Colour polymorphism and sex-ratio variation in Aphidecta obliterata (L.) (Coleoptera: Coccinellidae) in eastern Scotland

By W. H. PARRY and I. D. PEDDIE

Abstract

Male: female sex ratios varied from 65:35 to 45:55 in samples from different areas immediately following adult emergence. During autumn the ratios of branch samples changed with time to give increased proportions of females which were inseminated prior to diapause. On branch samples in spring females outnumbered males by 3:1. No differential mortality occurred during overwintering beneath bark scales. Dark coloured elytra were commoner among male adults but light elytra were the most numerous in both sexes. A greater proportion of individuals with dark elytra survived until spring. Melanic pigmentation on both elytra and head capsules was greater in females. Mean length and width was greater in females. Despite these differences sex differentiation proved unreliable without dissection of the sexual organs.

1 Introduction

Colour polymorphism is a common feature in Coccinellidae e.g. FÜRSCH (1967) described over 150 different colour variants of *Adalia bipunctata* L. Nine elytral colour variants of *Aphidecta obliterata* (L.) have been described (MADER 1926–1934; KUHNT 1911; in EICHHORN and GRAF 1971), but only 5 variants were categorized in EICHHORN and GRAF's (1971) study of sex-linked polymorphism of this species in Germany. The sex-ratio of overwintering *A. obliterata* located beneath bark scales or from laboratory reared samples were unusual in that 60 to 66 % were female. EICHHORN and GRAF (1971) suggested that this may have been related to the (XX: XO) sex-determining mechanism in this species.

The aim of the present study was to compare colour polymorphism and sex ratios of the German A. obliterata populations with those obtained from Sitka spruce (*Picea sitchensis* [Bong.] Carr.) and Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco) under various conditions in eastern Scotland.

2 Materials and methods

Adult A. obliterata were collected at irregular intervals from Douglas fir foliage at Craibstone (PARRY 1978); from Sitka spruce foliage at Countesswells (PARRY 1973); from beneath bark scales on mature Sitka spruce at Craibstone during December, January and February; from Sitka spruce and Douglas fir foliage near Kirkcaldy (PEDDIE 1979) and from Sitka spruce foliage at Alltcailleach forest, Ballater, Aberdeenshire. Ballater was chosen to represent an inland, high altitude (ca.

U.S. Copyright Clearance Center Code Statement: 0044-2240/81/9105-0442 \$ 02.50/0 Z. ang. Ent. 91 (1981), 442-452 © 1981 Verlag Paul Parey, Hamburg und Berlin ISSN 0044-2240 / InterCode: ZANEAE 300 m) site for comparison with the other low altitude, coastal sites. In the event only one sample was obtained from Ballater.

Samples were obtained either by beating the foliage and collecting the falling insects on trays or by manually removing bark scales and collecting the beetles overwintering beneath them. All beetles were stored in glass tubes, transported to the laboratory and either immersed in 70 % ethanol or stored alive in an environmental cabinet at 5 ± 1 °C.

By contrast to the findings of WITTER and AMMAN (1969) head markings and body length proved unreliable for the identification of sex. Consequently, every beetle was dissected under a binocular microscope in order to examine the internal sex organs.

Chromosome numbers were determined in late autumn for male insects by removing the testes, fixing in ethanol and glacial acetic aid (3:1 v/v) and keeping at low temperatures until required. The testes were placed on glass microscope slides, stained with acetyl choline for 15 min and squashed with a cover-slip to spread the tissue prior to scanning under a microscope for the various stages of meiosis and mitosis. Similar steps were taken with ovarioles removed from female insects. However, no gametogenesis was observed at this time so attempts were made to stain midgut villi for evidence of mitosis. One hour prior to dissection colchicine was injected into the beetles in order to halt mitosis by inhibiting spindle formation and thus making the chromosomes appear larger and darker.

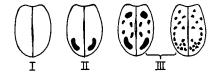


Fig. 1. Elytral colour patterns in A. obliterata L. in East Scotland

Elytra were coloured either fawn (= light) or orange-brown (= dark). Three main melanic spot patterns were superimposed on these colours which were classified into patterns I, II, III (fig. 1, after EICHHORN and GRAF 1971). The brown, dark-brown or black melanic head markings were divided into 4 patterns: whole, 1 break, 2 breaks or spotted (after WITTER and AMMAN 1969).

3 Results

3.1 Field observations

Adults of *A. obliterata* were to be found in every month of the year. Eggs were laid in early to mid-May, a heavy adult mortality occurring following egg deposition. Larvae were generally present in the latter half of May and June, pupation occurring in June with adults of the new generation appearing in July and August. Very few adults remained on foliage between mid-December and March, but were commonly to be found beneath bark scales, particularly of mature Sitka spruce.

