Oecologia (Berlin) (1983) 60:340–347

Oecologia

The influence of environmental factors on wing polymorphism in females of *Leptopterna dolobrata* (Heteroptera, Miridae)

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Summary. The females of *Leptopterna dolobrata* (Heteroptera, Miridae) occur either as flightless brachypters or as macropterous individuals, whereas all the males are long-winged and capable of flight. The expression of this alary dimorphism is influenced by both genetic and environmental factors. Population density and temperature conditions prevailing during larval development both affect the formation of macropterous females. The larval instars L_4 and/or L_5 are particularly sensitive to these environmental stimuli and are thus decisive for the determination of wing-morphs.

Experimentally crowded larvae developed a greater proportion of macropterous females than individuals reared at lower densities, and lower temperatures seem to counteract the stimulating effect of crowding. Larvae from different local populations varied in the proportion of macropters which developed, which could be ascribed to differences in the genetic constitution, although the genetic basis of wing-morph determination in *L. dolobrata* is not yet understood.

There is strong evidence that in crowded populations a high percentage of the emerging macropterous females will emigrate and perform dispersal flights to new habitats. The sexual maturation of macropterous females is retarded compared with the brachypterous morph, and the dispersal flights are likely to occur during the pre-reproductive period.

The underlying physiological mechanism of wing-morph determination and the adaptive significance of its environmental control are discussed on the basis of information available from other polymorphic species.

1 Introduction

Leptopterna dolobrata is strictly univoltine over the entire range of its holarctic distribution, hibernating in the egg stage which lasts about 10 months in the field (Braune 1971). This protracted embryonic period is caused by an obligatory diapause (Braune 1980), and serves to synchronize the seasonal appearance of the larvae and adults with that of their food resources (mainly the ears of several grass species).

L. dolobrata belongs to the Miridae, the biggest Heteropteran family, consisting of about 300 species in the German area. From the data presented by Wagner (1952), at least 48 species of this family show an alary polymorphism which is manifested either in both sexes or in the females only. *L. dolobrata* belongs to the latter category. Whereas all the males are long-winged and capable of flight, the females are polymorphic, occurring either as flightless brachypters or as macropterous individuals. The brachypterous females appear to be the common form in the majority of natural populations studied so far in the northern part of Germany.

As pointed out by Honek (1976a) in a literature review on wing polymorphism in insects, the manifestation of wing-form is considered generally to be governed by both intrinsic and extrinsic factors, i.e. the expression of the genetic background may be more or less controlled by environmental influences.

The aim of this work was to study the influence of environmental factors on wing-form determination in females of *L. dolobrata* and to elucidate the adaptive significance of the underlying mechanisms.

2 Material and methods

This paper is mainly based on laboratory studies carried out from the end of May to July in 1979 and 1982. The experimental material originated from the field and comprised first instar larvae of *L. dolobrata* which were collected from local populations in the vicinity of Kiel (Schleswig-Holstein). All the larvae for each set of trials derived from the same habitat. They were reared at different larval densities in standard size containers (30 cm × 22 cm × 35 cm), the walls and top of which were fitted with nylon gauze.

Fresh top-cuttings of the grass species *Dactylis glomerata* and *Alopecurus pratensis* served as food, the cut ends being inserted in a moist block of spongelike material at the bottom of the cage. The food was provided in equal quantities and was changed every second day. The animals were reared under a constant photoperiod of 12 h photophase/12 h scotophase at room temperature (varying between 17° and 25° C), at a constant temperature of 16° C, or under an alternating temperature regime of 22°/16° C (12 h/12 h). The individuals in each container were checked daily, and the number of larvae, males, and brachypterous and macropterous females determined. Dead animals were removed, only the adults being preserved in 70% alcohol for later measurements of their wings. Additionally, the incidence of copulations and the wing form of the mating females were registered during the regular checks.

As the wing form in *L. dolobrata* is always expressed symmetrically, the morphometric analysis could be restricted to the wings of one side. The fore- and hindwing of the right-hand side of each individual were dissected from the thorax and embedded on a microscope slide. The lengths of both wings, the areas of the corium and the membraneous part of the forewing, and the area of the hindwing were determined with a MOP-system Digiplan (Kontron, Munich) for manual-optical picture analysis. In order to increase the accuracy of the measurements, the micro-slides were placed in a commercial photographic enlarger and projected on the planimeter-plate at a final magnification of 10 times the natural size.

The percentage of macropterous females in natural populations was determined by analysis of the wing-forms of insects caught with a sweep-net.

