

Phenotypic variation in colour pattern and seasonal plasticity in *Eristalis* hoverflies (Diptera: Syrphidae)

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Abstract. 1. An examination of phenotypic variation in colour pattern was carried out on four *Eristalis* hoverfly species using museum material.

2. The amount of phenotypic variation varied substantially among the species with *E.arbustorum* being the most variable. The other species showed a wide colour pattern range but less variation within that range (*E.abusivus* and *E.nemorum*), or a narrow range of colour variation (*E.horticola*).

3. Sexual colour dimorphism was apparent in all four species, but most pronounced in *E.abusivus* and *E.nemorum*.

4. There were good phenotype–season relationships shown by both sexes in all species, except for female *E.abusivus* and *E.nemorum*, with paler insects being more abundant during the warmer summer months.

5. Female, but not male, *E.arbustorum* collected at inland sites were on average paler than those collected at coastal sites. This observation is considered with respect to temperature during the developmental stages.

6. The function of colour plasticity in hoverflies is discussed with reference to the need to maintain optimal thermal conditions for activity.

Key words. Syrphidae, *Eristalis*, phenotypic variation, phenotypic plasticity, colour variation, seasonal variation.

Introduction

Many hoverflies (Syrphidae) possess yellow and black colorations, particularly on the abdomen. Because of their, sometimes superficial, resemblance to wasps, particularly in many of the aphid feeding Syrphinae, these colours are thought to serve a mimetic purpose. Colour and pattern generally varies little among individuals of some of these species (e.g. *Chrysotoxum* spp.) which is consistent with the patterns having a mimetic function (Turner, 1977), although a certain amount of variation within a general aposematic scheme, even within well-known mimetic species such as ladybirds, can always be found (Dobzhansky & Sivertzev-Dobzhansky, 1927). Other hoverflies, for example *Eristalis tenax*, resemble honey bees more closely and it has been demonstrated in the laboratory that this resemblance can serve to protect hoverflies, to an extent, against vertebrate predation (Brower & Brower, 1962; Heal, 1982). However, *E.tenax*, along with many other

species in that genus, also show much quantitative colour variation. This suggests that the colours may serve other functions apart from or as well as mimicry.

The conditions under which insects live, especially multi-voltine temperate species such as *Eristalis* hoverflies, are not constant and it would make evolutionary sense for a developing insect to adjust its adult phenotype to increase its fitness in some way in response to an environmental variable. The ability of genetically identical organisms to produce different phenotypes in response to current environmental conditions is termed phenotypic plasticity (Bradshaw, 1965). It is becoming increasingly apparent that this type of phenotypic variation can often have a substantial influence on fitness (see Bradshaw, 1965; Schlichting, 1986; Stearns, 1989, for reviews) although probably not all plasticity is adaptive (Smith-Gill, 1983). Phenotypic plasticity is a very common phenomenon and because of this some scientists are predicting that far more attention will be devoted to studying phenotypic variation (Scharloo, 1989). Recently many studies have been carried out on phenotypic plasticity and its possible consequences for fitness (e.g. Dodson, 1974, 1989; Via, 1987; Via & Lande, 1985, 1987; Schlichting, 1989; Rice & Bazzaz,

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1989; Harvell, 1990; Rawson & Hilbish, 1991; Spitze, 1992; Strathmann *et al.*, 1992). However, many of these studies have been carried out in the laboratory and rather fewer descriptions of the relationship between phenotype and seasonal variation have been derived from the field. Exceptions include the work of Brakefield & Reitsma (1991) using *Bicyclus* butterfly species and Parejko & Dodson (1991) using *Daphnia pulex*. Monthly samples of *E. arbustorum* have been collected by Heal (1981) and here the fitness effect of the colour variation may be connected with thermal melanism, since darker insects are active under cooler conditions. However, it is unwise to assume that since one member of a genus shows seasonal variation in the field that all other species in the same genus show similar variation. This is highlighted by the *Bicyclus* butterfly species, of which there are seventy (Condamin, 1973), where some species are highly variable in response to environmental variation and others do not show any such plasticity whatsoever (H. Roskam, pers. comm.).