3.2 Sex ratios

In 1977–1978 a total of 571 *A. obliterata* were classified from collections made from foliage of Douglas fir and Sitka spruce. In the autumn of 1977 the proportion of females, originally c. 40 %, increased prior to diapause in mid-December, $F_{1,3} = 15.8$, P < 0.05 (fig. 2). More females than males were found on Douglas fir foliage following diapause (table 1). Therefore, there was no constant sex ratio on conifer foliage.

100 pupae were collected from Sitka spruce at Countesswells on June 24th, 1978 and maintained at 15 \pm 1 °C until adult emergence. 95 adults developed

Date		N	No o≉7	No q	% ¥
1978	May 2	50	20	30	60.0
	May 10	50	15	35	70.0
	Jun 13	55	19	36	65.5
1979	Apr 23	129	29	100	77.5
	May 7	116	27	89	76.7
	May 21	120	28	92	76.7

Table 1. Sex ratios of A. obliterata on Douglas fir at Craibstone following diapause and emigration in 1978 and 1979

of which 38 (40 %) were female. Field collection of adults soon after emergence revealed that in Countesswells c. 45 % were female, in Craibstone c. 35 % and in Kirkcaldy c. 55 %.

Regression analysis confirmed that the proportion of females on foliage in autumn increased in response to time at Countesswells ($F_{1,6} = 13.78$, P < 0.01), Craibstone ($F_{1,3} = 28.50$, P < 0.05) and Kirkcaldy ($F_{1,2} = 116.2$, P < 0.01). By October over 60 % of the total population of all three areas consisted of females.

Application of Bartlett's test (FREESE 1974) produced a $\chi^2 2df = 4.77$ (P < 0.1 > 0.05) which confirmed the homogeneity of the variance of the 1978 data from the three sites. The slopes and elevations were compared by analysis of variance. The null hypothesis assumption of common slope values was confirmed (F_{2,11} = 1.50, P > 0.05) whilst the null hypothesis assumption of common elevation as rejected (F_{2,13} = 14.56, P < 0.01). The regression

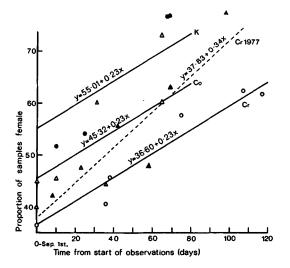


Fig. 2. Changes in the sex-ratios of A. obliterata in relation to time at Kirkcaldy (●), Craibstone (○) and Countesswells (△) in the summer of 1978 and Craibstone (▲) in the summer of 1977

Date	Total ♀ ♂ [≉] %♀		% Dead	ŧ	% age of live	% age of dead	
			[%]	9	്	beetles ¥	beetles ¥
5 Dec 1978	6	2		0	0		
22 Jan 1979		19			78.9	80.0	40.0
24 Jan 1979	63	-	51		62.3		34.5
20 Feb 1979	78	75	51	65.4	68.9	54.0	51.0
7 Mar 1979	112	91	55	69.6	75.8	60.7	52.3

 Table 2. Sex ratios of live and dead A. obliterata in diapause beneath bark scales of Sitka spruce at Craibstone

equations relating proportion of females (y) to time (x) were recalculated using the common regression coefficient (fig. 2).

Sex ratios of *A. obliterata* overwintering beneath Sitka spruce bark scales showed a reversion to approximate equality (table 2). A slightly lower level of female mortality resulted in around 60 % female survivors in March at the time of emigration commencement (table 2). The majority of overwintering *A. obliterata* died (table 2).

In 1979, following emigration from the overwintering site, over 75 % of the population on Douglas fir foliage consisted of females (table 1). Therefore, at the time of spring egg-laying a marked reversal of the immediate post-pupal sex ratios had occurred with females being 3 times as common as males.

3.3 Chromosome numbers

The chromosomes were small with no distinguishing features. The autosome number was 18. The sex determining system was XX : XO. At the time of the cytological investigation in October and November spermatogenesis had terminated. All females dissected carried spermatophores which indicated that female insemination had occurred in the period preceding diapause. Egg fertilization and ovary development appeared not to occur until after diapause.