3 Results

3.1 Wing morphology and its variability in field-collected adults

The term polymorphism is rather ambiguous (see discussions in Kennedy 1961; Honek 1976a; Vepsäläinen 1978). In this paper it is used in the sense of Vepsäläinen (1978) who defines polymorphism as "the occurrence together in the same population of two (dimorphism) or more discontinuous phenotypes (called morphs) belonging to the same stage in the life cycle of a species, in such proportions that the frequency of the rarest of them cannot be maintained merely by recurrent mutation". With regard to the variation of wing form the term sould be reserved for cases where the frequency distribution of forms is at least bimodal and transitional forms are either missing or scarce.

The application of this criterion is difficult in species where the variations of fore- and hindwings are not strictly correlated, as in *Pyrrhocoris apterus* (Seidenstuecker 1953). Honek (1976a) neglected the size of the hindwings and classified the imagines of *P. apterus* as macropters if their forewings exceeded the 7th tergite in females or reached to the middle of the 7th tergite in males. If the forewings reached only the anterior part of the 6th tergite, the individuals were assumed to be brachypterous. All intermediate instances were classified as semimacropters.

The use of such a relative measure seems unsuitable in *L. dolobrata* because the abdomen of the females becomes immensely swollen towards oviposition, thus changing the relative wing-size in proportion to the length of the abdomen with the progress of adult development. Therefore, it was tested whether it was possible to classify wing-morphs in *L. dolobrata* using a single absolute measure irrespective of the body length of the individuals.

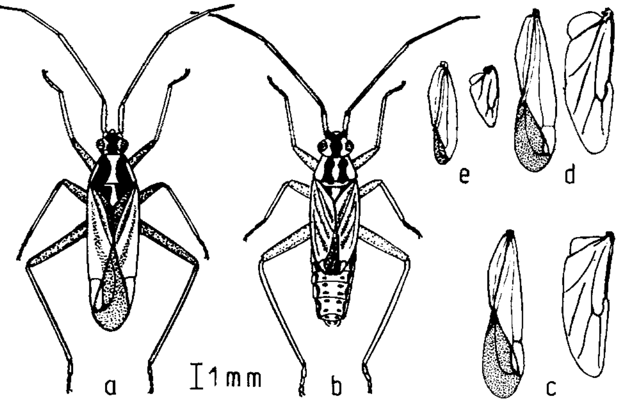

Fig. 1a–e. *Leptopterna dolobrata.* **a**: male; **b**: brachypterous female; **c–e**: fore- and hindwings of male (**c**), macropterous female (**d**) and brachypterous female (**e**)

The wing form of males and females is shown in Fig. 1, and its variability in 176 field-collected adults expressed as correlations between different morphometric parameters is presented in Fig. 2. In the following considerations, the values obtained for the obligatory macropterous males are always taken as a standard for comparison.

It is evident from Fig. 2a that in both sexes a strict correlation exists between the length of the forewing and that of the hindwing. In males the forewing length varies between 6.3 and 7.3 mm, whereas the variability in females is much higher and discontinuous, with a distinct group of individuals having wing-lengths similar to the males. The correlations between wing-length and wing-area are shown in Fig. 2b for both the fore- and the hindwings. If for each individual the area of the forewing is divided by that of the hindwing, the calculated quotients are relatively constant and independent of the absolute wing-lengths in males (Fig. 2c). They range from 0.78 to 0.95, which means that in males the hindwings are always larger than the forewings. Quotients of less than 1 are found in females only if the length of their forewings reaches or exceeds 6 mm. For the rest of the females the quotients increase with decreasing length of the forewing indicating that in these short-winged individuals the area of the hindwings is always smaller than that of the forewings.

Figure 2d refers to the forewings and shows the quotients between the areas of the corium and the membraneous part in relation to wing-length. This proportion is relatively constant and independent of the wing-length in males. Corresponding values are found in females only if their forewings exceed a length of 6 mm. In the short-winged individuals the quotients increase with decreasing wing-length indicating that a reduction of the forewing mainly affects the membraneous part.

To summarize, this analysis shows that wing form in females of *L. dolobrata* varies discontinuously, thus fulfilling an essential criterion in Vepsäläinen's definition of polymorphism. Since the changes of morphometric parameters in both the fore- and the hindwings are strictly correlated, the classification of wing-morphs can be based on a single measure which – for practical reasons – should be the length of the forewings. The choice of this measure seems justified because the frequency distribution of wing-lengths reveals a strict bimodal pattern (Fig. 3), indicating that females of *L. dolobrata* occur in two distinct morphs only, and thus exhibit an "all or none" alary dimorphism (Southwood 1961).

