Wing-length determination in two wing-dimorphic *Calathus* species (Coleoptera: Carabidae)[1,2]

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Wing dimorphism in the carabid beetles *Calathus cinctus* and *C. melanocephalus* was studied by rearing offspring of single-pair crosses. In both species wing dimorphism was found to be determined genetically according to a single-locus model with brachyptery dominant to macroptery. In *melanocephalus*, however, the expression of the long-winged genotype is modified by environmental factors such as temperature and food supply, whereas in *cinctus* wing-length is independent of these factors. Moreover, in *melanocephalus* the expression of the long-winged genotype was found to be favoured by relatively better environmental conditions (higher temperatures and abundant food) and to be more frequent in females than in males, both in the field and in laboratory experiments. It is argued that the resulting differences in phenotypic plasticity of the long-winged genotype (none in *cinctus* and a varying amount in *melanocephalus*) contribute to temporal and spatial differences in dispersal abilities between the two species. The adaptive significance of the two types of inheritance is discussed.

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Wing polymorphism is a very common phenomenom in insects, occurring in many groups (see HARRISON (1980) and DINGLE (1986) for recent reviews). In carabid beetles it has caught the attention of zoologists since the times of DARWIN (1859: flightless morphs on Madeira) and DARLINGTON (1936, 1943: wing development in relation to mountain tops and islands), but little experimental work has been done to unravel the background of wing development in this group. LINDROTH (1949, 1969) based his theory about the recolonization of Fennoscandia by Carabidae after the last glaciation on "the postulate that long-winged (macropterous) individuals are homozygotes and that populations entirely or very dominantly consisting of such individuals are pioneers (late colonizers)" (LINDROTH 1969: p. 181). This postulate was mainly based on his limited but thus far unique breeding experience (a progeny of 52 beetles of 7 parental females) with the wing-dimorphic *Pterostichus anthracinus* (Illiger) (LINDROTH 1946), which led him to the conclusion that wing dimorphism in this species is inherited in a simple

Mendelian fashion with the brachypterous condition dominant. The fact that JACKSON (1928) had already got similar results with the weevil *Sitonia hispidula* (Fabricius) tempted LINDROTH (1946) to the statement that "it therefore seems probable that the non-sexual wing dimorphism in the order of Coleoptera as a whole will prove to be of the same type". STEIN (1973) indeed got comparable results for another weevil, *Apion virens* Herbst.

Concerning carabid beetles, since then very few efforts have been made to confirm Lindroth's postulate. Breeding results with the wing-polymorphic *Agonum retractum* LeConte (CARTER 1976) and with *Bembidion lampros* (Herbst) (LANGOR and LARSON 1983) do not allow unambiguous conclusions concerning the type of inheritance involved in these species. DESENDER (1989a) showed a high heritability of relative wing development in the wing-polymorphic *Pogonus chalceus* (Marsham). DEN BOER et al. (1980) used some preliminary data of *Calathus cinctus* from the study presented here to illustrate their theory on the evolution of wing dimorphism in carabids.
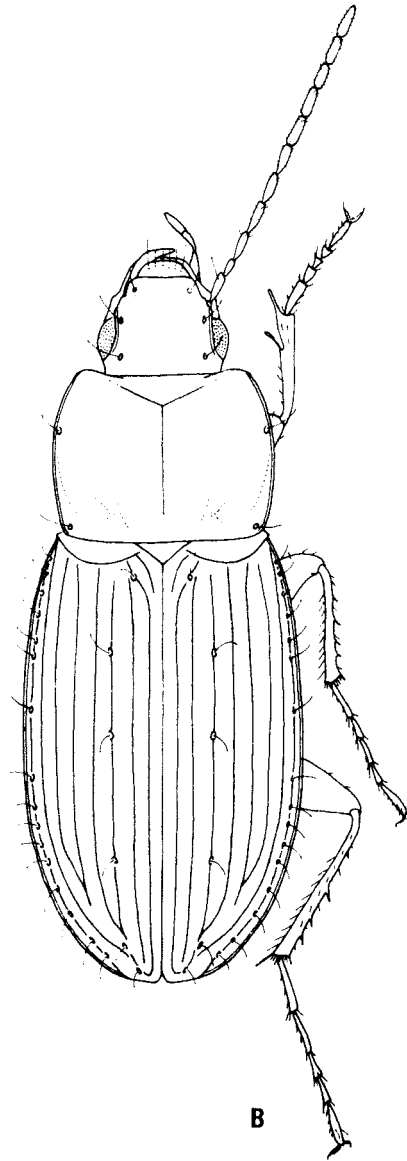
The aim of the work presented here was to study the inheritance of wing dimorphism in two closely related species of the genus *Calathus* Bonelli: *Calathus (Neocalathus) cinctus* Motschulsky (= *ery-*
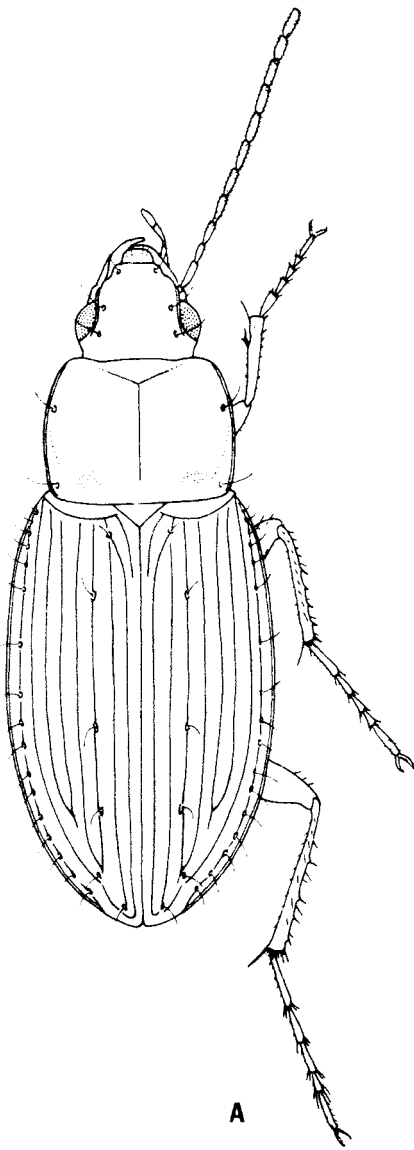
Fig. 1 A–B. Habitus of females of *Calathus* (scale 1 mm   **Fig. B.** *melanocephalus.*
Fig. A. *cinctus.*

throderus Gemminger & Harold) and *Calathus* *(Neocalathus) melanocephalus* (Linnaeus) and thus to test Lindroth's postulate of a single-locus model with dominance of the short-winged condition for these two species. A third species under investigation, the closely related *Calathus (Neocalathus) mollis* (Marsham), appeared to be monomorph macropterous in field samples, collection material as well as in breeding experiments (AUKEMA 1990).