3.4 Elytral colour

In autumn the proportion of adults with dark elytra was consistently lower than the proportion with light elytra (fig. 3). This proportion increased in response to time in both males, $F_{1,19} = 8.35$, P < 0.01 and females, $F_{1,19} =$ 6.19, P < 0.05 (fig. 3). Application of Bartlett's test failed to confirm variance homogeneity (χ^2 ldf = 7.26) thus invalidating statistical comparisons of the regressions. However, the results support the hypothesis that dark elytral colouration was partially sex-linked. There was no evidence to support an effect of sampling area or host species on elytral colouration.

In populations overwintering beneath Sitka spruce bark scales at Craibstone the majority of both males and females possessed light elytra even though the

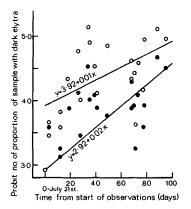


Fig. 3. The association between time and dark coloured elytra in male (\bigcirc) and female (\bullet) adult A. obliterata

Table 3. Elytral colour of a) diapausing adults of A. obliterata beneath bark scales of Sitka spruce at Craibstone and b) post diapause adults on foliage of Douglas fir at Craibstone

Date		Dark	Female Light	% Dark	Dark	Male Light	% Dark
a) .	Jan 24	9	80	10	12	49	20
I	Feb 20	5	70	7	16	59	21
I	Mar 7	18	87	17	28	62	31
ь) /	Apr 23	36	64	36	13	15	46
ı	May 7	40	49	45	16	11	59
ı	May 21	37	55	40	6	22	21

Table 4. A comparison of survival levels of dark and light forms of A. obliterata under Sitka spruce bark scales

		Light			Dark	
Date	Total	Alive	% Alive	Total	Alive	% Alive
27 Jan	121	70	57.9	21	18	85.7
20 Feb	84	37	44.0	21	13	61.9
7 Mar	132	21	15.9	63	35	55.5

proportion of males possessing dark elytra was higher than the proportion of females (table 3a). The mortality rate was higher in overwintering individuals with light elytra (table 4), this differential mortality being reflected in the increased proportions of males and females with dark elytra in the postdiapause populations of Douglas fir at Craibstone (table 3b).

3.5 Elytral pattern

Preliminary observations in 1977 indicated that three melanic elytral patterns were present in N.E. Scotland, the most common being type I with no elytral spots, the least common being type III (fig. 1). Types IV or V (EICHHORN and GRAF 1971) were not encountered.

In autumn 1978 the frequencies of types I, II and III were in the same order as observed in 1977 (table 5). However, the proportion of pre-diapause adults bearing melanic elytra increased in response to time, $F_{1,19} = 28.05$, P < 0.01 (fig. 4). The proportion of melanic females was greater than the proportion of melanic males (table 5). The proportions of each type did not change following migration to spruce bark scales (table 5) but post-diapause females on foliage exhibited a greatly innreased proportion of melanic type II elytra by contrast to post-diapause males in which the proportion remained steady (table 5).

Colour	Autumn 1978		In diap	ause	Spring	Spring 1979	
	o 7	Ŷ	ď	Ŷ	57	Ŷ	
I	95.03	74.09	96.50	72.93	95.24	53.02	
Π	4.44	15.14	3.50	22.18	4.76	42.70	
Ξ	0.53	10.77	0.00	4.89	0.00	4.27	
	5.55	,,	5100		0.00	,	

Table 5. Proportions of male and female A. obliterata with melanic spotted elytra in 1978-79. (Pooled data from all sources)

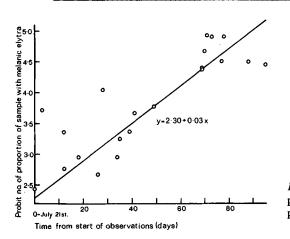


Fig. 4. The effect of time on the proportion of branch-caught, pre-diapause adult *A. obliterata* with melanic elytra (types II and III combined)

	Elytral pattern Type						TOTAL
	I		п	п			
	N	2	N	3	N	*	
Countesswells	74	74	25	25	1	1	100
Ballater	99	63	29	18	29	19	157
Kirkcaldy	28	54	12	23	12	23	52
TOTAL	201		66		42		

 Table 6. A comparison of sampling area and A. obliterata elytral pattern in late September, 1978

In late September a higher proportion of the melanic forms were present in samples from Kirkcaldy and Ballater, $\chi^2 4df = 21.49$, P < 0.001 (table 6). No association was established between overwintering mortality and elytral pattern or between pre-diapause and diapausing adults. However, a higher level of branch caught melanic forms occurred on Douglas fir than on Sitka spruce $\chi^2 1df = 16.90$, P < 0.001 (table 7).