Females with forewings of at least 6 mm in length have almost the same wing-proportions as males and are therefore classified as macropters. Those with forewings shorter than 6 mm have wing proportions deviating drastically from those of the males and represent the brachypterous morph.

3.2 The effect of larval density on the occurrence of macropterous females

Four environmental factors (photoperiod, temperature, population density, and food) have been widely demon-

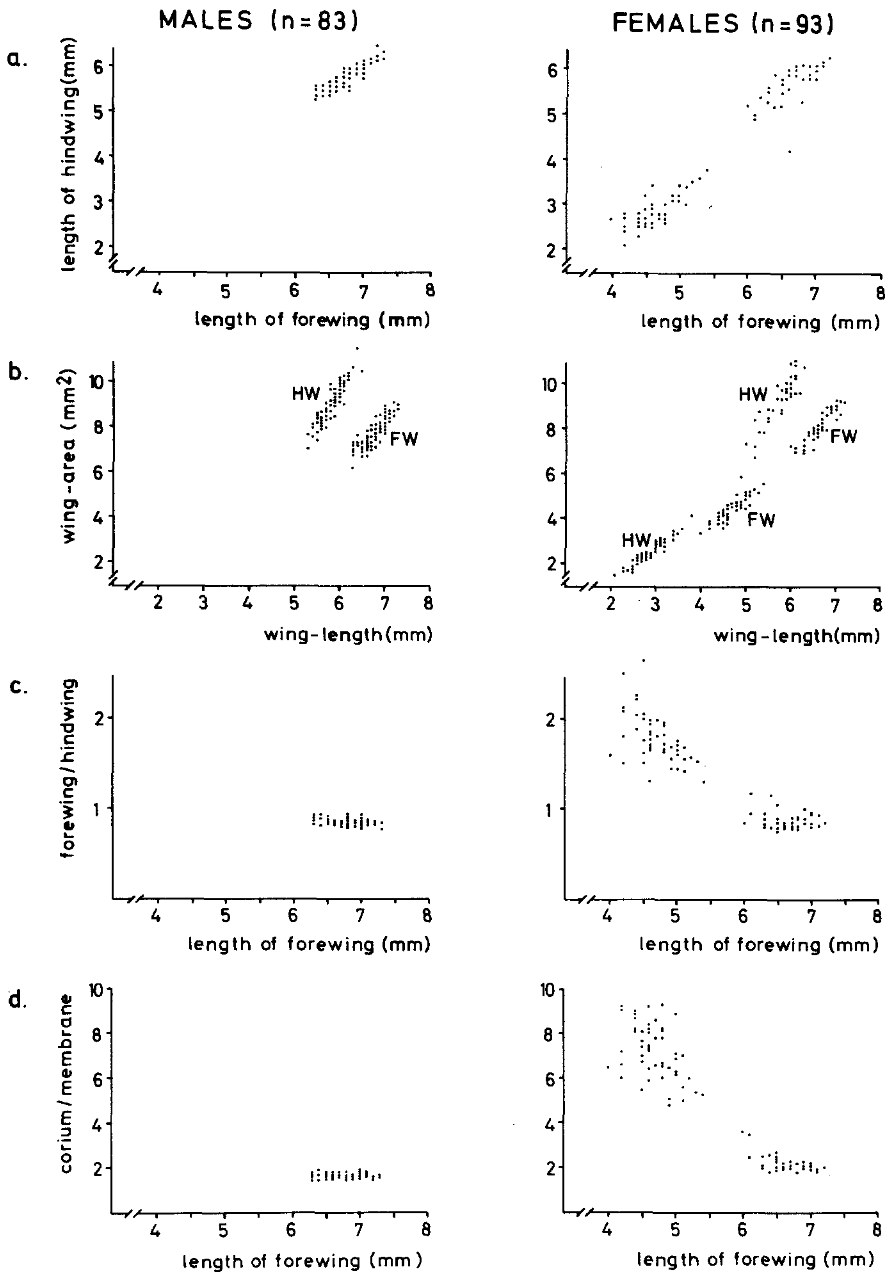

Fig. 2a–d. Correlations between various parameters of the fore- and hindwings in field-collected males and females of *L. dolobrata*. For further explanation see text

strated to affect the determination of wing-morphs in insects (see review by Honek, 1976a). Of these, population density seems to be especially important in *L. dolobrata*, because in our field surveys the highest percentages of macropterous females have always been found in habitats where *L. dolobrata* occurred at relatively high densities.

