Wing dimorphism and development in *Pterostichus melanarius* (Coleoptera: Carabidae)

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Abstract: Recently established populations of *Pterostichus melanarius* showed an extremely high proportion of long winged beetles (25.0-95.1%) in comparison to old populations (0.4-1.7%), and a large number of long winged beetles in samples collected at the end of June possessed fully developed flight muscles. In contrast with these observations flight was only reported occasionally. Preliminary results of single-pair crosses between supposed short winged heterozygous beetles indicate that wing dimorphism in *Pterostichus melanarius* is inherited in a simple Mendelian fashion with brachyptery dominant to macroptery.

Under outside conditions overwintering of larvae took place in the second and third instar. A thermic hibernation parapause in the larval stage was not necessary for development. Data on development times of the different stages are presented.

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Introduction

Pterostichus melanarius Illiger (= *P. vulgaris* (non Linnaeus): auct.) (fig. 1) is a medium sized 13.5-17.5 mm large, nightactive, eurytopic autumn breeder with a thermic hibernation parapause in the larval stage and no dormancy in the course of adult development (Thiele & Krehan, 1969; Krehan, 1970; Thiele, 1977). The larvae develop independently of photoperiod, but in the third larval stage they need a cold period to complete development (Krehan, 1970).

The species is wing-dimorphic with brachypterous and macropterous beetles. Brachy-

Fig. 1. *Pterostichus melanarius* (Photograph: Th. Heijerman).

pterous beetles have strongly reduced hind wings and are not able to fly, and macropterous beetles have well-developed hind wings. Data on wing dimorphism in *Pterostichus melanarius* are published by Den Boer (1970) for Dutch populations and by Desender (1989) for Belgian material. Den Boer found a high percentage of 25% long winged specimens in a young population in the recently reclaimed polder Oost-Flevoland (6 out of 24 specimens) in comparison with the rather low percentage (1.7%) in old populations in Drenthe (2 out of 119 specimens). Desender listed a percentage of 0.4% long winged *P. melanarius* for Belgium (36 out of 8451 specimens) and presented some data on wing size and flight muscle development. Actual flight, however, also depends on the possession of fully developed wing muscles and suitable weather conditions (Van Huizen, 1979) and was observed only occasionally in this species: in July 1969 a single female was caught in a window trap in the Lauwersmeerpolder, an area closed off from the sea shortly before in May 1969 (J. Meijer, personal communication) and Kádár & Szél (1995) reported the capture of four specimens in light traps in Hungary.

Den Boer (1977) accordingly classified *Pterostichus melanarius* as a species with uncertain dispersal power (C-species). Nevertheless it is assumed that one or more fully winged specimens founded the new populations in Oost-Flevoland (Den Boer, 1970; Den Boer et al., 1980).

Additional data on wing-morph frequencies in a number of young Dutch populations of *Pterostichus melanarius* are given, together with measurements of absolute and relative wing-size, and some observations on flight muscle development. Results of a limited cross-breeding program are presented, together with preliminary data on development time of eggs, larvae, pupae and adults for both short and long winged beetles.

Fig. 2. Sampling sites of *Pterostichus melanarius* in The Netherlands. 1, Province of Drenthe, surroundings of the Biological Station, Wijster: different localities sampled between 1959-1967 (Den Boer, 1977); 2, Bijlmermeer Polder: sampled in September 1972 by A.J. van Selm (Boomsma & Arntzen, 1985); 3, Oost-Flevoland, N60: sampled from March 1964 - March 1965 (Den Boer, 1970); 4, Oost-Flevoland, Ecological Nature Reserve: grass field sampled in 1968-1969 (Haeck, 1971) and in 1981-1984 (Aukema, 1990a); 5, Oost-Flevoland, C62: field with summer barley, sampled 20-27 June 1986 by J. Lahr & B. Aukema; 6-9, Zuid-Flevoland: four fields (6, Ez30; 7, Gz5; 8, Gz48; 9, Nz112) with summer barley, sampled 20-27 June 1986 by J. Lahr & B. Aukema; 10, Noordoostpolder, between Vollenhove and Marknesse: sampled on 13 July 1987 by A.J. Spee & Th. S. van Dijk.