	Colour Type T II				ш		TOTAL
	N	*	N	8	N	*	
Sitka spruce	74	74	25	25	1	1	100
Douglas fir	78	73	13	12	16	15	107
TOTAL	152		38		17		

Table 7. A comparison of A. obliterata elytral pattern and sampled tree (Douglas fir and Sitka spruce at Craibstone) in the pre-diapause period in 1978

3.6 Head pattern and colour

The four melanic head patterns and three colours were tested for independence by means of χ^2 contingency tables (table 8). Sex, in the form of darker females with whole patterns; host species, in which black individuals with whole patterns were more common on Douglas fir and broken pattern and brown colouration more common on Sitka spruce and sampling area, where black, whole patterns were commoner in Ballater and broken, brown patterns commoner elsewhere (table 8), all indicated that head pattern was dependent on at least 3 different factors.

Variable 1	Variable 2	χ²	df	Significance (P)	
Head pattern	Sex	380.4	3	< 0.001	
Pattern colour	Sex	248.8	2	< 0.001	
Head pattern	Host species	22.8	3	< 0.001	
Pattern colour	Host species	55.9	2	< 0.001	
o ⁷¹ Head pattern	Host species	0.4	3	> 0.05	
σ ^a Pattern colour	Host species	28.6	2	< 0.001	
9 Head pattern	Host species	23.8	3	< 0.001	
♀ Pattern colour	Host species	33.0	2	< 0.001	
Head pattern SS	Sex	14.5	3	< 0.01	
Pattern colour SS	Sex	23.2	2	< 0.001	
Head pattern DF	Sex	16.2	3	< 0.01	
Pattern colour DF	Sex	4.0	2	> 0.05	
♀ Head pattern	Sampling area	23.4	6	< 0.001	
9 Pattern colour	Sampling area	35.9	4	< 0.001	
o [#] Head pattern	Sampling area	7.8	6	> 0.05	
o ⁷ Pattern colour	Sampling area	15.0	4	< 0.01	

Table 8. Table of χ^2 values relating A. obliterata head pattern to various variables in pre-diapause samples

Observations on head patterns of overwintering insects indicated that no pattern or colouration differences existed in comparison with autumn adults.

In spring populations sex and head pattern and sex and pattern colour were again associated with higher than expected levels of black, whole patterned females and higher than expected levels of spotted, brown males thus maintaining the differences observed in the autumn samples.

Comparison of males and females in pre and post-diapause populations revealed that head pattern and colour differed significantly with higher levels of both black, whole and brown, spotted females in the pre-diapause populations and higher proportions of dark brown females in post-diapause populations. There were no differences in male head patterns but higher than expected levels of both black and light brown individuals occurred in prediapause populations.

3.7 Size

Samples of 21 males and 21 females were compared for length and width (table 9). Females were significantly longer with wider thoraxes than males. All measurements on male and female length obtained throughout the study

	Sex	N	x (mm)	F ratio	P	t (df = 20.00, $P = 0.05$)	t (n-1)
a)	ଟ୍ୟ ଦୁ		4.203 4.379	1.31	> 0.05	2.086	16.226
ь)	ہم 2		1.886 1.958	1.22	> 0.05	2.086	11.390

Table 9. Comparison of a) length and b) thorax width of male and female A. obliterata

confirmed these results but the overlap was sufficient to prevent their use in the differentiation of the sexes.

4 Discussion

Variability in the male adult colouration in both Germany (EICHHORN and GRAF 1971) and Scotland was considerably less than the variability in the female and mostly consisted of a greater degree of female melanisation (table 5). By contrast, dark elytral colouration unrelated to melanism was commoner in males (fig. 3). The proportion of foliage adults bearing dark elytra (fig. 3) or melanic spots (fig. 4) increased in response to time. The colour of the elvtra remained stable following the initial cuticular hardening process. Therefore, the most likely explanations for this change would be increased emigration of light forms, higher mortality rates in less pigmented individuals or later emergence of darker adults. The possibility of a delayed mortality of the pigmented forms is supported by the increase in the proportion of beetles with dark elytra on foliage following diapause (table 3) and the higher survival rate of the dark form beneath Sitka spruce bark scales (table 4). In addition prediapause head markings and colour were less melanistic than post-diapause markings. A similar change in the frequency of elytral colour forms has been noted in Adalia bipunctata L. by TIMOFÉEFF-RESSOVSKY (1940) where the black form prevalent in autumn was in the minority in comparison with the red form in the succeeding spring. This was attributed to a superior overwintering ability of the red form while the black forms were considered to have some advantages in summer e.g. ability to survive high temperatures (MAR-RINER 1926 quoted in FORD 1976) or higher activity (LUSIS 1961).

