EVIDENCE OF RESTRICTED MIMETIC COLOUR POLYMORPHISM IN THE LARGE NARCISSUS BULB FLY, *MERODON EQUESTRIS* FAB. (DIPTERA : SYRPHIDAE), IN THE PYRENEES

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Received 1.ix.75

SUMMARY

The large narcissus bulb fly, *Merodon equestris*, which mimics bumble bees, may be one of 34 colour types in the U.K. However in the Pyrenees individuals may be only one of 12 colour types owing to lack of variation at the *bulborum* gene locus. It is suggested that the simultaneous presence of other mimics in large numbers in the Pyrenees is responsible for this difference.

1. INTRODUCTION

THE large narcissus bulb fly, *Merodon equestris* Fab., is one of several hover fly mimics of bumble bees. Other hover fly mimics include *Volucella bombylans* Linn., *Criorrhina berberina* Fab., *C. floccosa* Meig., *Eristalis intricaria* Linn., *Arctophila bombiformis* Fall. as well as *Merodon flavus* Sack.

In the U.K. *M. equestris* is a highly polymorphic mimic with at least 34 discernible colour types all of which are more or less mimetic. These colour types are produced by the interaction of at least six gene loci (Conn, 1971, 1972a, b) three of which (*equestris*, *bulborum* and ground colour) are linked and two of which depend upon the presence and modify the expression of the dominant allele of the *bulborum* locus (the dominant alleles of both modifier *U* and modifier *V*). Three gene loci (*bulborum*, *equestris* and *transversalis*) were named after colour types that they produce and the other three (modifier *U*, modifier *V* and ground colour) were named to indicate the effects that one or other of the alleles produced. Briefly, the dominant allele of *bulborum* blackens all but the anterior hairs of the thorax, the dominant allele of *equestris* blackens only an interalar band of hairs on the thorax, *transversalis* produces a dark band of shortened hairs on the third abdominal segment, the dominant allele of modifier *U* modifies the colour type *bulborum* (produced by the dominant allele of the gene locus *bulborum*) to the colour type *subvalidus* and the dominant allele of the modifier *V* further modifies the colour type *subvalidus* to the colour type *validus*. Both *subvalidus* and *validus* colour types show sexual dimorphism. *Subvalidus* males resemble *bulborum* males except that the second abdominal segment has a mixture of black and coloured hairs arranged in a fairly constant pattern. *Subvalidus* females are harder to define and more variable. The hairs of the anterior of the thorax are darkened but not black and the hair colouration of the second abdominal segment is usually similar to the male though more variable. In *validus* colour types the sexual dimorphism is extended further. The *validus* male resembles the *subvalidus* male except that there are now only a few isolated coloured hairs on the second abdominal segment and the *validus*

female has a completely black thorax and the second abdominal segment is black except for a few isolated coloured hairs. The ground-colour locus behaves as a supergene and produces yellow and orange hairs distributed in bands (and masked whenever the dominant alleles of *bulborum*, *equestris* or *transversalis* are present). The colour types based on the expression of the ground-colour locus together with the recessive alleles of *bulborum*, *equestris* or *transversalis* are known as *narcissi* and may be YOYO, OOOY or OOOO—the letters referring to the yellow or orange colouration from the anterior of the thorax to the abdomen tip with the exception of the second letter which refers to the colour of the interalar band, *i.e.* YOYO indicates a yellow thorax, orange interalar band, yellow anterior abdomen (segment 2) and orange abdomen tip (segments 3 and 4). OOOY indicates an orange thorax (and interalar band) and an all yellow abdomen. Variants within YOYO and OOOY categories occur (YOYY, YYYO, YYYY and OOOY, OOOYO) and the genetics of these has been investigated.

The colour types of *M. equestris* are generally described as *narcissi* YOYO, *transversalis* YYYO, *equestris* OOOO, *bulborum* OOOY, *subvalidus* YOYO, male *validus* OOOO, etc. As female *validus* are more or less completely black except for the third and fourth abdominal segments they are usually described as female *validus* orange tail or female *validus* yellow tail. In the cases of *equestris*, *bulborum*, *subvalidus* and male *validus* the orange interalar band is masked, so this inconsistency of nomenclature should be borne in mind when one considers the genetic constitution of the insects. Another inconsistency of nomenclature is to be found in male *validus*, as the colouration of the few light-coloured hairs on the second abdominal segment is often difficult to distinguish.