Offspring of single-pair crosses between all pos-

sible combinations of wingmorphs of both species were reared under approximately outside conditions in an outdoor insectary as well as under fixed temperature conditions in incubators in the laboratory. In the case of *melanocephalus* also the effect of the quantity of available food during larval development on wing development was established.

Some preliminary data have already been published (AUKEMA 1986).

Material and methods

Species

Calathus cinctus (Fig. 1A) and *C. melanocephalus* (Fig. 1B) are both wing-dimorphic with either strongly reduced short wings (about half the length of the elytra) or fully developed long wings (about 1.5 times the length of the elytra) (Fig. 2; Table 1). Detailed information on biology of the species is given by AUKEMA (1990).

Parents and offspring of crosses carried out by VAN DIJK (1978) were used as starting material for a first crossing programme. Assumed parental genotypes were derived from phenotypes of parents and their offspring. Long-winged phenotypes were considered to represent the recessive homozygote, whereas short-winged offspring of long-winged females were supposed to be heterozygous. The short-winged homozygotes could not be established with certainty, but fully short-winged offspring of short-winged females from localities with a low to very low percentage of long-winged individuals were used as such.

All three assumed genotypes of *cinctus* were obtained from offspring of females caught at Nuil and Dwingeloo in the surroundings of the Biological Station.

Supposed long-winged homozygotes and short-winged heterozygotes of *melanocephalus* were reared from females collected in the in 1957 reclamed polder of Oost-Flevoland from a population with a relatively high percentage of long-winged beetles (23 % in 1978). Short-winged offspring of females collected at the heath of Kraloo (a population with a very low percentage of macropterous beetles—estimated as 0.23 % by DEN BOER (1977) —were used as short-winged homozygotes. In *melanocephalus* males and females with asymmetric wing development (a fully developed wing on the left or the right side and a short wing on the opposite side) occur in both field populations and in laboratory bred offspring (see also DESENDER 1989b). In this study those specimens are considered to represent long-winged genotypes.

Cross-breeding

For both *cinctus* and *melanocephalus* single-pair crosses between all combinations of wingmorphs were carried out during the years 1978/1979 and 1979/1980 under approximately outside conditions in an outdoor insectary. Selected pairs were kept in petri dishes in ground peat litter. Eggs were separated from the peat with the sieve-wash technique

of MOLS et al. (1981) and further incubated at a constant temperature of 19°C. Larvae were transferred to glass tubes, in which they were reared individually in sieved peat litter in the outdoor insectary. During the winter months (from the end of November until the end of March) the larvae were moved to a climate room at 5°C under short-day (SD 10/14) conditions. Crosses and origin of the beetles used are given in Table 2.

Offspring of crosses conducted by VAN DIJK (1979) (F_1-offspring 1978 in Table 2) and specimens collected in the field before the start of the reproduction period (tenerals in the case of females) were used as starting material (Table 2). Furthermore, offspring of females inseminated in the field (*cinctus* from Nuil and Dwingeloo, and *melanocephalus* from Oost-Flevoland) was reared in order to get virgin females as starting material for the next crossing experiments.

In 1979/1980 crosses were carried out in the same way as in the preceding year. The larvae, however, were kept in small petri dishes and the food was changed from pieces of mealworm to small maggots. Information on these crosses is also summarized in Table 2.

The effect of temperature on wing development in both *cinctus* and *melanocephalus* was studied in 1981/1982 by rearing larvae of different groups of single pairs of long-winged parents collected in the field at three constant temperatures (8.5, 12 and 15.5°C) and natural daylight in incubators in the laboratory as well as under outside conditions in the outdoor insectary. Parental material of *cinctus* and *melanocephalus* was collected on the West Frisian Island of Ameland and in Oost-Flevoland, respectively.

During the winter months the larvae of the outside-group were kept in a wooden box sunk in the ground, where they stayed from the third week of December until the last week of April.

The effect of the amount of available food on wing development in *melanocephalus* was studied in 1982/1983 and 1983/1984 by rearing groups of larvae at two different levels of food supply under different temperature conditions.

In 1982/1983 offspring of different groups of long-winged parents collected in Oost-Flevoland was reared at three different constant temperatures as well as under outside conditions (the same temperature conditions as in the 1981/1982 programme).