Other variables, such as sampling area (table 8) and plant species on which collection occurred (tables 7, 8) also affected the frequency of dark elytra and melanic spot deposition. FORD (1976) indicated that both region and season had marked effects on ratios of *A. bipunctata* colour forms with industrialisation having a positive effect on the proportion of black forms. FÜRSCH (1967) considered that industrialisation and also maritime, humid climates increased the proportions of dark forms in Coccinellidae. These observations in eastern Scotland support the conclusion of EICHHORN and GRAF (1971) that FÜRSCH's general observation is not applicable to *A. obliterata*.

The superior overwintering ability of pigmented males and melanistic

females would be expected to act selectively against the continued existence of the light coloured forms. However, in *A. obliterata* mating occurred during the summer months when the vast majority of the males possessed light elytra. Consequently, the superior survival ability of pigmented males would have little evolutionary significance in terms of elytral colour.

The significance of melanistic females may be related to geographical area, a conclusion supported by the work of LUSIS (1961) and HAWKES (1920) on *A. bipunctata*. In inland, high altitude Ballater and in coastal Kirkcaldy, a higher proportion of melanistic individuals were found (table 6) while in Germany high proportions of completely melanised individuals occurred in the mountainous, continental areas (EICHHORN and GRAF 1971). The increased survival of dark forms in colder areas may be associated with a higher degree of radiation absorption by dark individuals, cf. LUSIS (1961) who related melanisation in *A. bipunctata* with a superior ability to utilize radiation. The dominance of the light form in East Scotland may be associated with the summer insemination period in which high levels of light coloured males occur at the time of mating. This may be the result of a lack of a sufficiently selective temperature mortality in the mild winters normally encountered by comparison to continental Germany. This may also account for the survival of males in Scotland (PARRY 1980) and their mortality in eastern France (WYLIE 1958).

Males accounted for about 40 % of surviving overwintering ladybirds under Sitka spruce bark scales and, although initial male mortality was higher, the total mortality at the termination of the period was comparable to that of the females (table 2). Therefore, extensive numbers of males survived into spring, PARRY (1980) suggesting that these survivors fed at lower rates than their female counterparts. There was no evidence to suggest that mating occurred in spring and insemination was considered to be exclusively prediapausal.

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Zusammenfassung

Der Farbpolymorphismus und die Unterschiede im Verhältnis männlicher und weiblicher Insekten bei Aphidecta obliterata (L.) (Coleoptera, Coccinellidae) im östlichen Teil Schottlands

Nach dem Erreichen der Geschlechtsreife variierte bei A. obliterata das Verhältnis von Männchen zu Weibchen bei den aus verschiedenen Gebieten stammenden Proben zwischen 65:35 und 45:55. Die Geschlechtsverhältnisse der von Ästen gesammelten Proben veränderten sich während des Herbstes mit fortschreitender Zeit, so daß sich ein erhöhter Anteil weiblicher Käfer ergab, die vor der Diapause befruchtet wurden. Auf den Zweigproben im Frühling waren die weiblichen Käfer den männlichen im Verhältnis 3:1 überlegen. Während der Überwinterung unter der Rinde trat keine unterschiedliche Sterblichkeit auf. Dunkelfarbige Deckflügel kamen unter den geschlechtsreifen Männchen häufiger vor, wobei jedoch die hellen Deckflügel unter beiden Geschlechtern am stärksten verbreitet waren. Verhältnismäßig mehr Käfer mit dunklen Deckflügeln überlebten bis zum Frühling. Dunkle Pigmentation sowohl auf den Deckflügel na suf der Kopfkapseł kam unter den weiblichen Käfern häufiger vor. Durchschnittslänge und -breite waren bei den Weibchen größer. Trotz dieser Unterschiede erwies sich die Geschlechtsdifferenzierung ohne eine Heranziehung der Geschlechtsorgane als unzuverlässig.

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The incidence of endoparasitism of *Dendroctonus frontalis* Zimm. (Coleoptera: Scolytidae) by Contortylenchus brevicomi (Massey) Rühm (Nematoda: Sphaerulariidae)¹

By D. N. KINN and F. M. STEPHEN

Abstract

Adults of the southern pine beetle, Dendroctonus frontalis Zimm., emerging from the lower and middle sections of infested boles usually had a higher incidence of endoparasitism by the nema Contortylenchus brevicomi (Massey) Rühm than did beetles emerging from the upper bole. But the incidence of parasitism was similar among beetles flying at different heights. Endoparasitism was significantly greater in emerging females than males, but significantly more infected males than

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