In order to test this, a total number of 1,500 first instar larvae (collected close to the southern bay of Kiel Canal on 29 May 1979) were transferred to the laboratory and reared at room temperature (17°–25° C) and a constant photoperiod (light/dark; 12 h/12 h). The larvae were kept in standard-size containers at densities of 25, 50, 100, 200, and 400 individuals per cage until the adults emerged. The set-up and the results of this experiment are shown in Table 1.

Rearing the larvae at densities of up to 100 individuals per cage resulted in a low incidence of macropterous fe-

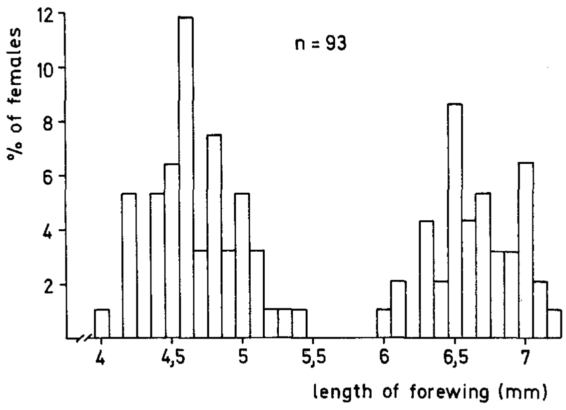

Fig. 3. Frequency distirbution of wing-lengths in field-collected females of *L. dolobrata*

Table 1. The effect of larval density on the occurrence of macropterous females

Number of larvae per cage	Number of cages	Initial number of larvae	Number of adults emerged: ♂	brachypterous ♀	macropterous ♀	Larval mortality (%)	Macropterous ♀ (%)
25	10	250	116	87	7	16.0	7.4
50	5	250	115	98	4	13.2	3.9
100	2	200	87	60	3	25.0	4.8
200	2	400	170	85	32	28.3	27.4
400	1	400	216	52	41	22.8	44.1

males. Less than 10% of the females belonged to the macropterous morph. An increase of larval density to 200 and 400 individuals/cage drastically raised the percentage of macropters to 27.4% and 44.1% respectively. Thus, a high density during the larval period seems to favour the production of the macropterous morph.

It cannot be entirely excluded, however, that a concomitant effect of food availability is involved, which is difficult to separate from the pure effect of crowding. A comparison of larval mortality occurring during development at different densities (see Table 1) shows that larval mortality was lowest (16% and 13.2%) at densities of 25 and 50 individuals per cage and increased to values of 22.8%–28.3% at higher densities. Since there are no marked differences in the percentages of larval mortality between the experiments with 100, 200, or 400 individuals/cage, food availability can be excluded as a limiting factor. Furthermore, there is no correlation between larval mortality and the occurrence of macropters as shown by a comparison of the values obtained for the experiments with 100 and 400 larvae per cage. This finding corroborates the view that the increased production of macropterous females in this experiment is substantially due to the effect of crowding rather than to dietetic influences.

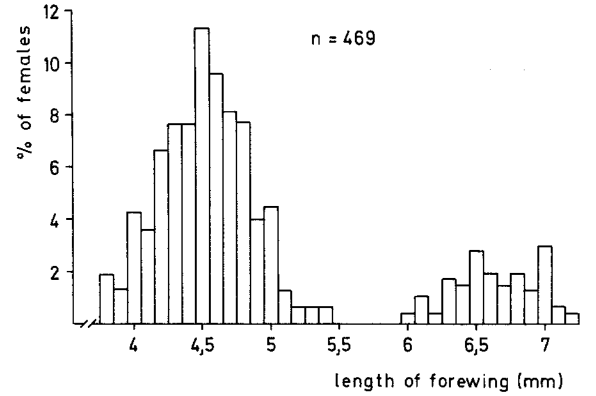

Fig. 4. Frequency distribution of wing-lengths in laboratory-reared females of *L. dolobrata*

Additionally, the lengths of the forewings of all the females ($n = 469$) that developed in this laboratory experiment were measured. A comparison of the resulting frequency distribution (Fig. 4) with that of field-collected females (Fig. 3) shows similar strict bimodal patterns in both groups and thus confirms that females of *L. dolobrata* occur in two distinct wing-morphs only, with transitional forms either absent or extremely scarce.

