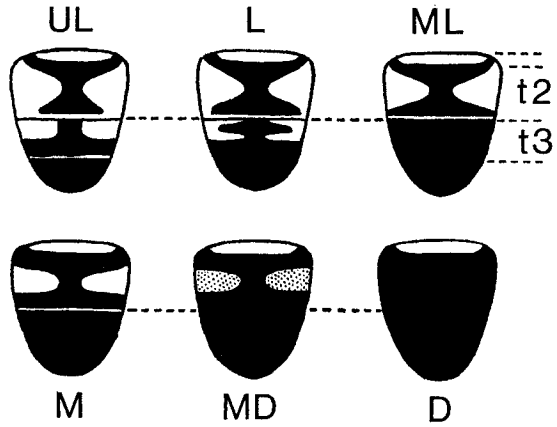


FIG. 1.—*Eristalis tenax*: classification of abdominal pattern (see text for explanation). Heavy shading = dark brown or black. Stippled = dull brown. Unshaded = orange or light brown. Tergites 2 and 3 are indicated (t2, t3). First segment is dark but hidden by scutellum.

Males tended to have, on average, slightly lighter patterns than female *E. tenax*. The side markings were more " triangular " in shape on males but more " rectangular " in the case of females. A common scheme was used for convenience, but male and female data are always given separately.

## 3. Results

### (i) *Progeny of wild females*

In *Eristalis tenax*, females fertilised in autumn hibernate in crevices and oviposit in spring (Kendall and Stradling, 1972). Females from autumn samples rarely laid eggs. Most of the broods were obtained from females collected in March and April. Fertile eggs were laid by 3 out of 14 spring females in 1973, 15 out of 25 in 1974 and 10 out of 14 in 1975. Data for all years are summarised in table 1.

Some broods from wild females were unimodal in both sexes, either for dark or for light abdominal pattern (tables 1a and 1b). Others were bimodal, although in some cases the bimodal distribution was unclear in the female offspring (tables 1c and 1d). The antimodes in these bimodal broods usually lay between grades ML and M in the male offspring, but between M and MD in the females. The two groups of patterns on either side of the antimode were considered equivalent to the single groups occurring in the two types of unimodal brood. This suggests the underlying segregation of a major gene affecting colour pattern. Yet no universal separation was found between the two morphs because of much variation from other sources. For analysis, some consistent means of separating light and dark patterns was necessary. Therefore in all broods flies were divided into two phenotypic categories, defined as follows:

(i) Light Phenotype (L.ph.): ♂ UL, L, ML
♀ UL, L, ML, M

(ii) Dark Phenotype (D.ph.): ♂ M, MD, D
♀ MD, D

Grade M is defined as L.ph. if female, but D.ph. if male because males tend to have lighter patterns (compare males and females in the broods shown in tables 1a and 1b). This division was justified by later breeding experiments and also agreed with the particular bimodal distribution of patterns recorded in wild populations of *E. tenax* (Heal, 1977 and in preparation).

Thirteen broods which were entirely or mainly dark phenotype are shown in table 1a. These were all produced by D.ph. females. Some broods contained a few " inappropriate " patterns (*i.e.* L.ph.) but these may be due to the broad spread of a unimodal curve. This interpretation seems reasonable for the progeny of T74/16 and T75/59 because whilst these " inappropriate " flies were scored as L.ph. grades from the size of their side-markings, the colour of these markings was usually dull brown as in other D.ph. flies. Several M females were obtained from T74/1, but subsequent crosses (T74C and T74U in tables 2c and 2b) indicated that in this case the M pattern corresponded to a dark genotype.

The all-light broods in table 1b can be examined in a similar manner. Four of them were entirely of the light phenotype (as defined previously). The progeny of T74/19 may have been unimodal for the light morph with

a broad spread of patterns. In these light broods the modal grade of females was always ML (although this is not always so, see table 2e) but the male mode fell at either L or UL. Thus males had distinctly lighter patterns than females in the same brood.

Using the same L.ph./D.ph. division, the segregating broods were of two types:

(i) Broods segregating approximately 1 : 1 for L.ph. and D.ph. (table 1c).
(ii) Broods segregating in an approximate ratio of 3 L.ph. to 1 D.ph. (table 1d).

These results provide evidence for the segregation of alleles at a single locus. The implication of the 3 : 1 broods is that the light allele is dominant to the dark allele with respect to colour pattern. The dominance of light over dark is also suggested by the all-light brood from T75/54 which had a dark phenotype (MD) pattern.

The locus for this major gene will be referred to as *Ap* (abdominal pattern) and its two alleles denoted by $Ap^{L}$ and $Ap^{d}$, for light and dark pattern respectively. In general, L.ph. flies will be $Ap^{L}$ $Ap^{L}$ or $Ap^{L}$ $Ap^{d}$ and D.ph. will have the genotype $Ap^{d}$ $Ap^{d}$.