The purpose of the present study was three-fold: (1) to examine the degree of phenotypic variation in a number of *Eristalis* species using field derived material; (2) to examine the differences among the relationships between season and phenotype from very closely related species to determine whether the degree of relatedness results in very similar phenotype–season relationships; and (3) to determine whether geographic variation has a noticeable effect on the phenotype–season relationship in one species.

Materials and Methods

Museum material was used to examine plasticity and to derive the phenotype–season relationship in four species: *E. arbustorum*, *E. abusivus*, *E. horticola* and *E. nemorum*. Only insects collected in the Netherlands were used. The insects had been collected randomly from each site (P. van Helsdingen, pers. comm.) so that the sample of each species was not biased by an excessive number of unusual variants. Most of the insects were collected between 1960 and 1990, but a substantial number were also collected between 1940 and 1945.

The colour variation in the *Eristalis* species is largely limited to the extent of the pale patches (yellow to yellowish brown) on tergites 2 and 3. The yellow pigment in a preserved specimen often changes colour slightly, although the extent of the yellow coloration could always be seen. It is also the case that among living specimens the intensity of yellow often varies, but this source of variation was not considered in the present study. For each specimen, sex, colour category (see below), date and place of collection was recorded. Colour was scored according to a system similar to that used by Heal (1981) (see Fig. 1). *E. arbustorum* were placed into categories ranging from 1 (no yellow on tergites 2 or 3) to 7 (extensive areas of yellow on both tergites and yellow spreading out along trailing edge of tergite 3). Categories 2 and 3 differed slightly between the sexes in *E. arbustorum* as shown in Fig. 1. Fig. 1 also shows the range of variation that existed in male

E. arbustorum placed into category 6. *E. abusivus* and *E. nemorum* were placed into six categories, as shown in Fig. 1, and *E. horticola* was placed into only four categories.

For each species the data on sex, colour category and month of collection were used for analysis. Each month's data were split into half months: insects collected from 1st to 15th and 16th to the end of each month. The largest data set was for *E. arbustorum* and here the data was further split into collected at coastal site or collected at inland site. The purpose of this was to investigate the effect of geographic variation on adult phenotype. To split the complete data set objectively the 7.5°C April isotherm of average daily temperature in the Netherlands was used (Fig. 2) (cf. climatic maps K.N.M.I., 1972). Inland from this isotherm the average April daily temperature increases to about 10°C, and towards the coast and northwards towards the Wadden Sea the average daily temperature drops to around 5°C. The average daily temperature changes, of course, through the year, but from April through to September the temperature increases by around 2°C inland of this line and decreases by approximately 2°C towards the coast. Furthermore, this isotherm split the data set approximately equally.

All data analysis was carried out using the Minitab Statistical Package. Because of the non-normal distributions of the data sets, analyses were carried out using Kruskal-Wallis (*H*) non-parametric tests (Siegel, 1956). All of the *H* values presented are adjusted for ties. Two-weekly periods with less than five records were not included in the analysis to avoid small sample influences. The standard deviation bars indicated in Fig. 3 should be treated as approximate guides.

Results

A total of 5490 individuals was scored. The numbers of flies collected during each time period are shown in Table 1. Table 2 summarizes the degrees of phenotypic variation shown by the four species. *E. arbustorum* showed the greatest phenotypic variation of the four species considered here with male phenotypes ranging from category 2 to 7 (mean 5.531) and female phenotypes ranging from category 1 to 4 (mean 2.635) (see Fig. 1). The mean phenotype differed significantly between the sexes ($H = 2310$, $df = 1$, $P < 0.001$). 97.6% of the male phenotypes lay within the range 4–7 but substantial overlap occurred between the sexes within category 4.

In *E. abusivus* the sexual dimorphism was more pronounced than in *E. arbustorum* with the sexes not overlapping at all (male mean 5.857, female mean 2.021; $H = 704$, $df = 1$, $P < 0.001$). However, the amount of phenotypic variation shown by *E. abusivus* was considerably less than *E. arbustorum* with nearly 99.5% of the male insects falling into either category 5 or 6, 85% being category 6, and females produced a reasonably even distribution of category 1, 2 and 3 phenotypes.