Table 1. *Pterostichus melanarius*: wing-morph frequencies in field populations. N: number of beetles; SW: short winged; LW: long winged. Localities: see fig. 2.

			Males			Females			Total		
Region/year(s)	locality	N	SW	LW	%LW	SW	LW	%LW	SW	LW	%LW
Drenthe											
1959-1967	1	119							117	2	1.7
Bijlmermeer											
1972	2	151	50	22	30.6	54	25	31.6	104	47	31.1
Oost-Flevoland											
1964	3	24							18	6	25.0
1968	4	221							121	100	45.2
1982	4	29	12	3	20.0	5	9	64.3	17	12	41.4
1983	4	18	4	6	60.0	3	5	62.5	7	11	61.1
1984	4	54	25	11	30.6	12	6	33.3	37	17	31.5
1986	5	551	183	178	49.3	95	95	50.0	278	273	49.5
Zuid-Flevoland											
1986	6	36	9	9	50.0	6	12	66.7	15	21	58.3
1986	7	345	40	104	72.2	54	147	73.1	94	251	72.7
1986	8	213	29	62	68.1	50	72	59.0	79	134	62.9
1986	9	41	1	21	95.4	1	18	94.7	2	39	95.1

Material and methods

Wing development of *Pterostichus melanarius* was examined on the basis of material from pitfall samples of relatively young populations in the Bijlmermeer polder (an artificial sand deposit, created in 1969 for building housing estates; Boomsma & Arntzen, 1985), and in the polders Oost- and Zuid-Flevoland, which were reclaimed in 1957 and 1967 respectively (Haeck, 1970). Sampling localities are depicted in fig. 2. Specimens collected between 20 and 27 June 1986 in cereal fields at the localities 5 (C62 in Oost-Flevoland) and 8 (Gz48 in Zuid-Flevoland) were dissected for both measurement of wings and elytra, and examination of flight muscle development of short and long winged beetles. Measurements of wings and elytra were made according to Aukema (1990a). Wing-morph frequencies were compared with data from the literature (Den Boer, 1970; Desender, 1989).

Relative wing size was estimated by the quotient of wing surface (wing-length x wing-

Table 2. Measurements of wing-length in *Pterostichus melanarius*. N: number of beetles measured; NM: number of beetles with fully developed flight muscles; WL: wing-length (in mm); RWL: relative wing-length (wing-length/elytrum-length); RWS: relative wing-surface (wing- surface/elytrum-surface; surface: length x width). Localities: see fig. 2.

Sex	Wing-morph	Locality	N	NM	WL (± SE)	RWL (± SE)	RWS (± SE)
♂	long winged	5	30	8	14.44 (± 0.294)	1.46 (± 0.030)	2.64 (± 0.078)
		8	25	9	13.65 (± 0.276)	1.45 (± 0.021)	2.61 (± 0.081)
	short winged	5	15	0	4.78 (± 0.454)	0.49 (± 0.046)	0.31 (± 0.069)
		8	15	0	4.59 (± 0.277)	0.49 (± 0.029)	0.29 (± 0.037)
♀	long winged	5	30	13	15.44 (± 0.315)	1.43 (± 0.030)	2.57 (± 0.117)
		8	25	13	14.59 (± 0.218)	1.45 (± 0.010)	2.60 (± 0.067)
	short winged	5	15	0	5.27 (± 0.320)	0.49 (± 0.025)	0.31 (± 0.037)
		8	15	0	4.82 (± 0.218)	0.48 (± 0.023)	0.27 (± 0.061)

Table 3. Mortality during development among offspring of single-pair crosses of supposed heterozygous short winged *Pterostichus melanarius*. N: number of specimens; M: mortality.