The 12 females producing 1 : 1 broods yielded 806 L.ph. and 766 D.ph. offspring. These figures do not differ significantly from expected ($\chi_1^2 = 1{\cdot}02$, $P > 0{\cdot}3$) and so there is no evidence for differential viability between the two morphs. Likewise, the 3 : 1 broods contained 526 L.ph. and 170 D.ph. which are very close to the expected numbers ($\chi_1^2 = 0{\cdot}12$, $P > 0{\cdot}7$) despite an apparently poor correspondence in some broods between the ratios in each sex (*e.g.* T75/52).

### (ii) *Laboratory crosses*

Several crosses were set up between males and females of known phenotypes to test the hypothesis of a major gene (see tables 2a-h). Of the 36 possible pair-wise combinations (of the six grades), only 23 were done due to the shortage of UL and L females. Four crosses were set up with single pairs, but otherwise the cages contained more than one of each sex. Two separate egg clusters taken from a single cage may therefore be derived from different parents (*e.g.* compare T74E2 and T74E3).

If the dark allele is recessive, flies scored as Dark Phenotype will usually carry a homozygous genotype ($Ap^{d}$ $Ap^{d}$). When two such flies are mated, an all-dark brood is expected. This is confirmed by 11 crosses in table 2a. Broods contained very few offspring that were not scored as D.ph. (the exceptions were all ML males and M females). The modal grades were not constant, being either MD or D for females and M, MD or D for male progeny. Also included here (table 2b) are two cases in which the parental females had been scored as grade M, and thus by definition were L.ph. Cross T74U indicates that all progeny from T74/1 were genetically " dark " despite showing a broad spread of patterns (see table 1a). Cross T74$\eta$ may clarify the apparently deviant assortment amongst females from T74j (table 2d).

Crosses between L.ph. and D.ph. *E. tenax* will yield either 1 : 1 broods (if the L.ph. parent is heterozygous) or entirely light patterns (if L.ph. is

TABLE 1

*Offspring reared in the laboratory from eggs laid by captured female* Eristalis tenax. *Total numbers of Light and Dark Phenotype shown in bold type. Note that D.ph. comprises M, MD, D males but only MD and D females*

| | | | ♂ | | | | | | ♀ | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Female | Pattern | Comments† | UL | L | ML | M | MD | D | UL | L | ML | M | MD | D | L.ph. | D.ph. |
| 1(a) "*All-dark*" *broods* | | | | | | | | | | | | | | | | |
| T73/5 | D | M, 1 | 0 | 0 | 0 | 10 | 11 | 0 | 0 | 0 | 0 | 0 | 3 | 6 | **0** | **30** |
| T73/36 | D | J, 1 | 0 | 0 | 0 | 0 | 6 | 25 | 0 | 0 | 0 | 0 | 2 | 29 | **0** | **62** |
| T73/49 | D | A, 1 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 5 | **0** | **12** |
| T74/1 | MD | M, 4* | 0 | 0 | 4 | 70 | 36 | 3 | 0 | 0 | 0 | 23 | 71 | 38 | **27** | **218** |
| T74/6 | D | M, 2 | 0 | 0 | 0 | 10 | 18 | 8 | 0 | 0 | 0 | 0 | 5 | 21 | **0** | **62** |
| T74/13 | MD | M, 1 | 0 | 0 | 0 | 3 | 23 | 30 | 0 | 0 | 0 | 1 | 29 | 29 | **1** | **104** |
| T74/16 | D | M, 3* | 0 | 3 | 7 | 18 | 24 | 19 | 0 | 0 | 1 | 16 | 22 | 30 | **27** | **113** |
| T74/18 | MD | M, 2 | 0 | 0 | 0 | 10 | 9 | 4 | 0 | 0 | 0 | 1 | 10 | 25 | **1** | **58** |
| T74/23 | D | M, 1 | 0 | 0 | 0 | 9 | 17 | 10 | 0 | 0 | 0 | 1 | 3 | 31 | **1** | **70** |
| T75/53 | D | A, 2 | 0 | 0 | 0 | 20 | 25 | 34 | 0 | 0 | 0 | 2 | 12 | 51 | **2** | **142** |
| T75/59 | MD | A, 2* | 0 | 11 | 28 | 36 | 38 | 6 | 0 | 0 | 8 | 13 | 63 | 55 | **60** | **198** |
| T75/60 | MD | A, 3 | 0 | 0 | 0 | 0 | 29 | 105 | 0 | 0 | 0 | 0 | 2 | 134 | **0** | **270** |
| T76/1 | MD | F, 1 | 0 | 0 | 0 | 10 | 19 | 7 | 0 | 0 | 0 | 1 | 14 | 7 | **1** | **57** |
| 1(b) "*All-light*" *broods* | | | | | | | | | | | | | | | | |
| T73/4 | M | M, 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | **7** | **0** |
| T74/19 | M | M, 1* | 26 | 39 | 20 | 10 | 0 | 0 | 0 | 2 | 44 | 20 | 2 | 0 | **151** | **12** |
| T74/21 | ML | M, 3 | 62 | 41 | 2 | 0 | 0 | 0 | 0 | 4 | 105 | 36 | 0 | 0 | **250** | **0** |
| T75/54 | MD | A, 2 | 47 | 81 | 2 | 0 | 0 | 0 | 0 | 31 | 115 | 7 | 0 | 0 | **283** | **0** |
| T75/62 | M | A, 1 | 31 | 29 | 3 | 0 | 0 | 0 | 0 | 0 | 39 | 27 | 0 | 0 | **129** | **0** |