E. nemorum was similar to *E. abusivus* in that there was hardly any overlap between the sexes and the level

Table 1. Numbers of flies captured during each half month period beginning with 1 for April through to 14 for the second half of October. The abbreviations arb., abu., hor. and nem. refer to *E.arbustorum*, *E.abusivus*, *E.horticola* and *E.nemorum*, respectively.

Sp.	Sex	April		May		June		July		Aug.		Sept.		Oct.		Total
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	
arb.	♂	12	56	140	71	142	253	194	143	240	169	126	84	6		1636
	♀	7	35	103	54	112	200	213	136	187	220	135	114	16	1	1533
abu.	♂		2	39	24	91	111	39	21	34	80	7	5	2		455
	♀		3	17	15	53	67	50	22	34	84	32	10	1		388
hor.	♂	1	6	39	81	58	43	35	16	20	29	9	6			343
	♀	1	1	18	47	36	50	45	30	28	40	8	5			309
nem.	♂	3	16	54	56	48	90	91	45	39	60	5	4			511
	♀	3	4	16	26	25	61	50	38	27	42	12	11			315

Table 2. Summary of the numbers of insects of each sex assigned to the various colour categories (see Fig. 1) in samples of four *Eristalis* species.

Species	Sex	Category						
		1	2	3	4	5	6	7
<i>E. arbustorum</i>	♂		2	37	109	504	910	74
	♀	257	349	624	303			
<i>E. abusivus</i>	♂				1	65	387	2
	♀	114	152	122				
<i>E. horticola</i>	♂	18	74	162	89			
	♀	81	172	56				
<i>E. nemorum</i>	♂			7	401	65	38	
	♀	49	122	142	2			

of phenotypic variation was fairly low. The mean male phenotype was 4.262, while the mean female phenotypic value was 2.308. The difference between the sexes was significant ($H = 653$, $df = 1$, $P < 0.001$). 98.6% of the males were categorized as phenotype 4, 5 or 6, although most of them were category 4 (78%), and 99.4% of the females fell into categories 1, 2 or 3.

The range of phenotypic variation in *E. horticola* across both sexes combined was much less than in *E. arbustorum*, *E. abusivus* and *E. nemorum* and was restricted to slight variation in the size of the yellow spots on tergite 2 and the presence or absence of small yellow stripes on tergite 3 (see Fig. 1). The difference between the sexes was also smaller (male mean 2.939, female mean 1.919), although it was still significant ($H = 211$, $df = 1$, $P < 0.001$).

Fig. 3 shows the relationships of the phenotypes of the four species with season. There was substantial variation among months in the mean phenotype of both sexes in *E. arbustorum* ($\delta H = 484.53$, $df = 12$, $P < 0.001$; $\eta H = 164.23$, $df = 13$, $P < 0.001$). Both sexes also showed a striking relationship with season with the flies becoming progressively paler through the year. However, in both sexes the flies become darker after early September. *E. abusivus* and *E. nemorum* both showed less plasticity

than *E. arbustorum*, but the difference among the months for both sexes was still significant ($\delta H = 74.19$, $df = 9$, $P < 0.001$; $\eta H = 17.74$, $df = 9$, $P = 0.04$ and $\delta H = 50.99$, $df = 9$, $P < 0.001$; $\eta H = 21.73$, $df = 9$, $P = 0.01$, respectively), although the H values for females were quite small. In the males there was a clear but weak relationship with season and in the females there was no good evidence of a phenotypic relationship with season, particularly so in *E. abusivus* (Fig. 3). Both sexes of *E. horticola* showed among month variation in phenotype ($\delta H = 77.70$, $df = 10$, $P < 0.001$; $\eta H = 19.75$, $df = 9$, $P = 0.02$), despite the limited amount of phenotypic variation shown by *E. horticola* (Fig. 1). Also, in both sexes there was a clear phenotypic relationship with season (Fig. 3), although, as with *E. abusivus* and *E. nemorum*, both the variation among months and the relationship with season was more impressive in males than in females.