3.3 *The period sensitive to crowding and the effect of temperature on wing-morph determination*

Since the period when the wing-morph is determined is relatively short in many species (Honek 1976a), we investigated whether any portion of larval life in *L. dolobrata* was particularly sensitive to environmental stimuli and thus decisive for the induction of macropterous development. Both the

Table 2. The influence of population density and temperature during different phases of larval development on the formation of macropterous females

trial	larval development L_1	L_2	L_3	L_4	L_5	number of replications	total number of larvae	number of adults emerged: ♂	brachypt.♀	macropt.♀	macropt. ♀ %
1	☐	☐	☐	☐	☐	8	400	171	112	44	28.2
2	▥	▥	▥	▥	▥	2	400	154	61	93	60.4
3	■	■	■	■	■	2	400	174	92	59	39.1
4	☐	☐	☐	▥	▥	3	600	248	99	113	53.3
5	▥	▥	▥	☐	☐	3	600	256	129	81	38.6
6	■	■	■	▥	▥	2	400	169	68	75	52.4
7	▥	▥	▥	■	■	2	400	157	91	69	43.1

☐ 50 larvae/cage at 22°/16°C (12 hrs./12 hrs.)
▥ 200 larvae/cage at 22°/16°C (12 hrs./12 hrs.)
■ 200 larvae/cage at 16°C

effects of larval density and temperature were studied at different periods of larval development (for descriptions and drawings of the 5 larval instars see Braune 1971). For this experiment we used 3,200 first instar larvae collected from a local population south of Kiel Canal on 25 May 1982. The set-up of the different trials and the results are shown in Table 2.

If larvae were reared continuously at a density of 50 individuals per cage at an alternating temperature of 22°/16° C (12 h/12 h), 28.2% of the emerging females were macropterous (Trial 1). This percentage of macropters is much higher than that obtained at the same density in the 1979 trial (for explanation see 3.4.). By rearing the larvae at the same alternating temperature but at a density of 200 individuals/cage (Trial 2) the percentage of macropterous females was drastically raised to a value more than twice as high as in Trial 1.

If larval development took place at the same density (200 larvae/cage) but at the lower constant temperature of 16° C (Trial 3), the percentage of macropters decreased to 39.1%. Since this value is still higher than that of Trial 1 but much lower than that of Trial 2, it may be concluded that the lower temperature during larval development partially counteracted the effect of crowding.

Trials 4 and 5 were both carried out at an alternating temperature of 22°/16° C (12 h/12 h). The 600 larvae of Trial 4 were reared in 12 cages at equal densities (50 larvae/cage) during the first three larval instars. Subsequently they were confined in 3 cages of 200 individuals each until the adults emerged. In Trial 5 the treatments were set in the reverse sequence (3 cages of 200 individuals → 12 cages of 50 individuals). If the percentages of macropterous females obtained in Trial 4 (53.3%) and Trial 5 (38.6%) are compared with those of Trial 1 (28.2%) and Trial 2 (60.4%), the values reveal the following order: Trial 1 < Trial 5 < Trial 4 < Trial 2.

An increase of larval density from 50 to 200 individuals per cage for a limited period of time, either during the initial phase (Trial 5) or during the later part of larval life (Trial 4), raised the percentage of macropterous females above the value of Trial 1. Since the percentage of macropters in Trial 4 is much higher than in Trial 5, it may be concluded that the instars L_4 and/or L_5 are particularly sensitive to crowding and thus decisive for the determination of macropterous development.

In both Trials 6 and 7 the larvae were reared at equal densities, but the temperature conditions were changed during the course of development (Trial 6: 16° C → 22°/16° C; Trial 7: 22°/16° C → 16° C). The percentages of macropterous females obtained in Trials 6 and 7 and those of Trials 2 and 3 reveal the following order: Trial 3 < Trial 7 < Trial 6 < Trial 2. Obviously, an influence of temperature is present throughout larval development such that higher temperatures favour the induction of macropterous development. However, this effect is less pronounced during the initial phase of larval life.

Summarizing the results, it becomes evident that both the temperature conditions and the population density during larval development affect the determination of wing-morph in *L. dolobrata*. The stages of larval life particularly sensitive to these environmental factors are L_4 and/or L_5. Consequently, the environmental conditions prevailing during late larval development are especially important for the determination of wing-morphs. The stimulating effect of high population densities on the induction of macropterous development is partially counteracted by lower temperatures.

3.4 Evidence for the involvement of hereditary factors in the determination of wing-morphs

According to Vepsäläinen (1978), the mechanisms of wing-morph determination in insects include both environmental and genetic switches with a single gene (or supergene) operating. In those few cases where the genetics of wing-length determination have been studied, the allele for short wings has been shown to dominate over that for long wings. Heterozygous or dominant homozygous individuals are predetermined to differentiate short wings (genetically short-winged), whereas recessive homozygous individuals are genetically long-winged. The realization of the wing-morph, however, can be modified by environmental factors during larval development in a way that genetically long-winged individuals may develop short wings. The susceptibility of the genotypes to environmental factors may vary between populations of the same species. Consequently, the frequency of the genotypes within a population and the environmental conditions prevailing during the sensitive period of larval development both affect the proportion of long- and short-winged individuals.