1(c) *Broods assorting approximately 1 : 1*

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| T73/2 | M | M, 1 | 0 | 1 | 3 | 2 | 0 | 0 | 0 | 0 | 1 | 4 | 4 | 0 | **9** | **6** |
| T73/34 | ‡ | J, 1 | 4 | 11 | 6 | 3 | 13 | 2 | 0 | 0 | 3 | 6 | 0 | 2 | **30** | **20** |
| T74/4 | D | M, 1 | 6 | 11 | 1 | 2 | 10 | 5 | 0 | 7 | 9 | 2 | 2 | 18 | **36** | **37** |
| T74/8 | ML | M, 2 | 17 | 31 | 1 | 1 | 33 | 15 | 0 | 1 | 35 | 3 | 14 | 29 | **88** | **92** |
| T74/10 | M | M, 4 | 4 | 31 | 2 | 19 | 17 | 2 | 0 | 1 | 17 | 30 | 27 | 12 | **85** | **77** |
| T74/24 | MD | M, 3 | 0 | 44 | 28 | 19 | 55 | 5 | 0 | 0 | 24 | 47 | 45 | 41 | **143** | **165** |
| T74/25 | rM | A, 1 | 4 | 43 | 18 | 17 | 8 | 5 | 0 | 0 | 14 | 26 | 21 | 22 | **105** | **73** |
| T75/56 | M | A, 3 | 17 | 56 | 4 | 13 | 54 | 9 | 0 | 7 | 64 | 5 | 11 | 50 | **153** | **137** |
| T75/61 | M | A, 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 2 | 6 | **5** | **9** |
| T75/64 | M | A, 1 | 2 | 23 | 0 | 12 | 10 | 9 | 0 | 0 | 20 | 9 | 7 | 14 | **54** | **52** |
| T75/83 | rM | S, 1 | 10 | 18 | 8 | 6 | 15 | 6 | 0 | 0 | 10 | 11 | 1 | 21 | **57** | **49** |
| T76/811 | ‡ | M, 1 | 6 | 15 | 0 | 5 | 22 | 1 | 0 | 1 | 13 | 6 | 3 | 18 | **41** | **49** |

1(d) *Broods assorting approximately 3 : 1*

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| T73/35 | ‡ | J, 1 | 9 | 11 | 5 | 1 | 2 | 4 | 0 | 0 | 3 | 4 | 1 | 5 | **32** | **13** |
| T74/12 | ML | M, 3 | 21 | 36 | 24 | 1 | 16 | 8 | 0 | 1 | 62 | 37 | 5 | 17 | **181** | **47** |
| T74/20 | M | M, 1 | 8 | 31 | 6 | 0 | 4 | 11 | 0 | 0 | 25 | 17 | 3 | 20 | **87** | **38** |
| T75/52 | M | M, 2 | 13 | 43 | 14 | 2 | 8 | 4 | 0 | 5 | 30 | 23 | 11 | 18 | **128** | **43** |
| T75/58 | M | A, 1 | 1 | 4 | 2 | 0 | 4 | 1 | 0 | 0 | 9 | 0 | 0 | 1 | **16** | **6** |
| T76/21 | M | A, 1 | 7 | 34 | 5 | 0 | 1 | 13 | 0 | 1 | 11 | 24 | 0 | 9 | **82** | **23** |

† Comments — letter indicates month of capture (F = February, M = March, A = April, J = July, S = September) and figure indicates the number of broods reared. Data are for the total offspring from each female.

* Unimodal broods with wide spread — see text. Modifying genes probably involved.

‡ Batch of eggs from cage containing both M and MD females.

TABLE 2

*Details of laboratory matings of* E. tenax: *data for broods containing at least 10 flies. Origin of parents refers to brood of wild female or previous cross. Totals of Light and Dark Phenotype in bold type. Note that D.ph. comprises M, MD, D males and MD, D females*