	Cross					
Stage	1	2	3	4	N	M (%)
Larva I	41	25	11	23	100	15.0
Larva II	35	24	11	12	85	20.0
Larva III	32	17	10	6	68	26.5
Pupa	25	9	7	6	50	28.0
Adult	18	8	6	4	36	
Mortality (%)	56.1	68.0	45.4	82.6	64.0	

Table 4. F2-beetles from four single-pair crosses of short winged *Pterostichus melanarius* reared under outside conditions in 1983/1984. N: number of offspring; SW: short winged; LW: long winged.

	Offspring			
	Observed phenotypes (males/females)			
Cross	N	SW	LW	%LW
1	18	5/5	5/3	
2	8	3/3	2/-	
3	6	-/5	1/-	
4	4	1/1	-/2	
Total	36	9/14	8/5	47.1/26.3

width) and elytrum surface (elytrum-length x elytrum-width) (Den Boer, 1977). Flight muscles were examined and classified according to Tietze (1963). Beetles with well-developed direct and indirect flight muscles in the classes IV and V according to Tietze (almost full-grown and full-grown muscles respectively) are assumed to be able to fly (see also Nelemans, 1987).

A limited cross-breeding experiment was carried out in 1983/1984 by breeding offspring of four single-pair crosses between supposed heterozygous short winged beetles individually. The latter were obtained from laboratory-bred offspring of a single long winged female collected in September 1982 at the Ecological Nature Reserve, Oost-Flevoland. Breeding took place in an outdoor insectary with overwintering in a wooden box sunk in the ground (see Aukema, 1990b, for breeding conditions). The larvae were fed twice a week with an excess of small blowfly larvae.

Additional breeding experiments were done in 1987/1988 to test the necessity of a thermic hibernation parapause at the larval stage. Offspring of mainly short winged beetles collected on 13 July in the Noordoostpolder (fig. 2) were reared at three different temperatures and two food-supply levels. Groups of 20 newly hatched larvae were reared at constant temperatures of 8.5 and 15.5 °C and under approximately outside conditions in an outdoor insectary comparable to the first experiment. The larvae were fed three times a week. Larvae of the high food-supply group each time got four to six small maggots of about 1.5 mg and those of the low food-supply group got about one quarter of that quantity. Wing development was not checked in this experiment.

Results

Wing-morph frequencies

Wing-morph frequencies in field populations are given in table 1. All populations sampled in recently established populations showed

Table 5. Development time (days) of immature stages of short and long winged *Pterostichus melanarius* under outside conditions in 1983/1984. N: number of beetles. LI, LII and LIII: first, second and third larval instar respectively. Oviposition period: 6-27 September 1983.

Sex	Wing-morph	N	Egg	LI	LII	LIII	Pupae	Total (± SE)
♂	long winged	8	12.6	34.6	158.9	89.5	16.8	316.4 (± 5.37)
	short winged	9	12.6	38.8	171.7	82.3	14.4	319.8 (± 3.11)
♀	long winged	5	12.4	35.6	182.0	80.3	13.8	320.0 (± 1.64)
	short winged	14	11.6	31.4	181.9	84.3	14.9	324.1 (± 2.58)

Table 6. Development (number of specimens) of *Pterostichus melanarius* at three temperature conditions and two food-supply levels in 1987/1988. LI, LII and LIII: first, second and third larval instar respectively; M: total mortality during development; DT: total development time in days.