To avoid maternal effects of using different groups of parental females at different temperatures, which might have affected the preceding
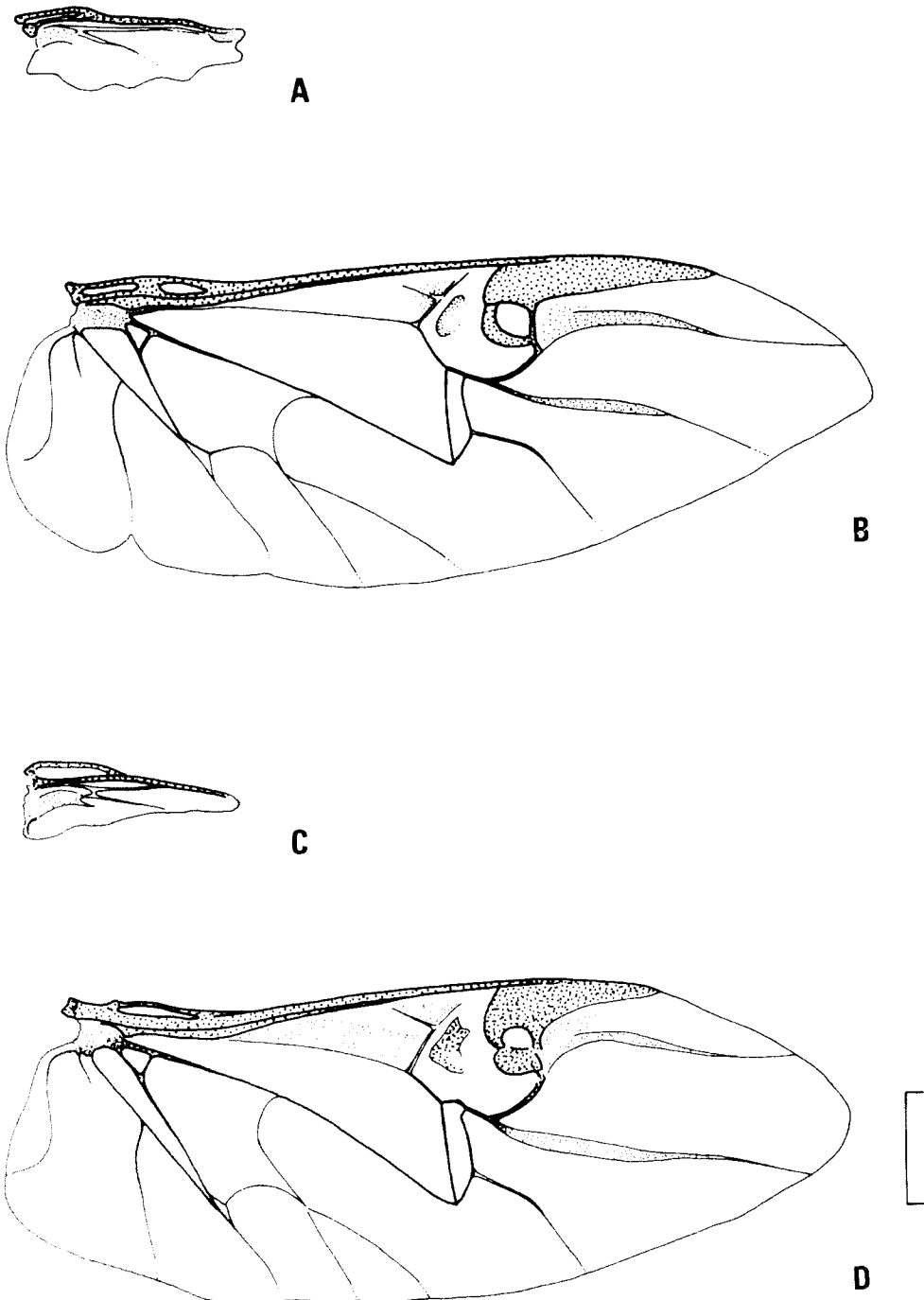
Fig. 2 A–D. Wing morphs in *Calathus* (scale 1 mm). **Fig. A.** *cinctus*, short-winged. **Fig. B.** ibid., long-winged. **Fig. C.** *melanocephalus*, short-winged. **Fig. D.** ibid., long-winged.

Table 1. Measurements (in mm) of wing-length and elytron-length. RWL: relative wing-length = wing-length/elytron-length. N: number of measurements. Measurements were made according to AUKEMA (1990)

Sexes	Wing-morph	Species	Locality	N	Wing-length		Elytron-length		RWL	
					Mean	95 % c.l.	Mean	95 % c.l.	Mean	95 % c.l.
Males	Short-winged	*cinctus*	Nuil	25	1.98	1.95–2.03	4.48	4.42–4.54	0.44	0.44–0.45
			Texel	20	1.93	1.85–2.01	4.17	4.07–4.29	0.46	0.45–0.47
		melanocephalus	Texel	20	1.93	1.86–2.00	4.09	4.00–4.18	0.47	0.46–0.49
	Long-winged	*cinctus*	Dwingeloo[1]	30	7.18	7.02–7.35	4.65	4.59–4.72	1.54	1.52–1.57
			Texel	11	6.26	5.89–6.62	4.12	3.98–4.25	1.52	1.47–1.57
		melanocephalus	Oost-Flevoland[2]	25	7.34	7.17–7.51	4.69	4.60–4.78	1.57	1.53–1.60
			Texel	7	7.10	6.86–7.35	4.32	4.19–4.32	1.64	1.62–1.67
Females	Short-winged	*cinctus*	Nuil	25	2.16	2.11–2.20	4.82	4.73–4.90	0.45	0.44–0.45
			Texel	20	2.14	2.08–2.20	4.54	4.44–4.64	0.47	0.46–0.48
		melanocephalus	Texel	20	2.06	1.99–2.13	4.45	4.36–4.53	0.46	0.45–0.48
	Long-winged	*cinctus*	Dwingeloo[1]	30	7.77	7.63–7.91	5.03	4.96–5.11	1.54	1.53–1.56
			Texel	11	6.49	6.15–6.82	4.34	4.18–4.50	1.49	1.45–1.54
		melanocephalus	Oost-Flevoland[2]	29	7.60	7.47–7.62	5.02	4.96–5.08	1.51	1.49–1.54
			Texel	20	7.51	7.38–7.65	4.80	4.72–4.88	1.57	1.54–1.59

[1] Measurements M. G. J. Oudewesselink

[2] Measurements A. Spee

experiments, in 1983/1984 newly hatched larvae of the same eight pairs of long-winged F_1-parents were distributed as equally as possible over six different rearing conditions: four constant temperatures (8.5, 12, 15.5 and 19°C) with natural daylight (adjusted once a week), one alternating temperature (12 hours light at 15.5°C and 12 hours dark at 8.5°C), and approximately outside conditions (comparable to the experiment carried out in 1981/1982).

In both years larvae of the high food-supply group were fed twice a week with about their own weight in small maggots, whereas larvae of the low food-supply group only got two milligrams of maggots twice a week during their whole development. Larvae were weighed twice a week during the entire developmental period.