| Cross | Parents ♀ | | | ♂ | | Progeny ♂ UL | L | ML | M | MD | D | ♀ UL | L | ML | M | MD | D | L.ph. | D.ph. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2(a) *D.ph.* × *D.ph. crosses: only dark offspring expected* | | | | | | | | | | | | | | | | | | | |
| T74G | T74/10 | MD | × | T74/1 | M | 0 | 0 | 1 | 20 | 4 | 0 | 0 | 0 | 0 | 6 | 33 | 11 | **7** | **68** |
| | | | | | | 0 | 0 | 0 | 4 | 5 | 0 | 0 | 0 | 0 | 0 | 7 | 9 | **0** | **25** |
| T74T | T74/18 | D | × | T74/10 | M | 0 | 0 | 1 | 33 | 28 | 5 | 0 | 0 | 0 | 6 | 36 | 19 | **7** | **121** |
| T74W | T74/6 | D | × | T74/16 | D | 0 | 0 | 0 | 0 | 9 | 23 | 0 | 0 | 0 | 0 | 1 | 42 | **0** | **75** |
| T74X | T74/1 | MD | × | T74/4 | D | 0 | 0 | 0 | 4 | 8 | 0 | 0 | 0 | 0 | 0 | 7 | 6 | **0** | **25** |
| T74a | T74W— | D | × | T74X— | M | 0 | 0 | 0 | 0 | 9 | 24 | 0 | 0 | 0 | 0 | 1 | 31 | **0** | **65** |
| T74x | DB73— | MD | × | DB73— | M | 0 | 0 | 0 | 4 | 9 | 6 | 0 | 0 | 0 | 0 | 1 | 12 | **0** | **32** |
| T74α | T74a— | D | × | T74T— | M | 0 | 0 | 0 | 10 | 9 | 1 | 0 | 0 | 0 | 1 | 12 | 2 | **1** | **34** |
| T75E | T75/60 | D | × | T75/53 | MD | 0 | 0 | 0 | 5 | 12 | 1 | 0 | 0 | 0 | 0 | 4 | 23 | **0** | **45** |
| | | | | | | 0 | 0 | 0 | 1 | 13 | 1 | 0 | 0 | 0 | 0 | 2 | 14 | **0** | **31** |
| T75F | T75/53 | MD | × | T75/60 | D | 0 | 0 | 1 | 5 | 15 | 0 | 0 | 0 | 0 | 0 | 12 | 11 | **1** | **43** |
| | | | | | | 0 | 0 | 0 | 23 | 20 | 0 | 0 | 0 | 0 | 3 | 19 | 35 | **3** | **97** |
| T75Q | T75E— | D | × | T75C— | MD | 0 | 0 | 0 | 0 | 5 | 13 | 0 | 0 | 0 | 0 | 1 | 21 | **0** | **40** |
| T75T§ | T75J— | MD | × | T75J— | MD | 0 | 0 | 0 | 1 | 11 | 8 | 0 | 0 | 0 | 0 | 3 | 16 | **0** | **39** |
| 2(b) *"All-dark" broods from cross between D.ph. male, and female of borderline L.ph. pattern but probably* $Ap^d$ $Ap^d$ *genotype* | | | | | | | | | | | | | | | | | | | |
| T74U | T74/1 | M | × | T74/23 | D | 0 | 0 | 0 | 5 | 34 | 21 | 0 | 0 | 0 | 0 | 20 | 43 | **0** | **123** |
| T74η | T74j— | rM | × | T74d— | MD | 0 | 0 | 2 | 23 | 14 | 0 | 0 | 0 | 0 | 3 | 24 | 2 | **5** | **63** |
| 2(c) *Crosses between heterozygous L.ph. and D.ph.—1 : 1 assortment expected. Significant deviation from 1 : 1 ratio indicated* | | | | | | | | | | | | | | | | | | | |
| T74C†† | T74/1 | M | × | T74/24 | L | 0 | 15 | 1 | 26 | 3 | 0 | 0 | 0 | 11 | 16 | 20 | 4 | **43** | **53** |
| T74D | T74/8 | ML | × | T74/16 | M | 3 | 6 | 3 | 0 | 0 | 1 | 0 | 0 | 9 | 2 | 4 | 1 | **23** | **6**‡ |
| | | | | | | 8 | 4 | 3 | 1 | 4 | 2 | 0 | 1 | 8 | 11 | 3 | 6 | **35** | **16**‡ |
| T74M | T74/4 | D | × | T74/10 | L | 3 | 25 | 1 | 1 | 16 | 2 | 0 | 0 | 10 | 11 | 7 | 24 | **50** | **50**‡‡ |
| | | | | | | 0 | 1 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 4 | 0 | 5 | **6** | **9** |
| T74S | T74/24 | M | × | T74/18 | M | 0 | 13 | 11 | 4 | 11 | 1 | 0 | 0 | 4 | 24 | 11 | 12 | **52** | **39** |
| T74e | T74M— | M | × | T74C | M | 5 | 16 | 0 | 1 | 14 | 9 | 0 | 3 | 6 | 13 | 2 | 17 | **43** | **43** |