There is some evidence for the existence of a similar twofold mechanism in females of *L. dolobrata*, as indicated by the deviating percentages of macropterous females obtained by rearing larvae at identical densities in the trials of 1979 and 1982 (Tables 1 and 2). The experimental material of both years originated from the same local population, but the percentages of macropters were much higher in 1982. Unfortunately, this result is not conclusive because the temperature conditions were not identical in both trials so that the deviating percentages of macropters could partially be ascribed to the effect of temperature.

This was excluded in an additional experiment. On 2 June 1982, groups of first instar larvae were collected from three local populations in the vicinity of Kiel and reared in identical conditions (200 larvae/cage at an alternating temperature of 22°/16° C; 12 h/12 h). The percentages of macropterous females obtained were highly variable and amounted to 10%, 39.1%, and 60.4%, respectively. This result might be explained by different frequency distributions of genotypes in these three populations. However, selection and crossbreeding experiments seem to be the only way to elucidate the genetics of wing-morph determination in *L. dolobrata*. Such a project will be greatly impeded by the obligatory long-term diapause during the egg stage of this species.

3.5 The "oogenesis-flight syndrome" and the occurrence of flight in macropterous females

In species showing alary polymorphism it is generally taken for granted that the macropterous forms are the means of dispersal and the colonization of new habitats. However, the wing form is merely one outward and visible sign of a functioning flight apparatus which requires a concomitant set of features including the development of wings and wing muscles as well as biochemical processes associated with their functioning. During ontogenesis the gonads and the flight apparatus develop differentially, and the development

Table 3. Changes in the proportions of macropterous and brachypterous females and the occurrence of mating in a high-density population of *L. dolobrata*

Date	Number of adults caught	Number of males	Number of females		Macropterous ♀ (%)	Number of copulations observed with:	
			brachypterous	macropterous		brachypterous ♀	macropterous ♀
14/6/82	217	106	50	61	54.9	–	–
18/6/82	200	112	60	28	31.8	13	–
21/6/82	435	194	160	81	33.6	29	–
25/6/82	200	100	74	26	26.0	19	–
29/6/82	208	110	86	12	12.2	3	–
7/7/82	257	100	151	6	3.8	–	2

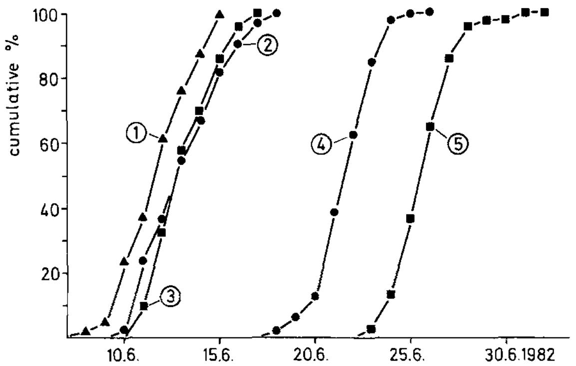

Fig. 5. Time course of adult emergence and the occurrence of mating in *L. dolobrata* reared at an alternating temperature of 22°/16° C (12 h/12 h) from the first larval instar. The data are presented in form of cumulative curves. *Curve 1*: males (total number: 829≙100%); *curve 2* brachypterous females (*n*: 401≙100%); *curve 3* macropterous females (*n*: 331≙100%); *curve 4* mating brachypterous females (number of copulations observed: 69≙100%); *curve 5* mating macropterous females (copulations observed: 52≙100%)

of either system can be influenced by environmental factors. As has been repeatedly shown in migrating species, the adult life of the females is characterized by an "oogenesis-flight syndrome" (Johnson 1969) such that the development of the flight apparatus retards the maturation of the ovaries and dispersal flights occur prior to the onset of reproduction.

In attempting to analyse the situation in *L. dolobrata*, it seemed necessary first to prove that the macropterous females are really capable of flight. Long-winged females were flight-tested in the field by placing them on a fingertip and raising them in the air. In these tests ($n = 57$), most of the individuals took off actively and commenced sustained flights over distances of up to 30 m, which clearly shows that they are capable of flight.