2. METHODS

Four sites in the Pyrenees were sampled. Three were in Andorra (Vallée d'Incles at an altitude of 1800 m, Encamp at 1350 m and above El Serrat at approximately 2100 m) and one site was in France at Bareilles (altitude 1100 m), Hautes Pyrénées. Models (bumble bee females and workers) and mimics (including bumble bee males and hover fly species) were sampled by simple netting and a total of 86 specimens of *M. equestris* were caught. Twenty museum specimens of *M. equestris* from various parts of the Pyrenees were also examined in the British Museum (Natural History) and Hope Department, Oxford collections.

3. RESULTS AND DISCUSSION

The samples of *M. equestris* taken, and the museum collections examined, all lacked individuals of the *bulborum*, *subvalidus* and *validus* colour types (table 1, *a* to *e*). The dominant allele of the *bulborum* locus was absent. Furthermore, most specimens caught were *equestris* YOYO or *equestris-transversalis* YOYO. In comparison with samples from the U.K. (see Conn, 1972*b*) the range of colour types of *M. equestris* present in the Pyrenees is very restricted.

At the time that *M. equestris* is flying in the Pyrenees (in August) there are many other bumble bee mimics out as well. The major mimic of female and

TABLE 1

Numbers of different morphs of M. equestris captured at four sites in the Pyrenees
(For explanation of colour types see text)

Colour type	Males	Females	Total
(a) <i>Vallée d'Incles</i> (18-19.8.71)			
<i>Equestris</i> YOYO	9	3	12
<i>Equestris</i> YYYY	0	2	2
<i>Equestris</i> OOOY	1	0	1
<i>Equestris-transversalis</i> YOYO	1 (?)	7	8
<i>Equestris-transversalis</i> YYYY	0	6	6
<i>Transversalis</i> YYYYO	0	2	2
	11	20	31
(b) <i>Vallée d'Incles</i> (5-9.8.73)			
<i>Equestris</i> YOYO	3	1	4
<i>Equestris</i> OOOO	1	0	1
<i>Equestris transversalis</i> YOYO	3 (?)	0	3
<i>transversalis</i> YYYYO	1 (?)	0	1
	8	1	9
(c) <i>Encamp</i> (7-9.8.73)			
<i>Equestris</i> YOYO	9	1	10
<i>Equestris</i> YYYY	1	0	1
<i>Equestris</i> OOOY	1	0	1
<i>Equestris-transversalis</i> YOYO	1 (?)	4	5
<i>Equestris-transversalis</i> OOOY	1 (?)	0	1
<i>Narcissi</i> YYYYO	2	0	2
	15	5	20
(d) <i>Above El Serrat</i> (6-8.8.73)			
<i>Equestris</i> YOYO	2	0	2
<i>Equestris</i> YYYY	0	2	2
<i>Equestris-transversalis</i> YOYO	0	2	2
<i>Narcissi</i> YYYYO	0	1	1
	2	5	7
(e) <i>Bareilles</i> (12-13.8.73)			
<i>Equestris</i> YOYO	4	0	4
<i>Equestris</i> OOOY	2	0	2
<i>Equestris-transversalis</i> YOYO	0	2	2
<i>Equestris-transversalis</i> YYYY	0	3	3
<i>Equestris-transversalis</i> OOOY	0	2	2
<i>Transversalis</i> YYYYO	0	1	1
<i>Transversalis</i> YYYY	0	1	1
<i>Narcissi</i> YYYYO	1	0	1
<i>Narcissi</i> OOOY	1	1	2
<i>Narcissi</i> OOOY	1	0	1
	9	10	19

worker bumble bees is the male bumble bee (table 2, *a* to *c*) and other mimics include *Arctophila bombiformis*, *M. flavus* and *Volucella bombylans*. *A. bombiformis* is an excellent mimic. To the human eye it is a better mimic than *M. equestris* var. *bulborum*, so that it is likely that *bulborum* colour types may be unfit at any frequency when compared with *equestris*, *transversalis* and *narcissi* colour types. On higher ground *M. equestris* co-exists with its sibling species *M. flavus*—of which the male resembles *M. equestris* var. *narcissi* and the female, *M. equestris* var. *transversalis*. The only other bumble bee mimic with colouration akin to that of *M. equestris* var. *equestris* and var. *equestris-transversalis* is *V. bombylans* var. *haemorrhoidalis* and this species, because of its