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| T74k | T74L— | M | × | T74G | M | 4 | 15 | 7 | 8 | 23 | 0 | 0 | 0 | 9 | 11 | 8 | 19 | **46** | **58** |
| | | | | | | 0 | 3 | 1 | 0 | 1 | 4 | 0 | 0 | 1 | 9 | 0 | 3 | **14** | **8** |
| T74δ | T74c— | ML | × | T74a— | D | 1 | 1 | 0 | 4 | 0 | 0 | 0 | 0 | 2 | 1 | 3 | 2 | **5** | **9** |
| T75J | T75/59 | MD | × | T75/64 | L | 17 | 1 | 1 | 4 | 11 | 8 | 0 | 7 | 8 | 2 | 8 | 19 | **36** | **50** |
| 2(d) *Crosses of D.ph.* × *L.ph. (genotype uncertain) which produced segregating broods. Deviation from 1 : 1 ratio indicated* | | | | | | | | | | | | | | | | | | | |
| T74E3 | T74/19 | ML | × | T74/20 | D | 0 | 6 | 3 | 0 | 0 | 5 | 0 | 0 | 1 | 5 | 0 | 15 | **15** | **20** |
| T74F | T74/20 | M | × | T74/1 | MD | 0 | 4 | 4 | 0 | 1 | 0 | 0 | 0 | 2 | 3 | 0 | 1 | **13** | **2**‡ |
| | | | | | | 1 | 11 | 1 | 1 | 7 | 4 | 0 | 0 | 1 | 8 | 1 | 13 | **22** | **26** |
| T74c | T74C— | MD | × | T74I— | UL | 14 | 12 | 0 | 7 | 16 | 2 | 0 | 11 | 13 | 3 | 10 | 14 | **53** | **49** |
| T74j | T74G— | MD | × | T74A— | L | 6 | 8 | 1 | 13 | 3 | 1 | 0 | 0 | 15 | 9* | 11 | 1 | **39** | **29** |
| T75C | T75/56 | D | × | T75/54 | L | 1 | 11 | 0 | 1 | 7 | 5 | 0 | 1 | 9 | 3 | 4 | 12 | **25** | **29** |
| | | | | | | 11 | 14 | 0 | 4 | 34 | 0 | 0 | 0 | 18 | 1 | 9 | 14 | **44** | **61** |
| T75D | T75/54 | ML | × | T75/56 | MD | 8 | 6 | 0 | 1 | 11 | 0 | 0 | 2 | 6 | 0 | 10 | 5 | **22** | **27** |
| T75G§ | T75/60 | D | × | T75/54 | UL | 10 | 3 | 0 | 2 | 12 | 1 | 0 | 0 | 13 | 2 | 6 | 4 | **28** | **25** |
| T75N§ | T75/59 | MD | × | T75/62 | UL | 10 | 5 | 0 | 2 | 6 | 0 | 0 | 2 | 10 | 2 | 2 | 11 | **29** | **21** |
| 2(e) *Crosses of D.ph.* × *L.ph. which yielded " all-light " broods* | | | | | | | | | | | | | | | | | | | |
| T74A | T74/21 | ML | × | T74/8 | MD | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 1 | 6 | 8 | 0 | 0 | **20** | **0** |
| | | | | | | 4 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 7 | 0 | 0 | **35** | **0** |
| T74E2 | T74/19 | ML | × | T74/20 | D | 1 | 5 | 11 | 0 | 0 | 0 | 0 | 0 | 3 | 14 | 0 | 0 | **34** | **0** |
| T74H† | T74/13 | MD—D | × | T74/19 | UL | 1 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 8 | 0 | 0 | **23** | **0** |
| | | | | | | 1 | 14 | 3 | 0 | 0 | 0 | 0 | 0 | 5 | 7 | 0 | 0 | **30** | **0** |
| T74L | T74/16 | D | × | T74/21 | UL | 15 | 54 | 15 | 1 | 0 | 0 | 0 | 2 | 23 | 49 | 0 | 0 | **158** | **1** |
| | | | | | | 1 | 7 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 26 | 0 | 0 | **37** | **3** |
| T74P† | T74/6 | D | × | T74/12 | L.ph. | 0 | 3 | 8 | 0 | 0 | 0 | 0 | 0 | 3 | 17 | 0 | 0 | **31** | **0** |
| 2(f) *Crosses between two heterozygous L.ph. parents—a 3 : 1 ratio expected (deviation indicated)* | | | | | | | | | | | | | | | | | | | |
| T74I | T74/10 | ML | × | T74/4 | L | 9 | 9 | 1 | 0 | 2 | 4 | 0 | 4 | 2 | 8 | 2 | 1 | **33** | **9** |
| | | | | | | 24 | 11 | 3 | 5 | 5 | 0 | 1 | 20 | 16 | 17 | 5 | 7 | **92** | **22** |
| T74R | T74/24 | M | × | T74/24 | L | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 0 | 1 | 1 | 3 | 3 | **6** | **9**‡ |

* Some M females were of " rM " pattern and probably homozygous $Ap^{d}$ $Ap^{d}$ (cross T74j).
† Exact patterns of both parents not known—flies of different grades within same " morph " used.
‡ Significant deviation from expected ratio ($P<0{\cdot}01$ in each case).
§ Single-pair cross.
†† T74G included in table 2c—females of pattern M but $Ap^{d}$ $Ap^{d}$ genotype.
‡‡ T74M—heterogeneity between sexes (het. $\chi^2 = 4{\cdot}01$, $P<0{\cdot}05$).