The large *E. arbustorum* data set was split into coastal and inland observations using a line corresponding to the April 7.5°C mean daily temperature isotherm (see Fig. 2). This split produced 1426 (781♂ and 645♀) coastal records and 1743 (855♂ and 888♀) inland records. The purpose behind splitting the data set into two was to test for an effect of temperature in the field on the mean phenotype,

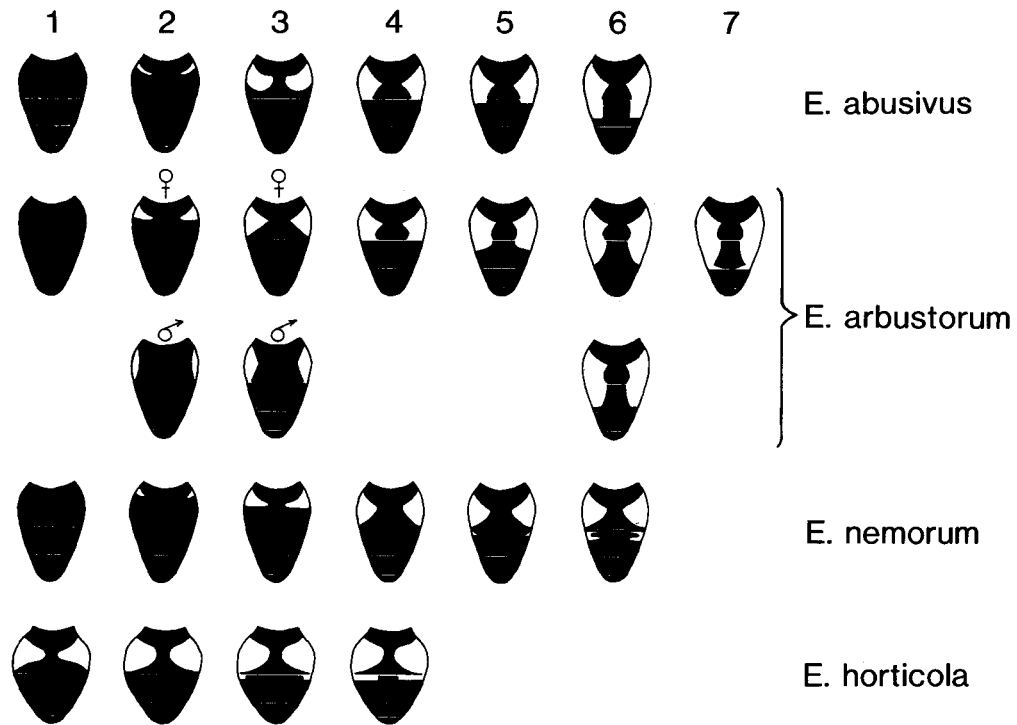


Fig. 1. Scheme used to classify extent of yellowish markings on abdominal tergites in four species of *Eristalis* hoverflies. Range of patterns in *E. arbustorum* placed into category 6 is shown. Categories 2 and 3 differed between the sexes in *E. arbustorum* as indicated.

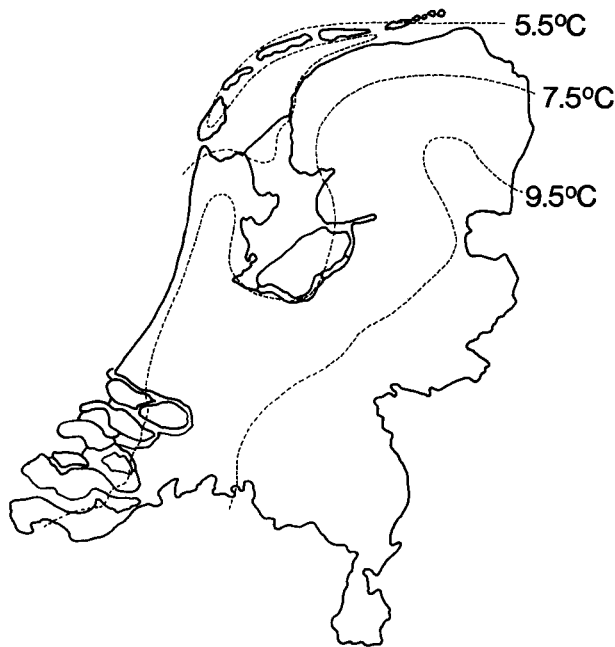


Fig. 2. Map of the Netherlands showing the positions of the 5.5°C, 7.5°C and 9.5°C mean daily temperature isoclines during April.