TABLE 2

Numbers of models and mimics caught by net sampling at three sites in the Pyrenees

	Colour type in terms of <i>M. equestris</i> *				
	<i>n/t</i>	<i>e</i>	<i>e-t</i>	<i>b-t</i>	<i>s</i> and <i>v</i>
(a) <i>Vallée d'Incles</i> (5-9.8.73)					
Female and worker bumble bees (models)	0	0	38	6	1
Male bumble bees (mimics)	2	10	23	14	8
<i>Merodon equestris</i>	1	7	1	0	0
<i>Volucella bombylans</i>	—	—	3	0	0
<i>Arctophila bombiformis</i>	—	—	—	5	—
(b) <i>Encamp</i> (7-9.8.73)					
Female and worker bumble bees (models)	25	9	20	21	0
Male bumble bees (mimics)	4	3	5	3	0
<i>Merodon equestris</i>	0	10	8	0	0
<i>Merodon flavus</i>	1	—	—	—	—
(c) <i>Above El Serrat</i> (6-8.8.73)					
Female and worker bumble bees (models)	9	1	42	8	0
Male bumble bees (mimics)	7	0	20	6	0
<i>Merodon equestris</i>	1	4	2	0	0
<i>Merodon flavus</i>	9	—	—	—	—
<i>Volucella bombylans</i>	—	—	1	0	0

* Key: *n/t* = *narcissi/transversalis*; *e* = *equestris*; *e-t* = *equestris-transversalis*; *b-t* = *bulborum-transversalis*; *s* and *v* = *subvalidus* and *validus*.

larval history as a scavenger or parasite of bumble bee nests, would probably be incapable of outnumbering *M. equestris*. The above may explain the preponderance of *equestris* and *equestris-transversalis* in the samples. At Bareilles, the lowest location and well below where *M. flavus* is to be found, there is a higher proportion of non-*equestris* and non-*equestris-transversalis* colour types. It is worth noting in passing that in the Pyrenees many male *M. equestris* express *transversalis*, or something akin to it, rather weakly (table 1, *a* to *c*). In the U.K. it is very rare for any male *M. equestris* to express *transversalis*. The difference may be the result of the same selective forces that give rise to the high frequency of female *transversalis* in the Pyrenees when compared to the U.K.

The principle reason for restricted colour polymorphism of *M. equestris*

in the Pyrenees may lie in the short summer, resulting in most other bumble bee mimics flying at the same time as *M. equestris*. The length of the season in the U.K. allows different mimics to fly at different times in the season. In the U.K., *M. equestris* adults are on the wing between mid-May and the end of June. They are out before most male bumble bees and before *V. bombylans* and, although *A. bombiformis* and *M. flavus* are not found in the U.K., *M. equestris* co-exists with *C. berberina*, *C. floccosa* and *E. intricaria*. However, none of these three species is every locally as common as *M. equestris*, unlike *A. bombiformis* and *M. flavus* in the Pyrenees. As one comes down the Pyrenees the summer season lengthens and it would be interesting to discover what happens to the mimicry of bumble bees and the mimetic colour polymorphism of *M. equestris* in the lower Pyrenees.

Acknowledgments.—I am extremely grateful to the staff of the British Museum (Natural History) and the Hope Department of Entomology, Oxford for allowing me to examine specimens of *M. equestris* and South European bumble bees, and to Dr I. H. M. Yarrow who suggested the Vallée d'Incles as a suitable site. I also thank Dr W. D. Hamilton for supervision, Professor T. R. E. Southwood for facilities at Imperial College Field Station, Professor J. W. S. Pringle for enabling me to complete this work and the Agricultural Research Council for the research assistantship from 1967 to 1971.

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