TABLE 2 contd.

| Cross | Parents ♀ | | | ♂ | | Progeny ♂ UL | L | ML | M | MD | D | ♀ UL | L | ML | M | MD | D | L.ph. | D.ph. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2(f) *Crosses between two heterozygous L.ph. parents—contd.* | | | | | | | | | | | | | | | | | | | |
| T74b | T74F— | M | × | T74F— | L | 1 | 4 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 4 | 0 | 3 | **12** | **4** |
| | | | | | | 2 | 12 | 7 | 0 | 4 | 0 | 0 | 0 | 4 | 16 | 1 | 4 | **41** | **9** |
| T74m | T74D— | ML | × | T74L— | L | 23 | 5 | 0 | 11 | 0 | 0 | 0 | 8 | 24 | 30 | 12 | 0 | **90** | **23** |
| T74n | T74A— | ML | × | T74D— | ML | 0 | 5 | 1 | 0 | 1 | 0 | 0 | 0 | 3 | 1 | 1 | 1 | **10** | **3** |
| T74q | T74H— | ML | × | T74E2— | L | 9 | 11 | 5 | 0 | 4 | 6 | 0 | 1 | 7 | 5 | 0 | 7 | **38** | **17** |
| T74r | T74E2— | M | × | T74H— | L | 5 | 20 | 12 | 0 | 4 | 6 | 0 | 0 | 7 | 28 | 3 | 7 | **72** | **20** |
| T74s | T74H— | M | × | T74P— | ML | 4 | 14 | 0 | 0 | 3 | 3 | 0 | 3 | 6 | 5 | 0 | 6 | **32** | **12** |
| | | | | | | 0 | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 4 | 2 | 0 | **11** | **3** |
| T74y | T74S— | M | × | T74S— | L | 4 | 14 | 2 | 8 | 0 | 0 | 0 | 0 | 9 | 21 | 4 | 0 | **50** | **12** |
| T75S§ | T75G— | ML | × | T75D— | L | 24 | 19 | 3 | 0 | 3 | 14 | 0 | 4 | 28 | 7 | 0 | 15 | **85** | **32** |
| | | | | | | 5 | 11 | 6 | 0 | 1 | 8 | 0 | 0 | 14 | 8 | 0 | 6 | **44** | **15** |
| 2(g) *Crosses of L.ph. × L.ph. (where at least one parental genotype was uncertain) that produced 3 : 1 assortments.* | | | | | | | | | | | | | | | | | | | |
| T74d | T74I— | M | × | T74F— | L | 6 | 6 | 1 | 5 | 3 | 0 | 0 | 1 | 10 | 6 | 0 | 0 | **30** | **8** |
| T75M | T75/62 | ML | × | T75/62 | UL | 5 | 0 | 0 | 3 | 2 | 0 | 0 | 3 | 12 | 5 | 5 | 1 | **25** | **11** |
| 2(h) *Crosses of L.ph. × L.ph. (at least one genotype uncertain) producing "all-light" broods.* | | | | | | | | | | | | | | | | | | | |
| T74Q† | T74/8 | ML | × | T74/21 | L—UL | 34 | 26 | 7 | 0 | 0 | 0 | 0 | 1 | 45 | 20 | 0 | 0 | **133** | **0** |
| T74f | T74I— | L | × | T74I— | UL | 48 | 19 | 0 | 0 | 0 | 0 | 14 | 18 | 13 | 9 | 0 | 0 | **121** | **0** |
| T74t | T74Q— | ML | × | T74E3— | L | 10 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 7 | 0 | 0 | **41** | **0** |
| T74*y*† | T74m— | L.ph. | × | T74m— | L.ph. | 29 | 6 | 0 | 0 | 0 | 0 | 0 | 13 | 13 | 12 | 0 | 0 | **73** | **0** |
| T74*θ* | T74Q— | ML | × | T74b— | UL | 65 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 85 | 2 | 0 | 0 | **154** | **0** |
| Sel/2 | Sel/1— | ML | × | Sel/1— | UL | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 6 | 0 | 0 | 0 | **14** | **0** |
| T75A | T74*θ*— | ML | × | T75/52 | ML | 42 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 43 | 1 | 0 | 0 | **86** | **0** |
| | | | | | | 26 | 10 | 0 | 0 | 0 | 0 | 0 | 1 | 33 | 1 | 0 | 0 | **71** | **0** |
| T75B | T75/52 | M | × | T75/52 | UL | 26 | 9 | 1 | 0 | 0 | 0 | 0 | 10 | 9 | 0 | 0 | 0 | **55** | **0** |
| | | | | | | 42 | 18 | 2 | 0 | 0 | 0 | 0 | 21 | 22 | 3 | 0 | 0 | **108** | **0** |

† Exact patterns of both parents not known—flies of different grades within same "morph" used.
§ Single-pair cross.

homozygous $Ap^L$ $Ap^L$). L.ph. *E. tenax* should be heterozygotes if they come from L.ph. × D.ph. matings or from 1 : 1 broods of wild females (see table 2c), but otherwise their genotype is uncertain (see tables 2d and 2e). In most cases where a 1 : 1 ratio was expected from a L.ph. × D.ph. cross, the results were in agreement although sometimes there was a discrepancy between the sexes (only significant for a brood from T74M—heterogeneity $\chi^2_1 = 4{\cdot}01$, $P < 0{\cdot}05$). The poor results from T74D were associated with high pupal mortality. Selective mortality of one morph is possible, but the total numbers of L.ph. (353) and D.ph. (341) from the crosses shown in table 2c show no overall differential viability ($\chi^2_1 = 0{\cdot}21$, $P > 0{\cdot}5$).