Results

Calathus cinctus

Wing-morph frequencies among offspring reared from females inseminated in the field are given in Table 3 and data on wing-morph frequencies in the parental field populations are summarized in Table 4. Long-winged females produced significantly more long-winged offspring than did short-winged ones (x^2=208.59, df=1, p<<0.001) and for both groups of females there are no significant differences in the frequencies of long-winged offspring between males and females (long-winged females: x^2=1.84, df=1, 0.5>p>0.1; short-winged females: x^2=0.85, df=1, 0.5>p>0.1). Nine out of the 21 long-winged females (43 %) used in this experiment only produced long-winged offspring (137 males and 135 females, representing 43 % of the entire offspring). Rearing mortality, calculated from Table 2, varied between 35 and 45 %.

These preliminary data already suggest a genetic determination of wing development in this species.

Wing-morph frequencies of both the F_1- and the F_2-generation of *cinctus* (Tables 5–6) reared in 1978/1979 and 1979/1980, respectively, are in accordance with the expectations from the assumed single-locus model: fully long-winged offspring from long-winged parents, 50 % long-winged offspring from long-winged and assumed heterozygous parents, 25 % long-winged offspring from heterozygous parents and no long-winged offspring from crosses with one or both parents short-winged homozygotes.

Heterogeneity between different crosses of the same group, taken together in Tables 5 and 6, was considerable, but never significant. The six crosses between heterozygous short-winged beetles (Table 5), expected to segregate 3 short-winged: 1 long-winged, show a pooled chi-square of 0.18 (df=1,

Table 2. Wing-length determination in *Calathus cinctus* and *C. melanocephalus*: crossing program. LW: long-winged; SW: short-winged; N: number of crosses; NL: number of crosses, producing larvae; L: number of larvae reared; B: number of beetles reared

| Year | Species | Parents | | | | Crosses | | | |
| | | Wing-morph | | Origin | | | | | |
		Males	Females	Males	Females	N	NL	L	B
1978	*cinctus*	LW	LW	Parents 1977[1]	F₁-offspring 1978[1]	6	5	283	179
		LW	SW	F₁-offspring 1978	Parents 1977	6	4	114	48
		SW	LW	F₁-offspring 1978	Parents 1977	6	5	149	59
		SW	SW	F₁-offspring 1978	F₁-offspring 1978	6	6	295	182
		SW	SW	F₁-offspring 1978	Parents 1977	1	1	59	25
		–	LW	no males	Dwingeloo (23-8/22-9-1978)	16	16	734	471
		–	LW	no males	Nuil (23-8/22-9-1978)	5	5	253	158
		–	SW	no males	Dwingeloo (7-9-1978)	1	1	49	27
		–	SW	no males	Nuil (23/31-8-1978)	4	3	147	86
	melano-cephalus	LW	SW	Oost-Flevoland (20/27-9-1978)	F₁-offspring 1978	4	4	188	113
		SW	SW	Kraloo (30-8-1978)	Kraloo (30-8-1978)	6	6	60	40
		SW	SW	Kraloo (30-8-1978)	F₁-offspring 1978	2	2	90	51
		–	LW	no males	Oost-Flevoland (20-9-1978)	14	13	489	304
		–	SW	no males	Oost-Flevoland (28-9-1978)	13	10	371	236
1979	*cinctus*	LW	LW	F₁-offspring 1979	F₁-offspring 1979	2	2	120	43
		LW	LW	Ameland (28-6-1979)	F₁-offspring 1979	1	1	60	20
		SW	LW	F₁-offspring 1979	F₁-offspring 1979	2	2	85	41
		SW	LW	Ameland (28-6-1979)	F₁-offspring 1979	1	1	60	13
		LW	SW	F₁-offspring 1979	F₁-offspring 1979	2	2	116	68
		LW	SW	Ameland (28-6-1979)	F₁-offspring 1979	1	1	60	20
	melano-cephalus	LW	LW	F₁-offspring 1979	F₁-offspring 1979	4	4	238	85
		SW	LW	F₁-offspring 1979 (O-Flevoland)	F₁-offspring 1979	4	4	240	135
		SW	LW	F₁-offspring 1979 (Kraloo)	F₁-offspring 1979	4	4	217	139
		LW	SW	F₁-offspring 1979	F₁-offspring 1979 (O-Flevoland)	4	4	239	92
		SW	SW	F₁-offspring 1979 (O-Flevoland)	F₁-offspring 1979 (O-Flevoland)	4	4	240	130
		SW	SW	F₁-offspring 1979 (Kraloo)	F₁-offspring 1979 (O-Flevoland)	4	4	224	136
		LW	SW	F₁-offspring 1979	F₁-offspring 1979 (Kraloo)	4	4	160	96
		SW	SW	F₁-offspring 1979 (O-Flevoland)	F₁-offspring 1979 (Kraloo)	4	4	240	132
		SW	SW	F₁-offspring 1979 (Kraloo)	F₁-offspring 1979 (Kraloo)	4	4	240	112

[1] Crosses carried out by Th. S. van Dijk

Table 3. Offspring of females of *Calathus cinctus* and *C. melanocephalus* inseminated in the field (1978/1979, outside conditions/5°C, SD10). N: number of parental females; n: number of offspring; LW: long-winged; SW: short-winged; SD10: short day condition of 10 hours light/14 hours dark

| Species | Parents | | | Offspring | | | |
| | Female | | | Observed phenotype (males/females) | | | |
	Phenotype	Origin	N	n	SW	LW	% LW
cinctus	LW	Dwingeloo	16	471	38/ 26	198/209	83.9/88.9
		Nuil	5	158	7/ 6	75/ 70	91.5/92.1
	SW	Dwingeloo	1	27	3/ 10	5/ 9	62.5/47.4
		Nuil	3	86	43/ 27	8/ 8	15.7/22.9
melanocephalus	LW	Oost-Flevoland	13	304	120/131	14/ 39	10.4/22.9
	SW	Oost-Flevoland	10	236	100/ 92	16/ 28	13.8/23.3

Table 4. Wing-morph frequencies in pitfall samples of field populations of *Calathus cinctus* and *C. melanocephalus*. n: number of beetles trapped; LW: long-winged; SW: short-winged