as the mean inland temperature is higher than coastal temperatures throughout the year. If the relationships shown in Fig. 3 are adaptive and temperature is a significant factor in the field, then inland insects should on average be paler than coastal insects. Fig. 4 shows the season-phenotype relationships in male and female *E. arbustorum* from inland and coastal sites. There was no significant difference between the two male data sets ($H = 0.17$, $df = 1$, $P = 0.678$), but the females collected from inland sites were significantly paler than those collected from coastal sites ($H = 7.87$, $df = 1$, $P = 0.005$), particularly from June to the end of the year.

Discussion

Many hoverflies are aposematically coloured and those with a bright yellow and black pattern appear to mimic wasps. Some of these wasp mimic species show little among individual colour variation. A few, in particular the bumblebee mimics, such as *Merodon equestris* (Conn, 1976) and *Volucella bombylans* (Gabritchevsky, 1924), are polymorphic, as is the honey bee mimic *E. tenax* (Heal, 1979a). Certain species are also prone to producing unusual variants, such as var. *unicolor* in *Scaeva pyrastris* where the normal whitish abdominal markings are lacking, although this type of variation probably has little function. There are also several other groups of hoverflies that show considerable continuous colour variation. This is particu-

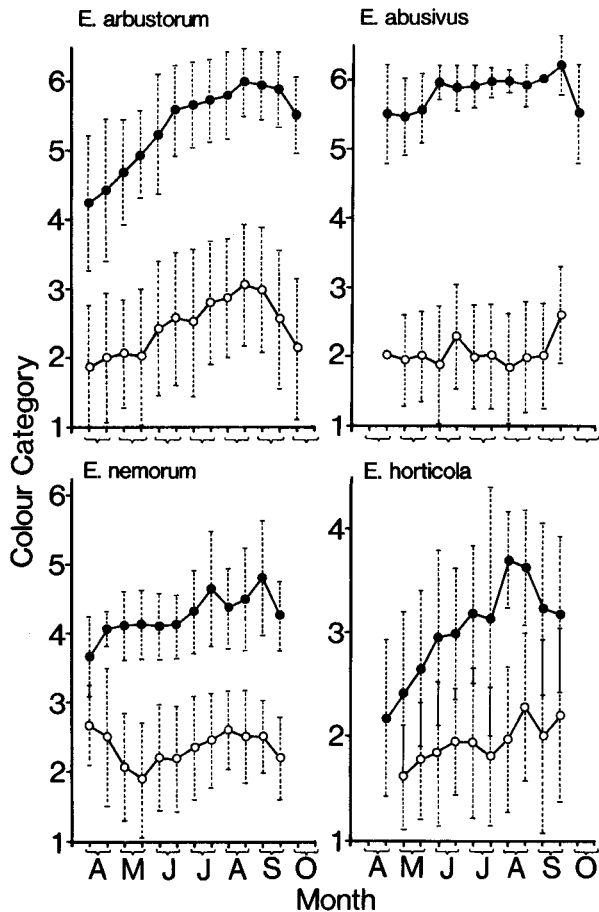


Fig. 3. The relationships between the mean colour category and season in four species of *Eristalis* hoverflies. Each monthly data set is split into two half months (see text). Half-monthly periods containing less than five observations are omitted. Solid and open circles refer to males and females, respectively. The dotted lines indicate one standard deviation.

larly obvious not only in many of the aquatic, detritus feeding hoverflies, such as *Eristalis* spp. and, although to a lesser extent, *Helophilus* spp., but also in several aphidophagous species, for example *Episyrphus balteatus*, *Melanostoma mellinum*, *Epistrophe eligans* and *Meliscaeva auricollis*. All of these species, as with *Eristalis* species, have long flight seasons, except for *E. eligans*, but this species does begin to appear in the field early on in the year during April.