Both all-light and 1 : 1 broods were obtained from matings where the genotype of the light parent was ambiguous. Two dissimilar broods from T74E were clearly from different females; this cage contained five females and three males. The anomalous ratio in the first brood of T74F was probably caused by high pupal mortality because it seems unlikely that the MD male could have carried an $Ap^L$ allele.

When a pair of L.ph. *E. tenax* are crossed, one expects the progeny to be all of the light phenotype or segregate 3 : 1. Where the origin of both parents indicated heterozygosity, a 3 : 1 ratio should occur (table 2f). The offspring of T74R were not as expected, but this cross was a sib-mating. Most of the L.ph. flies were malformed, and the deviant ratio could be the result of greater mortality amongst the light flies. That this is not a general feature of 3 : 1 broods is indicated by the close overall agreement to the predicted proportions (616 L.ph., 190 D.ph. – $\chi^2_1 = 0{\cdot}87$, $P > 0{\cdot}3$).

In the remaining broods, where at least one parental genotype was unknown, most cases produced only L.ph. progeny (tables 2g and 2h). Some crosses yielded more variable offspring than others, especially when females were examined (compare T74f with T74$\theta$). A possible factor is that some broods contained two genotypes (*i.e.* $Ap^L$ $Ap^L$ and $Ap^L$ $Ap^d$) and others only one. Therefore some of the variability within the L.ph. category may result from incomplete dominance of the light allele (Heal, 1977). The peculiar result from T74d suggests a sex-linked gene, but the rest of the data lead to the conclusion that the *Ap* locus is autosomal.

The analysis already presented shows that a major part of the colour pattern variation in *E. tenax*, namely the assortment into lighter and darker categories, can be explained by a major gene (the *Ap* locus) with two alleles, light pattern being dominant to dark. However it is also apparent that the two morphs are not discrete classes, and where overlap occurs, genotypes cannot always be inferred unambiguously from external appearance alone.

Since both L.ph. and D.ph. can be subdivided into a series of grades, other sources of variability must be involved, and could be either environmental factors or modifying genes. To estimate the heritability of the character, pattern grades were scored as $D = 1$ to $UL = 6$. Mean values for male and female offspring in each brood were evaluated ($\bar{m}$ and $\bar{f}$ respectively). Single sex comparisons between parent and offspring (*e.g.* sons with fathers) would overcome the problem of wider variation in males than females, but this approach is invalid because pairs were not chosen at random. Consequently, the best comparison is between the mid-parent value ($\bar{p}$) and the mid-offspring value ($\bar{o} = \frac{1}{2}(\bar{m}+\bar{f})$). The regression coefficient of $\bar{o}$ on $\bar{p}$ is an estimate of $h^2$. The overall heritability was very

high under the fairly constant conditions of the laboratory, being approximately 0·9 (see table 3).

However, a major contribution to the high overall $h^2$ estimate comes from the *Ap* gene. Its effect can be reduced by looking at crosses between *E. tenax* of the same " morph ", *i.e.* dark × dark, or light × light. Taking 15 dark patterned broods (those in tables 2a and 2b containing at least 10 of each sex), the regression coefficient obtained was:

$$b_{\bar{o}/\bar{p}} = 0{\cdot}52 \pm 0{\cdot}23$$

This is significantly different from both 0 and 1 ($P < 0{\cdot}05$ in each case). The figure of 0·52 is an estimate of the heritability of variation in pattern within the dark morph, *i.e.* for those flies shown to be homozygous for the $Ap^{d}$ allele. Crosses between light patterned flies may produce 3 : 1 broods, but in this analysis the mean score of L.ph. offspring only was compared to the mid-parent value. This will include both flies homozygous and also those heterozygous for the $Ap^{L}$ allele. From 21 broods (those in tables 2f-h with at least 20 L.ph. progeny) the estimated value for $h^2$ within the light morph was:

$$b_{\bar{o}/\bar{p}} = 0{\cdot}46 \pm 0{\cdot}17 \qquad \text{(L.ph. only)}.$$

Thus approximately half of the variation within the Light and Dark Phenotype categories considered separately is attributed to modifying genes, but further differences must result from environmental factors. Although broods were reared according to a standard procedure, it was inevitable that

TABLE 3

*Correlation ($r$) between male and female offspring, and regression of mid-offspring ($\bar{o}$) on mid-parent ($\bar{p}$) values. Data from broods in table 2 containing at least 10 flies of each sex*

| Year | No. of broods | $r(\bar{m}, \bar{f})$ | $b_{\bar{o}/\bar{p}}$ |
|---|---|---|---|
| 1974 | 41 | 0·95 | 0·88 ± 0·08 |
| 1975 | 19 | 0·96 | 0·90 ± 0·12 |
| Combined | 60 | 0·95 | 0·89 ± 0·06 |

$b_{\bar{o}/\bar{p}}$ is taken as an estimate of the overall heritability.

