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Colour polymorphism in *Agriotes ustulatus* (Coleoptera: Elateridae): Absence of geographic and temporal variation

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Abstract. The proportion of melanic (with dark elytra) and non-melanic (yellow-brown elytra) adults of *Agriotes ustulatus* (Schaller) was established in populations from central Europe (Bohemia, Czech Republic) and the Mediterranean region (Veneto, northern Italy). Both areas, although separated by only 500 km distance, have dramatically different climate. The average proportion of melanic individuals was slightly (by 8%) but significantly greater in populations from Veneto than from Bohemia. The frequency of melanics was identical in both sexes and stable over a 11 year period as well as during the season. The apparent stability of morph frequencies in *A. ustulatus* contrasts with other insect species where melanic freguencies often vary greatly, both in space and in time.

INTRODUCTION

Colour polymorphism, consisting of the presence of dark (melanic) and light (non-melanic) forms, in populations of a species, are widespread in several insect taxa including moths, ladybeetles, spittlebugs, psocids, hoverflies, bumble bees, carabid beetles, bugs and drosophilids.

Usually, the percentage of melanic forms varies between local populations, with the course of the season or over a long time period. This variation provides an opportunity of investigating the causes of the change in morph frequency. Usually, they are inferred from correlations of morph frequencies with relevant environmental factors (Cleve, 1970; Brakefield, 1988). Industrial melanism is probably the best studied example (Kettlewell, 1973; Lees, 1981). Climatic selection or cryptic protection against visual predators were advocated strongly as explanations for the differences in melanic frequencies. Arguments in favour of climatic selection include variation in proportion of melanic forms along the climatic gradients (Halkka et al., 1975; Thompson, 1984, 1988; Capy et al., 1988) and the high effect of temperature on the expression of genetically determined melanism (Watabe, 1977; David et al., 1990). Body coloration has an important role in maintenance of insect body temperature (Wasserthal, 1975; Roland, 1982; Brakefield & Willmer, 1985) and, thus, affects the overall fitness of the species.

In contrast to frequently observed geographic and temporal variation in frequencies of melanics, stable polymorphisms are rather rare. In some species, e.g. coccinellid beetles *Adalia bipunctata* (L.) (Honěk, 1975; Klausnitzer & Schummer, 1983) or *A. decempunctata* (L.) (Brakefield, 1985) morph frequencies may be relatively stable over large geographic areas but highly variable in other regions. This study provides a further example of the stability found in *Agriotes ustulatus* (Schaller). This common elaterid of central and

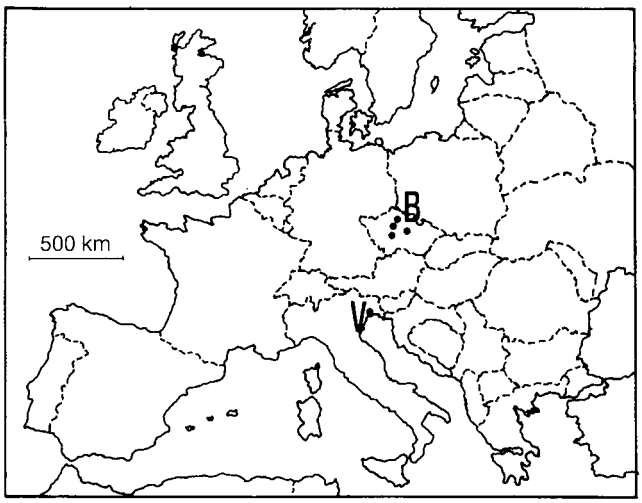

Fig. 1. The localities of collection of *A. ustulatus* populations in Bohemia (B) and Veneto (V). The 8 localities of Veneto which are proximal are represented by a single point.

southern Europe, has very conspicuous colour dimorphism. Either, the adults have a dark scutum and head and yellow-brown elytra (light, non-melanic form), or the dorsum is black throughout (dark, melanic form). Variation in the frequencies of morphs in local populations has yet to be studied. Only Méquignon (1929) mentioned the prevalence of light over the dark form in western Europe. The biology of this species is well known. In northern Italy the greatest proportion of the subterranean larvae overwinter twice and pupate 24 months after the eggs were laid (Furlan, in press). Adults emerge from the soil from June to early September. Development in central Europe is longer and lasts 3 or 4 years (Rambousek, 1928; Miller, 1956) but the period of adult emergence is the same as in northern Italy.

In this study the morph frequency in *A. ustulatus* populations from two areas with different climate, Bohemia (the western part of the Czech Republic) and Veneto (wide surroundings of Venice in north-east Italy is compared. The data provide information on annual and seasonal variation of the morph proportions.

MATERIAL AND METHODS

Adults of *A. ustulatus* were collected (Fig. 1) at 4 localities of Bohemia situated between 49°40′ and 50°15′ N, at elevations 200–400 m a.s.l. All localities were within 70 km from Prague. The populations from Veneto were colected at 8 localities grouped in an area of ca 40 km diameter, on the plains of the lower branch of Piave River (45°30′ N), at elevations of 8–15 m a.s.l. Although the distance between Bohemian and Veneto localities is only ca. 500 km the climate of both regions is dramatically different (Table 1) due to separation of both areas by the Alpine massive. Temperature, rainfall and sunshine data were obtained from meteorology stations near the centres of the investigated areas: Praha-Ruzyně and San Donà.

At both areas, the localities of sampling were situated in an agricultural landscape with intensive crop production. The adults of *A. ustulatus* were collected from late June to early August, largely from flowering umbellifers, or by sticky traps. The morph frequencies were recorded and the Veneto populations were also sexed. Bohemian populations were separated by 50–70 km distance and were considered separately. Veneto populations were closely aggregated and therefore pooled into one sample. The contingency tables of differences in morph freguencies were evaluated by chi-square tests.