Food-supply	Temperature	Starting date	LI	LII	LIII	Pupae	Adults	M (%)	DT (mean ± SE)
Low	8.5 °C	18.viii.1987	20	20	19	18	9	55.0	427.8 (± 4.12)
	15.5 °C	11.viii.1987	20	19	19	17	12	40.0	319.3 (± 5.53)
	outside	20.viii.1987	20	20	16	7	7	65.0	318.0 (± 4.43)
High	8.5 °C	14.viii.1987	20	19	18	17	7	65.0	433.0 (± 4.51)
	15.5 °C	10.viii.1987	20	18	18	16	12	40.0	327.8 (± 4.93)
	outside	17.viii.1987	20	20	18	15	14	30.0	305.0 (± 2.17)

extremely high percentages of long winged beetles (between 25 and 96%) in comparison to figures for old populations as given by Den Boer (1970) for Drenthe, The Netherlands (1.7%), and Desender (1989) for Belgium (0.4%). However, large differences were found between different populations in the same area (Zuid-Flevoland: 58-95%) and between years for the same population (the Ecological Nature Reserve, Oost-Flevoland: 31-61%). Comparing data for Oost-Flevoland and Zuid-Flevoland, in general higher frequencies of long winged beetles were observed in Zuid-Flevoland, which was reclaimed 10 years later than Oost-Flevoland.

Wing size

Relative wing sizes (table 2: RWS), estimated for populations in Oost-Flevoland (locality 5) and Zuid-Flevoland (locality 8), were about 2.6 for both long winged males and females and about 0.3 for short winged beetles of both sexes. In comparison with the data compiled by Den Boer (1977) for other species the vast majority of the long winged beetles of *Pterostichus melanarius* measured showed quotients comparable to species with a high dispersal power (B-species), which were capable to fly under certain conditions.

Cross-breeding

The results of four single-pair crosses between supposed heterozygous short winged *Pterostichus melanarius* are given in tables 3-4. The total mortality of 64% was rather high, and especially the pupae showed a remarkably high mortality in relation to the short duration of this stage (table 3). All crosses produced both short and long winged offspring (table 4). The proportion of long winged beetles (36.1%) did not differ significantly from the expected value of 25% for crossing short winged heterozygous beetles of a species in which wing dimorphism is inherited according to a single locus system with dominance of the brachypterous condition ($\chi^2 = 1.42$; $p < 0.05$).

Total development time on the average took about 320 days for both short winged and long winged males and females (table 5). In 35 of the 36 beetles reared overwintering took place in the second larval stage and adult beetles hatched between early July and early September (fig. 3).

Flight muscle development

Fully developed flight muscles were found in a significant number of long winged males and females in samples taken between 20 and 27 June 1986 at the localities 5 (Oost-Flevoland) and 8 (Zuid-Flevoland), the only two samples dissected (table 2: 26.7 and 36.0% for males, and 43.3 and 52.0% for females at the two localities respectively). No flight muscle development was found in short winged beetles.

Flight muscle development in *Pterostichus melanarius* was already reported by Desender (1989): 20% out of the 15 long winged beetles dissected by this author possessed functional flight muscles.

Breeding

The results of the breeding experiments in

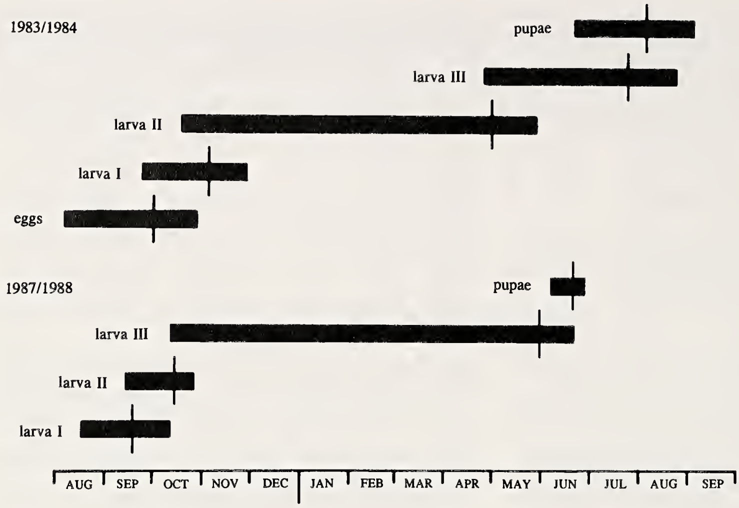

Fig. 3. Development in time of eggs, larvae and pupae of *Pterostichus melanarius* under outside conditions in 1983/1984 (35 specimens) and 1987/1988 (14 specimens). Cross bars: median values.