TABLE 4

*Estimates of $h^2$ within dark and light morphs derived from broods of L.ph. × D.ph. crosses (tables 2c-e). Comparisons made between D.ph. progeny and D.ph. parents, L.ph. progeny and L.ph. parents*

| Parental type considered | N | $b_{\bar{m}/p}$ | $b_{\bar{f}/p}$ | Estimated $\frac{1}{2}h^{2}$‡ | Within-morph heritability§ |
|---|---|---|---|---|---|
| D.ph.♂ | 6 | 0·45 | 0·10 | 0·28 | 0·55 |
| D.ph.♀ | 8* | 0·38 | 0·16 | 0·27 | |
| L.ph.♂ | 11 | 0·24 | 0·15 | 0·20 | 0·49 |
| L.ph.♀ | 7† | 0·20 | 0·43 | 0·32 | |

Data were used from the largest brood of each cross provided that there were at least 20 of the relevant phenotype.

† Excluding deviant results of T74D.

* This includes T74C—see note to table 2.

‡ Mean of regression coefficients.

§ Using a weighted mean of the separate estimates.

temperature, degree of larval crowding and other conditions were not always the same.

Some further confirmation for a within-morph heritability of about 0·5 is shown in table 4. Data from L.ph. × D.ph. crosses (tables 2c-e) have been used to calculate the regressions of dark or light progeny of each sex on the parent of the same phenotypic category. In these single parent comparisons, the regression coefficient is equivalent to $\frac{1}{2}h^2$. Individual values of b may not be significantly different from 0, but all are positive and the mean estimates of the within-morph heritability are in surprisingly close agreement with the figures given above (*i.e.* approximately 0·5).

## 4. Discussion

The control of colour pattern variation in *Eristalis tenax* differs from that in other hoverfly species that have been studied. In two bumblebee mimics, *Volucella bombylans* and *Merodon equestris*, a number of distinct phenotypes are present and particular aspects of the patterns have been attributed to individual loci (Gabritchevsky, 1924; Conn, 1972). This is not unlike the control of mimetic patterns in some polymorphic butterflies (Sheppard, 1975).

If the range of phenotypes cannot be divided into two or more distinct morphs, the genetic analysis becomes more complicated. This was particularly true for *E. tenax* because both size and shade of the abdominal markings vary. However, the presence of a continuous range of patterns does not mean that only polygenic inheritance is involved. Breeding experiments indicated the presence of two alleles at a locus for abdominal pattern. The light allele ($Ap^L$) is dominant but it is not certain whether dominance is complete because there is considerable variability within the Light Phenotype class. Despite the segregation of alleles at the major pattern locus, and thus a genetic polymorphism, one does not find two discrete varieties and so the homozygous recessive genotype is not identifiable in every case. Segregating broods show a bimodal distribution but often with slight overlap between the two morphs. A further complication is the sexual difference in expression. This required a different division between L.ph. and D.ph. categories in males and females.

The major gene is an important contributory factor towards the high overall heritability for colour pattern of 0·9. When its effect is minimised—by analysing variation within L.ph. and D.ph. groups separately—the data suggested a " within-morph " heritability of approximately 0·5. Therefore both polygenic influences and environmental factors are important, and it is their combined effect which produces the continuous range of patterns present in *E. tenax*. No modifying genes have been located, but further genetic studies require more rigorously controlled rearing conditions and a more detailed classification of the different patterns. Some experiments have shown that rearing temperatures during the pupal, and also larval, stages influenced the final pattern. Pupae kept in cold conditions produced darker adults (Heal, 1977).

Two questions may be posed:

1. If disruptive selection for pattern has produced a genetic polymorphism, why has it not yielded two discrete morphs mimicking the two principal varieties of *Apis mellifera* in Britain?

2. Why is there differential expression between the sexes in a species of which both males and females are apparently mimetic?

In areas where *E. tenax* were collected (*i.e.* North-West England), most *Apis* workers could be classified as either dark brown or orange-banded, although intermediate patterns were not uncommon. From crosses between dark *carnica* and banded *ligustica* honeybees, Kulincevic (1967) showed a clear dominance of the yellowish pigmentation. The absence of discrete morphs in *E. tenax* is not adequately explained by suggesting that Italian bees (*ligustica*) were introduced into Britain relatively recently, because the same range of patterns is found in *E. tenax* from continental Europe. Distinct varieties have evolved in mimetic butterflies such as *Papilio dardanus* (Sheppard, 1975) but *Eristalis tenax* lacks a suitable range of conspicuously different models. Since the two types of *Apis mellifera* are not greatly dissimilar, avian predators may not discriminate between them. Moreover, *E. tenax* is often abundant and in urban areas may outnumber the model species. This would also influence discrimination by predators and at higher densities variability could be generated by apostatic selection. Behavioural differences between the sexes affecting exposure to predation could be the cause of the differential expression.

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