A substantial amount of colour variation was found in the four *Eristalis* species examined here. It is apparent, however, that although the species are closely related (the only qualitative character available to separate *E. arbustorum* and *E. abusivus* is the length of the hairs on the arista (Goot, 1981; Stubbs & Falk, 1983)) the species differ substantially in the amount of colour variation shown (Table 2). Other *Eristalis* species also show remarkable among species differences in degree and type of colour variation. *E. intricarius* is a polymorphic bumblebee mimic that also shows a considerable range of intermediates

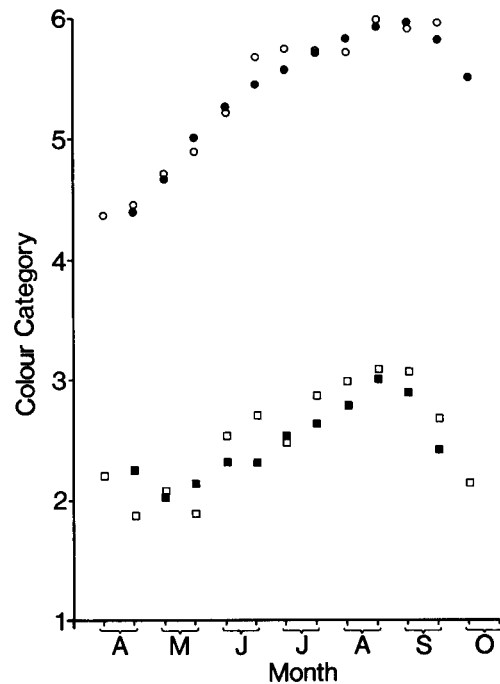


Fig. 4. The relationship between the mean colour category and season in *E. arbustorum* collected from inland and coastal sites. Each monthly data set is split into two half months (see text). Half-monthly periods containing less than five observations are omitted. Open symbols refer to inland sites and solid symbols to coastal sites. Circles refer to males and squares refer to females.

(Heal, 1979b). *E. tenax* carries a genetic polymorphism that contributes substantially to colour variation (Heal, 1979a), and *E. pertinax* varies mainly in intensity of the yellowish coloration but not so much in the extent of the yellow (pers. obs.). The variation shown by *E. arbustorum* is primarily environmentally induced and no genetic polymorphism affecting colour has been found in this species (Heal, 1981).

Heal found that the temperature under which *E. intricarius* (Heal, 1989) and *E. arbustorum* (Heal, 1981) pupae developed influenced adult phenotype with warmer conditions generally producing paler flies. This effect was considerably more marked in male *E. arbustorum* than females and temperature had a very limited effect in *E. tenax* (Heal, 1989). Temperature fluctuations may be responsible for the seasonal changes shown in Fig. 3. The temperature under which the immature stages of some other insects develop also influences adult phenotype, such as in the tropical butterflies *B. anynana* (Lepidoptera: Satyridae) (Brakefield & Reitsma, 1991) and *B. safitza* (Windig, 1993). However, closer examination of the system showed that the pupae respond not to the temperature *per se*, but rather to the length of the development period (Brakefield & Reitsma, 1991; Windig, 1993). For these butterflies many cues signalling the onset of the dry season, e.g. temperature, quality and availability of food, etc., are bundled into one character, development period. Heal's (1981, 1989) studies on the effect of temperature were

carried out in the laboratory. The mean phenotypes collected from inland sites in the Netherlands were significantly paler than those collected at coastal sites in females, but not in males (Fig. 4). The temperature difference between the coast and inland averages 3–4°C and it is tempting to interpret these phenotypic differences as the result of temperature variation. David *et al.* (1985) also showed geographic variation in the amount of pigmentation possessed by individuals of different populations of *Drosophila melanogaster*. However, this variation occurred across very large distances (between 30° and 50° latitude) rather than the relatively local scale considered here. Heal (1981) showed in *E. arbustorum* that male phenotypes were very susceptible to temperature but most females emerged from pupae with a category 3 phenotype (see Fig. 1) irrespective of development temperature. Thus Heal's findings and the results of the present study are apparently not consistent. It may be that other factors, as well as temperature, influence phenotype in the field, as with the *Bicyclus* butterflies (Windig, 1993).