If the macropterous females mediate dispersal to new habitats, the optimum time for migratory flights would be the pre-reproductive period, for mechanical reasons related to wing-loading. Males and macropterous females of *L. dolobrata* have been shown to possess almost identical wing lengths and proportions (Fig. 2). Since the body weight of young sexually immature females (12.75 ± 1.37 mg; $n = 14$) does not differ drastically from that of males (11.76 ± 0.44 mg; $n = 17$) both groups of individuals presumably have similar degrees of wing-loading. However, the body weight of females increases enormously with the progress of ovarian development and reaches 26.93 ± 3.71 mg ($n = 22$) at the time of oviposition. This increase in weight results in a higher degree of wing-loading which consequently increases the power requirements for flight. Based on this criterion the occurrence of dispersal flights during the pre-reproductive phase of adult life seems to be of advantage.

Although dispersal flights of macropterous females have never been directly observed during our field surveys, there is some indirect evidence for their occurrence. This is deduced from changes in the proportion of macropterous and brachypterous females in a high-density population of *L. dolobrata* monitored in a small and isolated habitat north of Kiel Canal from 14 June to 7 July 1982 (see Table 3).

At each of the field-surveys the percentages of wing-morphs were determined from sweep-net catches always covering the entire area of approximately 25 m × 115 m. Whenever mating pairs were caught, the wing-morph of the female was recorded. On 14 June, more than half the females were macropters. In the later surveys the percentages of macropterous females were much lower decreasing to 3.8% on 7 July. Based on this result it seems likely that a considerable portion of the macropterous females emigrated from the crowded habitat. If dispersal flights had really taken place, they would have occurred during the pre-reproductive stage, as indicated by the absence of macropterous females in the mating couples which were caught from 18 June to 29 June.

Another possible explanation would be that the brachypterous females had a prolonged larval development in comparison to the macropterous morph. If on 14 June all the macropterous individuals but only some of the brachypters had reached the adult stage, the decreasing percentages of macropterous females obtained in the subsequent surveys could be due to the later occurrence of the brachypterous morph and the earlier death of the macropters. However, this possibility is excluded by the results of the laboratory experiments which clearly show that both morphs occur simultaneously. Figure 5 presents the data on the occurrence of males, macropterous and brachypterous females as well as the incidence of mating summarized from Trials 1, 2, 4 and 5 in 1982 (Table 2).

It is evident from these laboratory rearings that the males of *L. dolobrata* emerged before the females and there was no difference between the occurrence of brachypterous and macropterous females. Mating, however, occurred much earlier in the brachypterous females than in the macropterous morphs. This result corresponds well with the data obtained in the field (Table 3) corroborating the view that the sexual maturation of macropterous females is retarded in the sense of the "oogenesis-flight syndrome". It may be concluded that pre-reproductive dispersal flights of macropterous females do occur at least in crowded populations.

4 Discussion

To summarize, alary polymorphism in *Leptopterna dolobrata* is restricted to the females. Whereas all the males are long-winged and capable of flight, the females are dimorphic, occurring either as flightless brachypters or as macropterous individuals. As shown by analysis of wing-forms in both field-collected and laboratory-reared adults, the females occur in two distinct morphs only, and thus exhibit an "all or none" wing dimorphism (Southwood 1961). Females with forewings of at least 6 mm in length have almost the same lengths and proportions of the fore- and hindwings as the males. They are classified as macropters and have been shown to be capable of flight. In females with forewings shorter than 6 mm the wing-proportions differ drastically from those of the males. The reduction of their wings mainly affects the area of the hindwings and the membraneous part of the forewing. These individuals represent the brachypterous morph.

The phenotypic manifestation of wing form is considered generally to be governed by both intrinsic (genetic) and extrinsic factors such that the expression of the hereditary potentiality of each individual is more or less under environmental control (Honek 1976a). Many environmental factors such as photoperiod, temperature, population density, and diet have been demonstrated to affect the determination of wing-morphs. However, in a given species, one factor is usually the most important, while the others can only modify its action.

Photoperiod and temperature have been shown to be the key factors in bivoltine species in which drastic changes in the frequency of the wing-morphs are related to the season (Vepsäläinen 1978). A major role of photoperiod seems unlikely in *L. dolobrata* because of its strictly univoltine life cycle. The changes of daylength experienced during larval development (May–July) are only moderate.

In this species, population density during larval development is of utmost importance for the manifestation of the wing-morphs. Crowding is also the main factor responsible for the production of alatae in aphids (Lees 1967) and for the development of macropters in leaf hoppers (Kisimoto 1956). Experimentally crowded larvae of *L. dolobrata* produced a greater proportion of macropterous females than individuals reared at lower densities. However, the responses to experimental crowding varied drastically between groups of individuals collected from different local populations in the same year. This variation in the tendency to produce macropters could be ascribed to differences in the genetic constitution between the different populations (Honek 1976b), although the genetic basis of wing-morph determination in *L. dolobrata* is not yet understood.