Species	Locality	Year	Observed phenotypes (males/females)			
			n	SW	LW	% LW
cinctus	Dwingeloo	1978	180	21/ 25	63/ 71	75.0/74.0
	Nuil	1978	33	1/ 4	13/ 25	92.9/86.2
melanocephalus	Oost-Flevoland	1978	982	389/365	91/137	19.0/27.3

Table 5. F$_1$-beetles from single-pair crosses of *Calathus cinctus* with assumed genotypes (1978/1979, outside conditions/5°C, SD10). *B*: short-winged allele; *b*: long-winged allele; LW: long-winged; SW: short-winged; N: number of crosses; n: number of offspring. SD10, see Table 3

Parents					Offspring				
Phenotype		Genotype			Phenotype (males/females)				
		Assumed			Observed				Expected
Male	Female	Male	Female	N	n	SW	LW	% LW	% LW
LW	LW	*bb*	*bb*	5	179	–/–	93/86	100/100	100
LW	SW	*bb*	*Bb*	4	48	9/11	12/16	57.1/59.3	50
SW	LW	*Bb*	*bb*	5	59	14/22	13/10	48.1/31.2	50
SW	SW	*Bb*	*Bb*	6	182	23/25	69/65	25.0/27.8	25
SW	SW	*BB*	*BB*	1	25	10/15	–/–	–/–	0

Table 6. F$_2$-beetles from single-pair crosses of *Calathus cinctus* with assumed genotypes (1979/1980, outside conditions/5°C, SD10). Symbols, see Table 5

Parents					Offspring				
Phenotype		Genotype			Phenotype (males/females)				
		Assumed			Observed				Expected
Male	Female	Male	Female	N	n	SW	LW	% LW	% LW
LW	LW	*bb*	*bb*	3	63	–/–	27/36	100/100	100
LW	SW	*bb*	*Bb*	2	88	18/27	25/18	58.1/40.0	50
SW	LW	*Bb*	*bb*	2	41	12/10	5/14	29.4/58.3	50
SW	LW	*BB*	*bb*	1	13	5/8	–/–	–/–	0

Table 7. F$_1$-beetles from single-pair crosses of long-winged *Calathus cinctus* from Ameland reared at different temperatures (1981/1982, natural daylight). Symbols, see Table 5

		Offspring			
		Observed phenotypes (males/females)			
Temperature	N	n	SW	LW	% LW
8.5°C	7	118	–/–	59/59	100/100
12 °C	7	120	–/–	61/59	100/100
15.5°C	5	68	–/–	29/39	100/100
Outside	2	50	–/–	26/24	100/100

ns, 0.5<P<0.9), a summed chi-square of 6.61 (df=6, ns, 0.1<P<0.5) and a heterogeneity chi-square of 5.42 (df=5, ns, 0.1<P<0.5).

Furthermore, offspring of single-pair crosses of *cinctus* collected on Ameland and reared at constant temperatures of 8.5, 12 and 15.5°C and natural daylight as well as under outside conditions was entirely long-winged in all cases (Table 7).

From these data it is concluded that in *Calathus cinctus* wing dimorphism is inherited in a simple Mendelian fashion with brachyptery dominant to macroptery. Asymmetric wing development was not observed in this species, neither in the field nor in breeding experiments.

Under the assumptions of the Hardy-Weinberg Equilibrium (genetically static, randomly breeding populations, see GOODENOUGH 1978), it is possible to calculate the frequency of alleles and the frequency of genotypes for populations of *cinctus* (Table 4). The frequencies of the *b* allele of populations of Dwingeloo and Nuil are 0.862 and 0.940 respectively and the populations contain 1.9 and 0.4 % homozygous short-winged genotypes and

Table 8. F$_1$-beetles from single-pair crosses of *Calathus melanocephalus* with assumed genotypes (1979/1980, outside conditions/5°C. SD10). Symbols, see Table 5

Parents					Offspring				
Phenotype		Genotype			Phenotype				
		Assumed			Observed (males/females)				Expected
Male	Female	Male	Female	N	n	SW	LW	% LW	% LW
LW	LW	*bb*	*bb*	4	85	38/34	7/6	15.6/15.0	100
SW	LW	*Bb*	*bb*	4	135	67/58	4/6	5.6/ 9.4	50
SW	LW	*BB*	*bb*	4	139	66/73	–/–	–/–	0
LW	SW	*bb*	*Bb*	4	92	38/50	1/3	2.6/ 5.7	50
SW	SW	*Bb*	*Bb*	4	130	55/68	–/7	–/ 9.3	25
SW	SW	*BB*	*Bb*	4	136	75/61	–/–	–/–	0
LW	SW	*bb*	*BB*	4	96	47/49	–/–	–/–	0
SW	SW	*Bb*	*BB*	4	132	75/56	1/–	0.8/–	0
SW	SW	*BB*	*BB*	4	112	66/46	–/–	–/–	0

23.6 and 21.2 % heterozygous short-winged genotypes respectively. The (isolated) island population on the West Frisian island of Ameland, on the other hand, contained in 1979 only 13 % (29/223) long-winged beetles, i.e., a much lower frequency of the *b* allele (0.360), 40.9 % homozygous short-winged genotypes, and 46.1 % heterozygous short-winged beetles.

Calathus melanocephalus

Calathus melanocephalus, collected in Oost-Flevoland, did not show differences between the proportion of long-winged offspring reared from long- and short-winged females, respectively (Table 3; $\chi^2=0.06$, df=1, p>0.5). For both long- and short-winged females the proportion of long-winged offspring is higher in females, but this difference is only significant for long-winged females (long-winged females: $\chi^2=7.28$, df=1, p<0.01; short-winged females: $\chi^2=2.94$, df=1, 0.1>p>0.05). Six crosses between short-winged males and females, collected at the heath of Kraloo, as well as two crosses between such males and F$_1$-offspring of similar crosses carried out in 1977 by Th. S. van Dijk (Table 2) only produced short-winged offspring. Four crosses between long-winged males collected in Oost-Flevoland and (short-winged) offspring of short-winged males and females collected at Kraloo (Table 2), however, produced not only the expected short-winged offspring (110 beetles), but three out of the four crosses each produced a long-winged female as well.