Fig. 3 shows that in all species, at least in the males, there was a good relationship between adult phenotype and season. The average colour of the flies closely follows seasonal temperature fluctuations with the flies captured after late August/early September becoming progressively darker. David *et al.* (1985, 1990) and Cagy *et al.* (1988) showed an effect of temperature on amount of pigmentation in *D. melanogaster* and *D. simulans*, respectively, as did Heal (1989) in *E. intricarius*. Heal (1981) also noted an effect of season on phenotype in *E. arbustorum*, but only in males. Heal (1981) further demonstrated that a proportion of females became darker with age in the laboratory whilst males did not. This, he argued, was the reason why he found a seasonal relationship in males but not in females. The females that Heal (1981) examined for ageing effects on colour all lived longer than 30 days in the laboratory. Estimates of average longevity in hoverflies from the field have produced values of 11–17 days and 3–11 days for *M. equestris* (Hodson, 1932; Conn, 1976, respectively), 3.4 days for *H. hybridus* (Nielsen, 1969), 10.1 days for *Sericomyia silentis* (Nielsen, 1969) and 4.2 days for *E. pertinax* (Holloway & McCaffery, 1990), all well short of 30 days. Whether these ageing effects on phenotype occur in the field is therefore still a matter for study. It can be seen from Fig. 3 that both sexes in both *E. arbustorum* and *E. horticola* showed clear season phenotype relationships. Re-examination of Heal's (1981) field-collected material shows that the palest females in 1975 were found in August, in 1976 July and in 1978 July and September. In the present study the palest females were found in late August so, in fact, the results of the two studies concur quite well. In view of the weak season phenotype relationship for female *E. arbustorum* shown in Fig. 3 though, a very large sample may be required in order to detect it. This could possibly be the reason why such a relationship was not found in *E. abusivus* and *E. nemorum* females, even though the samples sizes were 388 and 315, respectively. It should be born in mind, however, that the colour scale used here and by Heal is arbitrary and provides

convenient categories into which to place each fly. The phenotypic variation must have a biochemical basis and at that level the differences between consecutive colour categories may not be linear. This could also influence the ease with which season phenotype relationships can be demonstrated.

Heal (1989) split broods of *E. intricarius* over several temperatures and showed that single genotypes (approximated by using families) were capable of producing different phenotypes depending on environmental conditions during development, i.e. *E. intricarius* shows phenotypic plasticity. Split brood experiments have also been carried out by Ottenheim & Holloway (unpublished data) using *E. arbustorum* and they found similar phenotypic plastic responses to those described by Heal (1989). This demonstrates that the variation among months in Fig. 3 can probably be primarily attributed to phenotypic plasticity. The minimum range of adaptive phenotypic plasticity shown by each species can be estimated by the difference between the mean values during the cooler months and the warm summer/autumn months.

The function of the variation in adult colour pattern is not at all clear. In some other systems the function of the plasticity is much more clear cut. For example, the production of neck spines by *D. pulex* (Crustacea: Cladocera) are for defence against late juvenile instars of the phantom midge, *Chaoborus americanus* (Parejko & Dodson, 1991; Spitze, 1992). The variation shown by *Bicyclus* butterflies also has an anti-predator function (Brakefield & Larsen, 1984). In temperate regions temperature fluctuations substantially affect insect activity and several examples of phenotypic plasticity in colour in temperate insects have evolved which have been interpreted as thermoregulatory adaptations (e.g. Watt, 1968; Cagy *et al.*, 1988; Kingsolver & Wiernasz, 1991). Some authors have argued that colour plays a negligible role in influencing body temperature in insects (e.g. Bursell, 1974). Other studies, however, have indicated that colour can affect final body temperature (see Willmer, 1982, for review). Edney (1971), for example, showed that black desert beetles maintained a body temperature 1–2.5°C higher than white beetles under similar circumstances. Comparable results have been found in insects possessing different morphs (e.g. Watt, 1968, 1969; Douglas & Grula, 1978; Brakefield & Willmer, 1985; Stewart & Dixon, 1989), including honey bees (Cena & Clark, 1972) which are similar in size to many *Eristalis* species. Indeed, Heal (1981, 1989) speculated that thermal effects may have played a role in the evolution of colour variation in *Eristalis* hoverflies. If one assumes that the relationship between colour and season in some *Eristalis* species has some adaptive function, then it is curious that there is so much difference among the species in both their degree of phenotypic plasticity (Fig. 3) and the amount of phenotypic variation (Table 2). All four species can be found together as adults feeding on the same flowers at the same times of the year. The only species that appears to be slightly more discriminating about its breeding sites is *E. abusivus*. In the U.K., *E. abusivus* is found in marshland areas, particularly at coastal sites (Stubbs & Falk, 1983),