TABLE 1. Average monthly temperatures, precipitation and sunshine hours in Bohemia (B, Praha-Ruzyně, 1953–1972) and Veneto (V, San Donà, 1960–1993).

		Total	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Temperature	B	7.7	-2.8	-1.5	2.3	7.8	12.7	16.3	17.6	16.8	13.2	8.2	3.0	-0.7
(°C)	V	13.2	2.7	4.9	8.5	12.7	17.4	20.9	23.4	22.8	19.4	14.2	7.9	3.5
Rainfall	B	456.3	18.1	21.1	25.4	36.4	57.3	63.6	70.2	59.6	32.4	32.6	23.6	22.5
(mm)	V	924.3	63.0	58.6	67.0	71.6	81.1	93.4	70.7	95.2	78.4	87.7	95.0	62.6
Sunshine	B	1674	48	69	128	167	213	226	224	214	179	118	47	41
(h)	V	2417	101	139	166	197	248	311	357	325	224	148	107	94

RESULTS

There was no difference (Table 2) in the percentage of melanic individuals among males and females ($X^2 = 0.099$, df = 1, n.s.). Therefore for calculating differences between populations results of both sexes were pooled. The melanic frequencies in annual samples of Veneto (Table 3) varied little and were sufficiently homogeneous to be pooled into a total sample ($X^2 = 3.43$, df = 3, n.s.). The same was true for annual samples of Praha-Ruzyně ($X^2 = 1.82$, df = 3, n.s.) and for samples of Bohemia when data from Praha-Ruzyně were pooled ($X^2 = 3.59$, df = 3, n.s.). The difference among the average frequency of the melanic morph in Bohemia (32.2%) and Veneto (40.5%) populations was only 8.3%. However, this difference was significant ($X^2 = 18.95$, $p < 0.005$), due to large sample size.

TABLE 2. Proportion of dark and light morphs in males and females of Veneto, 1991 and 1992.

	Colour morph			
	Dark		Light	
	n	%	n	%
Males	265	40.2	395	59.8
Females	406	40.9	586	59.1

The annual differences were not significant. The frequency of melanics in Praha-Ruzyně varied within 11 years period by only 6.6%, in Veneto populations they varied over a 4 year period by 5.8%. This variation was far below the statistical significance (see above). The seasonal variation of melanic frequency was recorded in 1993 sample from Veneto (Table 4). There was no significant trend for increase or decrease of the proportion of melanics ($X^2 = 0.70$, df = 3, n.s.).

DISCUSSION

Our study revealed only small differences in frequency of melanic adults between geographic populations of *A. ustulatus*. Logically, the absence of large variation between a small number of populations does not imply the geographic stability of this polymorphism. Increasing number of samples would increase the probability of such generalization. However, accumulating greater data over the period of the study was difficult as *A. ustulatus*, previously thought to be an important field pest, became progressively scarcer in the Czech Republic since the late 1950's due to side effects of fertilizer application and

decreasing acreage of permanent crops. The comparison with Veneto populations is interesting due to the similarity of morph frequency in the warm Mediterranean climate of Veneto and the cooler continental climate of Bohemia. The average temperature for June to August (the period of adult activity in *A. ustulatus*) was 5.5°C higher and sunshine hours 1.5 times longer in Veneto than in Bohemia. However, large climatic effects on *A. ustulatus* melanism cannot be demonstrated from our data. If climatic selection were important, the local differences would affect the variation in melanic freqency. By analogy with well documented polymorphism of the lady beetle species *Adalia bipunctata*, it would be expected that there would be a decrease of melanic frequency with an increase of temperature and/or sunshine (Benham et al., 1974). By contrast, the proportion of melanics in *A. ustulatus* was slightly greater in warm Veneto than cooler Bohemia. The only factor which might favour the melanism in Veneto is the proximity of the sea. This was claimed an important factor of melanism in *A. bipunctata* (Scali & Creed, 1975; Bengtson & Hagen, 1977).

TABLE 3. Proportion of dark and light morphs in populations of Bohemia and Veneto.

Locality	Year	Colour morph			
		Dark		Light	
		n	%	n	%
Bohemia					
Čáslav	1976	30	38.0	49	62.0
Mladá Boleslav	1975	101	35.2	186	64.8
Praha-Ruzyně	1975	36	31.0	80	69.0
	1980	39	34.8	73	65.2
	1984	91	28.2	232	71.8
	1986	30	30.9	67	69.1
Votice	1982	4	28.6	10	71.4
Veneto					
Eraclea, S. Donà	1990	10	37.0	17	63.0
	1991	9	37.5	15	62.5
	1992	357	42.8	478	51.2
	1993	314	38.4	503	60.6

TABLE 4. Seasonal change of the proportion of colour forms in Veneto, 1993.

Date	Dark		Light	
	n	%	n	%
< June 30	11	40.7	16	59.3
July 1–15	62	41.1	89	58.9
July 16–31	62	40.5	91	59.5
> August 1	7	31.9	15	68.1

The apparent stability of *A. ustulatus* polymorphism is strange in comparison with the exaggerated local variation of moth (Kettlewell, 1973), lady beetle (Hodek & Honěk, in press) or spittlebug (Halkka & Halkka, 1990) populations. However, this stability is paralleled by polymorphisms in some coleopteran species, e.g. the chrysomelid *Orsodacne cerassi* (L.) (Honěk, unpubl). It is possible that the long subterranean development of *A.*

ustulatus might be a factor which prevents the effects of climatic variation on changing genetic composition of local populations.

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