These preliminary data strongly contrast with those of *cinctus* and suggest at least another type of wing-morph determination in *melanocephalus* than the simple genetic one found in *cinctus.*

Wing-morph frequencies among the F$_1$-generation of *melanocephalus* reared in 1979/1980 indeed deviated from the expectations of the single-locus model in that crosses which are expected to produce a certain proportion of long-winged offspring produced much lower ones (Table 8). Crosses which are expected to produce only short-winged offspring did so indeed, with only one exception: a long-winged male reared from one of the crosses between assumed heterozygous males and homozygous short-winged females (Table 8).

Additional crosses between F$_1$-individuals carried out at a constant temperature of 12°C under natural daylight in a temperature room in 1981/1982, on the other hand, resulted in rather high frequencies of long-winged offspring, which is difficult to explain (Table 9). Seemingly, all combinations involved are able to produce at least some long-winged offspring under certain conditions, even crosses between supposed short-winged homozygotes (three out of four of such crosses each produced one long-winged female!). The highest proportion of long-winged offspring, however, was produced by crosses between short-winged beetles resulting from crosses between long-winged parents (Table 9).

In all types of crosses females showed a higher frequency of long-winged individuals than males (Table 9).

Offspring of single pairs of long-winged *melanocephalus,* collected in Oost-Flevoland, and reared at three different constant temperatures as well as under outside conditions, showed clear temperature dependent wing-morph frequencies (Table 10) with the highest proportion of long-winged beetles at 12°C (56.2 %) and the lowest proportion at 8.5°C (13.3 %). Again, females were more frequently

Table 9. F$_2$-beetles from single-pair crosses of *Calathus melanocephalus* with assumed genotypes (1981/ 1982, 12°C, natural daylight). Symbols, see Table 5

Parents					Offspring				
Phenotype		Genotype			Phenotype				Expected
		Assumed			Observed (males/females)				
Male	Female	Male	Female	N	n	SW	LW	% LW	% LW
SW	SW	*bb*	*bb*	3	49	11/ 2	12/24	52.2/92.3	?
SW	SW	*Bb*	*bb*	1	4	2/ –	1/ 1	–/–	?
SW	SW	*Bb*	*Bb*	8	75	26/13	11/25	29.7/65.7	25
LW	SW	*bb*	*BB*	2	40	19/11	3/ 7	13.6/38.9	0
SW	SW	*BB*	*BB*	4	57	27/27	–/ 3	–/10.0	0

Table 10. F$_1$-beetles from single-pair crosses of long-winged *Calathus melanocephalus* from Oost-Flevoland reared at different temperatures (1981/1982, natural daylight). Symbols, see Table 5

| | | Offspring | | | |
| | | Observed phenotypes (males/females) | | | |
Temperature	N	n	SW	LW	% LW
8.5°C	9	128	54/57	4/13	6.9/18.6
12 °C	10	121	34/19	38/30	52.8/61.2
15.5°C	10	151	62/43	21/25	25.3/36.8
Outside	9	129	54/47	12/16	18.2/25.4

Table 11. F$_1$-beetles from single-pair crosses of short-winged *Calathus melanocephalus* from Ameland reared at different temperatures (1981/1982, natural daylight). N: number of crosses (between brackets: number of crosses with long-winged offspring). Symbols, see Table 5

| | | Offspring | | | |
| | | Observed phenotypes (males/females) | | | |
Temperature	N	n	SW	LW	% LW
8.5°C	10(2)	125	73/50	–/2	–/ 3.8
12 °C	9(2)	132	65/60	–/7	–/10.4
15.5°C	10(5)	111	55/47	2/7	3.5/12.9
Outside	10(5)	129	69/55	1/4	1.4/ 6.8

long-winged than males (Table 10), both for separate temperatures as well as for the combined set of temperatures, though not significantly so (χ^2=5.76, df=4, 0.1<p<0.5). Even single-pair crosses between short-winged *melanocephalus*, collected at the West Frisian Island of Ameland from an entirely short-winged population (all 421 specimens (212 males and 209 females) collected there in 1979, 1981 and 1984 were short-winged), gave similar results (Table 11).

In 1982/1983 a preliminary experiment to establish the effect of the amount of available food on the phenotypic expression of the assumed long-winged genotype was performed. Table 12 gives the phenotypes of the offspring of single pairs of long-winged *melanocephalus,* collected in Oost-Flevoland, and reared at constant temperatures of 8.5 and 15.5°C and natural daylight as well as under outside conditions. Since from these preliminary data it is clear that not only temperature but also food supply affects the expression of the assumed long-winged genotype, a larger experiment (more temperature conditions tested and more larvae reared) was carried out the next year. In that experi-

Table 12. F$_1$-phenotypes from single-pair crosses of long-winged *Calathus melanocephalus* from Oost-Flevoland reared under three different temperatures at two food-supply levels (1982/1983, natural daylight). NL: number of larvae used. Symbols, see Table 5

| | | | | Offspring | | | |
| | | | | Observed phenotypes (males/females) | | | |
Food supply	Temperature	N	NL	n	SW	LW	% LW
Low	8.5°C	7	35	24	11/13	–/–	–/–
	15.5°C	6	37	20	7/ 8	2/3	22.2/27.3
	Outside	4	30	23	8/12	1/2	11.1/14.3
High	8.5°C	4	15	14	6/ 5	–/3	–/37.5
	15.5°C	4	31	17	1/ 1	8/7	88.9/87.5
	Outside	4	43	37	15/17	–/3	–/15.0

Table 13. F$_2$-phenotypes of *Calathus melanocephalus* reared from the same parental long-winged single-pair crosses at different temperature conditions at two food-supply levels (1983/1984). NL: number of larvae used. Symbols, see Table 5

Food supply	Temperature	NL	Offspring Observed phenotypes (males/females)			
			n	SW	LW	% LW
Low	8.5°C	65	50	25/25	–/–	–/–
	12°C	64	37	20/17	–/–	–/–
	15.5°C	62	44	20/23	1/–*)	4.8/–
	19°C	65	36	27/ 9	–/–	–/–
	15.5/8.5°C	63	44	25/19	–/–	–/–
	Outside	58	48	20/28	–/–	–/–
High	8.5°C	66	64	29/31	1/ 3	3.3/ 8.8
	12°C	63	60	28/14	7/11	20.0/44.0
	15.5°C	58	54	10/ 8	17/19	63.0/70.4
	19°C	64	32	10/ 9	6/ 7	37.5/43.7
	15.5/8.5°C	61	58	16/21	5/16	23.8/43.2
	Outside	63	57	24/14	6/13	20.0/48.1

*) One fully developed wing on the right side only

ment possible maternal effects were excluded by using about equal numbers of larvae from the same eight single pairs in each group.