whereas the other three species occur much more generally. Clearly, more work needs to be done before the variation in colour described here is linked unequivocally with thermal regulation, although with the available evidence it is difficult to argue that the seasonal colour changes do not have some adaptive significance.

All four of the study species show sexual dimorphism for colour. This dimorphism is unlikely to serve as a sex recognition system as, in the field, roving male *E. arbustorum* and *E. nemorum* can be seen checking any insect in the vicinity of approximately the right size. It is likely that pheromones and/or tactile stimulations are more important than vision in this respect. In order for the dimorphism to have a thermal explanation connected with the need to remain active, females must occur more frequently in cool micro-habitats than males. Holloway & McCaffery (1990) found that female *E. pertinax* congregated around the edge of a damp woodland which contained suitable oviposition sites whilst the males were more likely to be found out in the open feeding on flowers. Females were also apparently more mobile than males judging by recapture rates. It is possible that the between sex colour variation is related to the differing ecologies of the two sexes. David *et al.* (1990), working with abdominal pigmentation in female *D. melanogaster*, concluded that melanin deposition in each tergite is controlled by different sets of genes since segmentation position affected the phenotypic plasticity of cuticular pigmentation. This is consistent with the findings of Scott & O'Farrell (1986) that several homeotic genes control the antero-posterior gradient during embryogenesis. Furthermore, for some metric characters a remarkable amount of sex-limited gene expression occurs (Holloway *et al.*, 1993). Given this, it is not difficult to envisage how sexual dimorphism largely limited to the presence (males) or absence (females) of yellow on tergite 3 has evolved.

It has already been mentioned (above) that colour variation occurs in several groups of hoverflies, including aphidophagous hoverflies. Future research may demonstrate that the colour of the adult hoverfly is determined directly by development period, but, of course, development period and temperature are very closely correlated in insects. In hoverflies that rely on aphids as a food source it is important to be mobile and many of the Syrphinae are well known as migrants (Torp, 1984). It could be that the development rate in these species determines the colour of the adult, but in this case the juvenile character may be influenced in the field more by the availability of an ephemeral food source than by temperature, although pupal development temperature has also been shown to effect adult colour in *E. balteatus*, *Metasyrphus corollae*, *M. luniger* and *Sphaerophoria scripta* (Dušek & Láška, 1974). A larva that takes a long time to develop in the field could be in an area where the aphid population is declining. The need to produce an adult with the capacity to migrate to better feeding areas is obvious. Here a phenotype may be produced that possesses characters more suitable for migration. Such phenotypes may be dark for increased activity under low light intensities as well as having other

characters suitable for migration, e.g. lower wing loading and larger glycogen reserves (Graves *et al.*, 1992). However, this remains speculative as no research has been done to date into this question, but work is currently being carried out into many of the problems highlighted by this study.

This study also shows that large museum collections can be used to carry out investigations into quantitative variation within and among species to examine ecologically relevant questions. The value of such collections for these studies, though, is largely determined by the way in which the specimens have been collected. A more or less random collection of insects across an area or country (if it is small enough, as is the Netherlands) is ideal, but this randomness can be influenced by one or two dipterists who donate their private collections to the museum and who were particularly active in their own areas. Also, there is a tendency for dipterists (as with many other entomologists) to collect unusual variants, too many of which can severely limit the usefulness of museum collections for quantitative comparisons among species. Species such as *Eristalis* spp. will generally not suffer from this problem though, since they are well known for being variable and unusual colour variants are not common. They are also extremely common with the result that museum collections of these species are often large. In principle, it may be possible to carry out similar studies using certain other species, such as *E. balteatus*.

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