1987/1988 are given in table 6. The total mortality varied between 30 and 65%. The best result was obtained under outside conditions with a high food-supply level, mainly due to an extreme low mortality of the pupae (6.7%) under these conditions.

Development times clearly depended on temperature: longer development times were found at lower temperatures. Total development under outside conditions took about 318 days and 305 days, with low and high food-supply levels respectively. These data are in accordance with those found in the cross-breeding experiment (table 5). Note that only in the first experiment egg development is included.

Under outside conditions all beetles reared at a high food-supply level overwintered in the third larval stage and adult beetles hatched between early June and the end of June (fig. 3). Beetles reared under outside conditions with a low food-supply, however, partly overwintered in the second larval stage (3 out of 7 beetles) and adults hatched between the end of June and the end of July.

At constant temperatures of 8.5 °C and 15.5 °C at both low and high food-supply levels '-hibernation' took place in the third larval stage.

Discussion

From the data on wing size and flight muscle development it can be concluded that at least under favourable conditions, as defined by Van Huizen (1979), flight activity in *Pterostichus melanarius* is to be expected. However, so far flight activity has been recorded only occasionally and, for instance, the species was never caught in window traps operating during four successive years (1981-1984) at the Ecological Nature Reserve in Oost-Flevoland, where a high frequency of long winged *P. melanarius* occurred (table 1, see also Aukema, 1995a). A comparable situation was found in *Calathus melanocephalus* Linnaeus, a species capable of flight under laboratory conditions but never intercepted during flight under natural conditions (Aukema, 1995a, 1995b). Nevertheless it is supposed that dispersal by flight occurs and that it is of great importance in establishing new populations, as for instance, in the newly reclaimed polders here involved. Niemela & Spence (1991) arrived at the same conclusion with regard to the recent expansion of *Pterostichus melanarius* in Central Alberta, Canada. They found a gradual increase in the frequency of long winged beetles from 20% in Edmonton, where it was recorded for the first time in Canada in 1959, to about 60-70% in the most distant populations. Furthermore, Powell & Waterhouse (1985) recorded a high frequency of long winged beetles in a recently established population of *P. melanarius* on an island in Lake Champlain, New York.

The cross-breeding data presented suggest that in *Pterostichus melanarius* wing dimorphism is inherited in a simple Mendelian fashion, with brachyptery dominant to macroptery. However, since only a limited number of crosses was performed and the mortality was rather high, additional work is necessary to corroborate this, the more so since in certain wing-dimorphic carabid beetles also environmental control of the expression of the long winged genotype was observed (Aukema, 1990b, 1995b).

A high mortality during the development of *Pterostichus melanarius* was experienced by Thiele & Krehan (1969), who got their best results - a total mortality of 72-76% - under outside conditions. However, contrary to their observations, overwintering in the present case took place in both the second and third larval instar and not exclusively in the third one. Most likely in the cross-breeding experiment this was due to the fact that the eggs were incubated at the end of the oviposition period, which probably was also reflected in the long development time and the late emergence of the adult beetles. However, only one reared beetle overwintered in the third larval instar, but it needed 338 days for development. In the breeding experiment under outside conditions overwintering in the second larval instar was only found at the low food-supply level. Obviously overwintering in the second larval instar is related to suboptimal conditions as late hatching of eggs and food shortage during early development.

Furthermore, from the breeding experiments at constant temperatures of 8.5 and 15.5 °C (table 6) it is clear that in *Pterostichus melanarius* a thermic hibernation parapause in the larval stage is not necessary to complete development. This was also observed in other autumn breeding carabids as, for instance, *Calathus melanocephalus* (Van Dijk & Den Boer, 1992; Aukema, 1995a), *C. cinctus* Motschulsky and *C. mollis* (Marsham) (Aukema, 1995a).

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