Again, the results of this experiment (Table 13) show a strong temperature-dependent expression of the long-winged genotype in the high food-supply group. The highest expression was found at a constant temperature of 15.5°C (66.7 %), lower proportions of long-winged offspring were found at 19 and 12°C (40.6 and 30.0 % respectively), whereas the lowest expression was found at 8.5°C. The results at the alternating temperature condition (36.2 % long winged) and under outside conditions closely resembles those at 12°C. Mortality in the high food-supply group was only significant at 19°C (Table 13). The difference in expression of the long-winged genotype between the high and the low food-supply group in this experiment turned out to be extremely large, since none of the 259 beetles reared with a low food supply was of the long-winged phenotype. Only a single male of the group reared at 15.5°C possessed a fully developed wing on the right side only. In general the mortality was substantially higher in the low food-supply groups than in the corresponding groups with a high food supply.

In this experiment, too, under all tested temperature conditions the frequencies of long-winged offspring were higher in females than in males. However, these differences were significant only at 12°C (χ^2=4.00, df=1, p<0.05) and under outside conditions (χ^2=5.08, df=1, p<0.05), whereas for the combination of all six temperature conditions

Table 14. Phenotypes of *Calathus melanocephalus* in pitfall-samples from the Ecological Nature Reserve, Oost-Flevoland. Symbols, see Table 5

Sampling period	Phenotypes (males/females)			
	n	SW	LW	% LW
19-8/29- 9-1975*)	968	195/446	75/252	27.8/36.1
28-6/21- 9-1976*)	857	188/361	83/225	30.6/38.4
28-9/25-10-1978	982	391/365	89/137	18.5/27.3
5-8/30-10-1981	428	156/105	81/ 86	34.2/45.0
18-5/28-10-1982	311	120/113	30/ 48	20.0/29.8
26-5/10-11-1983	58	18/ 21	7/ 12	28.0/36.4
21-6/29-11-1984	1005	332/409	86/178	20.6/30.3

*) Unpublished data of R. Hengeveld & J. Haeck, Institute for Ecological Research, Heteren.

the difference was insignificant (χ^2=12.55, df=6, 0.05<p<0.1).

Analysis of year-samples of *melanocephalus* collected in Oost-Flevoland (Table 14) showed that also in the field the proportion of long-winged beetles was higher in females than in males. The difference is significant for all years, with the exception of 1983 (the year with the lowest catch).

Asymmetric wing development in *melanocephalus* was established in a low frequency both in the field and in breeding experiments. For instance, among long-winged beetles reared in experiments at different temperatures and with different food supplies (Tables 10–13) for instance 1 of 130 males (0.7 %) and 11 of 191 females (5.8 %) showed asymmetric wing development.

From these data it is concluded that although in

Calathus melanocephalus wing dimorphism basically might be inherited according to a single-locus model too, at least the expression of the long-winged genotype is under environmental control in threshold response. During this study, however, also a small number of long-winged *melanocephalus* was reared from crosses which according to the above mentioned single-locus model should have produced short-winged offspring only (Tables 8–9, 11).

Discussion

HARRISON (1980) in his review of dispersal polymorphism in insects recognises two ways in which flight polymorphism might be controlled: by genes and/or by the environment. Concerning genetic determination Harrison states that "Only in the weevil *Sitonia hispidula* is there unambiguous evidence that winglength is determined by a single gene (or cluster of tightly linked genes) ... In other insect species, crossing experiments indicate that wing determination has a genetic compound but is not a simple Mendelian trait." In the first case he refers to the work of JACKSON (1928) and as instances of the latter type of inheritance he refers to studies on field crickets (Orthoptera) (HARRISON 1979; McFARLANE 1962), on Heteroptera (HONEK 1976), and on Homoptera (ROSE 1972). Harrison argues that "since it has been demonstrated that environmental factors directly influence wing and flight muscle development, much of the genetic data can be interpreted (or reinterpreted) in terms of individual variation in threshold response".

From a literature review ROFF (1986) concluded that the presence or absence of wings may be controlled by a single-locus, two-allele genetic system or by a polygenic system, and that *both* types of inheritance can be subsumed within a general threshold model. He suggests that suppression of wing development results when some hormone, perhaps juvenile hormone, exceeds a threshold value during a critical stage of development. In his view evolution towards wing dimorphism requires an increase in the rate of the wing-suppressing hormone and a change in the threshold level at which wing development is suppressed. Consequently, due to net gene-migration, selection in stable habitats will act against the long-winged morph, because beetles with a low production of wing-suppressing hormone and/or a low threshold level will tend to

leave the population. The kind of reasoning used by Roff is basically the same as DEN BOER et al. (1980) developed to construct a possible pathway for the evolution of the genetic dominance of brachyptery.

Returning to our species we found both types of inheritance: genetic determination according to a single-locus model in *Calathus cinctus* and a combination of both genetic determination and environmental control of the long-winged genotype in threshold response in *C. melanocephalus*.

The few deviating crossing results with assumed short-winged homozygotes, collected at the Heath of Kraloo or reared from short-winged parents collected there (Table 8–9), can be explained in terms of the 'Threshold theory'. In this stable habitat net gene-migration has led to both a low frequency of long-winged genotypes and a relatively high threshold for the wing-suppressing hormone of the remaining long-winged genotypes. Although a considerable part of the population might still consist of heterozygous short-winged beetles, the long-winged genotype will be expressed only incidentally in offspring of crosses with these beetles. For the isolated island population at Ameland, similar results (Table 11) can be explained in the same way.