As in many other species, the period sensitive to environmental stimuli is relatively short in *L. dolobrata.* The larval instars L_4 and/or L_5 are particularly sensitive to crowding, and thus the population density prevailing during late larval development is decisive for the manifestation of the wing-morphs. The stimulating effect of crowding on the formation of macropterous females is modified by the temperature conditions during larval development. Rearing crowded larvae at an alternating temperature regime of 22°/16° h (12 h/12 h) resulted in a higher percentage of macropterous females than in the corresponding experiment at the constant lower temperature of 16° C. If the influence of crowding is attributed to mutual tactile stimulation, the counteracting effect of lower temperatures could be ascribed to a lessened motility which would reduce the frequency of physical contacts.

As far as the physiological mechanism is concerned, it seems likely that the way in which crowding affects wing-formation has a humoral basis. The tactile stimuli are perceived by the nervous system and integrated by the brain. Neurosecretory cells and/or other hormone-producing glands could be activated according to the degree of stimulation. The resulting titre(s) of hormone(s) could influence the differentiation of the wings within the limits set by the genetic potentiality of the individual.

Southwood (1961) reviewed alary polymorphism in the Heteroptera, considering the brachypterous morphs either as adults with juvenile characters caused by an excess effect of juvenile hormone (JH), or as larval forms with adult characters caused by a lessening effect of JH. Experimental evidence for the influence of JH on wing differentiation has been gained in several species of aphids which are sensitive to crowding (von Dehn 1963; White 1968, 1971). In *Megoura viciae*, external application of JH to nymphs of presumptive macropters caused the individuals to develop apterous characters and only small wings, which suggests that alatae are produced when the corpus allatum is inactive. A similar effect was observed in *Aphis fabae*, when first instars were treated with farnesol (a JH analogue). In *Brevicoryne brassicae* the corpora allata are smaller in developing alatae than in apterae. According to Amiressami (1973), in parthenogenetic forms of *Pemphigus bursarius* a greater number of neurosecretory cells is present in winged than in wingless forms, whereas the corpora allata are relatively small in both forms. By contrast, the wingless sexuales had many neurosecretory cells and large corpora allata at the same time. Although the evidence is still fragmentary, it may be concluded that environmental stimuli such as crowding affect the neuro-endocrine system in such a way that their influence on the differentiation of wing-morphs is mediated by hormones.

As pointed out by Honek (1976b), it seems necessary from an ecological point of view to evaluate whether the varying proportions of wing-morphs found in natural populations are consistent with the experimental results obtained under laboratory conditions. According to preliminary field-surveys the brachypterous morph of *L. dolobrata* is the common form (more than 90% of the females) in the majority of local populations studied in the vicinity of Kiel. In these habitats the larvae obviously do not experience conditions favourable for maximum production of macropters implying that a considerable portion of potential macropters is not phenotypically manifested. An exceptionally high percentage of macropters (ca. 55% of the females) was found in a small and isolated habitat, however, where *L. dolobrata* developed in highly crowded conditions, which have been experimentally shown to favour the production of macropters.

According to the onset of mating both in the field and in the laboratory cultures, the sexual maturation of the macropterous females is retarded compared with that of the brachypterous morph. There is strong evidence that a high percentage of the macropterous females will emigrate from a crowded habitat and perform dispersal flights. These flights are likely to occur during the pre-reproductive period which is the optimum time for mechanical reasons related to wing-loading. The relation between retarded sexual maturation and the occurrence of pre-reproductive flights in macropterous females of *L. dolobrata* is interpreted in the sense of the "oogenesis-flight syndrome" (Johnson 1969) which is characteristic of many migrating species.

As far as the adaptive significance of an environmental control of wing-morph determination is concerned, a density-dependent mechanism such as that demonstrated in *L. dolobrata* will lessen the risk of overcrowding a habitat. The two morphs may be considered to fulfil different functions (Vepsäläinen 1978). Due to its greater local reproductive efficiency the brachypterous female will operate the optimum "within-site strategy" by exploiting the food resources of stable but isolated habitats. The macropterous morph increases the possibility of colonization of new sites and operates the "between-sites strategy". The plasticity of wing-morph determination to environmental conditions is understood as an adaptation which enables the polymorphic species to keep pace with changing environments but to exploit the resources of a given habitat as long as the conditions are favourable.

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Received April 20, 1983