These findings are in accordance with the other available data on wing-length determination in Carabidae and contrast with the polygenic control found in species of other taxonomic groups (especially Orthoptera, Heteroptera and Homoptera (see ROFF 1986, for a review)). In two other families of Coleoptera (Ptiliidae and Bruchidae) indications of polygenic control are found for respectively *Ptinella apterae* (Guérin–Meneville) and *Callosobrochus maculatus* (Fabricius) (TAYLOR 1981; UTIDA 1972), but in both cases no single-pair crosses were carried out. Different taxonomic groups apparently may exhibit different types of control of wing development (cf. ZERA et al. 1983; DESENDER 1989a; ZERA 1989).

Since also in carabids environmental factors may play an important role in wing-morph determination, the interpretation of data on wing-morph frequencies in natural populations (LINDROTH 1949; 1969) consequently should be done with care. PEARSON (1965), for instance, examined the distribution of wing-morph frequencies in *Bembidion grapei* Gyllenhal in relation to isotherms of maximum summer temperature. Note, that this is one of the most important species Lindroth used to illustrate his theory of postglacial recolonization of Fennoscandia (LINDROTH 1949; 1969; DARLINGTON 1971; THIELE 1977). Pearson showed that wing dimorph-

ism might be controlled by temperature, with the short-winged morph more cold-resistant than the long-winged one!

Observed differences in frequency of long-winged beetles between males and females (the latter more frequently long-winged) may result from differences in threshold or from differences in sensitivity between the two sexes. Although this difference in most cases was not significant in our breeding experiments, we believe it to exist because of the highly convincing field data (Table 13). Moreover, it must be realized that sample sizes required for detecting such a difference with 80 % certainty at the 5 % level of significance are much larger than those that could be realized in our breeding program (SOKAL and ROHLF 1969). For instance, in theory at least 504 individuals, instead of the 151 individuals actually reared, are needed to detect the difference between 25.3 and 36.8 % at 15.5°C (Table 10). Similar differences were observed by CARTER (1976) in *Agonum retractum* and BENGTSON and ERIKSTAD (1984) in *Amara quenseli* (Schönherr).

The adaptive significance of a higher frequency of long-winged beetles in females may only be understood if actual flight is preceded by insemination. while otherwise the chance of founding new populations will diminish due to the lower chance of a sufficient number of males arriving through the air at the right sites.

Concerning the resident population the relatively high amount of net migration of long-winged genes caused by the departure of females is at least partly balanced by the lesser amount in males.

Asymmetric wing development apparently is a rare phenomenon in carabids: from literature and from own observations DESENDER (1989b) lists only five species in which it has been found: *Agonum obscurum* (Herbst). *A. retractum, Bradycellus harpalinus* (Serville), *C. melanocephalus* and *Carabus clathratus* Linnaeus. If asymmetric wing development is linked to environmental control of the expression of long-winged genotypes as found in *melanocephalus,* this kind of wing-length determination consequently should be equally rare among carabids.

In general, dispersal activities (production of dispersal morphs included) are generally thought to be associated with adverse conditions, i.e., with detoriating environments (HARRISON 1980). In the case of wing-morph determination in *Calathus melanocephalus* the opposite was found, the dispersal morph being more frequently produced under relatively favourable conditions (i.e., high temperatures and

abundant food during larval development). Concerning carabids there is still very little and contradicting information on this point. NELEMANS (1987) found that flight muscle development in the autumn breeder *Nebria brevicollis* (Fabricius) depends on favourable environmental conditions (temperature and food supply) during the development of the larvae, whereas VAN SCHAIK ZILLESEN and BRUNSTING (1984) presented the opposite in the spring breeder *Pterostichus oblongopunctatus* (Fabricius).

Perhaps these differences might have to do with a more general difference in effect of environmental factors between quickly developing summer larvae (*P. oblongopunctatus*) and slowly developing and overwintering winter larvae (*C. melanocephalus* and *N. brevicollis*). In the first case a direct response to the quality of the environment could be more advantageous than in the second case, in which the higher unpredictability of environmental conditions during future adult life could favour a more opportunist 'strategy'. Furthermore, it should be realized that both the development of both wings and flight muscles will cost additional energy, which generally is not likely to be available under conditions in which food is scarce.

The differences in wing-morph determination between *C. cinctus* and *C. melanocephalus* result in different dispersal 'strategies'. In *cinctus* the dispersal potential is genetically fixed, which means that independent of environmental conditions the genetic potential of possible dispersers is always realized. In *melanocephalus,* however, the dispersal potential is under environmental control, allowing a more dynamic production of possible dispersers depending on environmental quality. Under relatively favourable conditions during larval development (such as a high amount of available food and/ or relatively high temperatures) a high proportion of the potentially long-winged genotypes will actually develop long wings, whereas in the opposite situation only a few beetles will do so.

Actual flight in both species, however, furthermore depends on the development of functional flight muscles and on appropriate weather conditions in the short period that functional flight muscles are present. In accordance with the oogenesis-flight syndrome (JOHNSON 1969) both species are only able to fly during a short period just before the start of reproduction. Moreover, during this period flight only occurs under special weather conditions: a minimum temperature of about 18°C, no rain and preferably no or little wind (VAN HUIZEN 1979). Details on wingmuscle development and ac-

tual flight of *cinctus* and *melanocephalus* will be treated elsewhere.

Under comparable stable conditions entirely genetic determination (referred to as the 'fixed system') will lead to a more rapid decrease of dispersal potential than a combination of genetic determination and environmental control (the 'dynamic system'), since in the first case relatively more of this potential will be lost by flying activities. Thus wing dimorphism will be maintained better with the 'dynamic system', but, on the other hand, the chance of establishing new populations on short terms will be greater with the 'fixed system'. Therefore, the 'fixed system' can be considered an opportunistic short-term 'between sites strategy', and the 'dynamic system' a flexible, more assuring long-term 'within-sites strategy'.

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