

ALARY POLYMORPHISM AND LIFE HISTORY OF A  
COLONIZING GROUND BEETLE,  
*BEMBIDION LAMPROS* HERBST  
(COLEOPTERA: CARABIDAE)

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ABSTRACT

Newfoundland populations of *Bembidion lampros* Herbst (Carabidae), a recently introduced Palaearctic species, contain three wing phenotypes: two short-winged (brachypterous) and one long-winged (macropterous). Breeding studies showed that macropterous parents gave rise to macropterous progeny, brachypterous parents to brachypterous progeny, and mixed parents to mixed progeny. The results suggest that at least three alleles or two genes are involved in controlling wing length and there was no clear evidence of any of the wing length factors being dominant. No flight muscles were present in brachypterous individuals and only 5.9% of macropters possessed flight muscles. It was not determined whether flight muscle development was under ontogenetic or genetic control, but as there was no evidence of flight muscle autolysis, genetic control is likely. There was no difference in the number of mature eggs carried by macropterous and brachypterous females. The distribution of the wing phenotypes on the Avalon Peninsula showed a higher frequency of macropters in populations towards the northern and western limits of the range and a higher frequency of brachypters in populations towards the southern limits. However, the geographical pattern of wing morph frequency did not conform to the centrifugal pattern expected if the macropters were the principal dispersal agents in expanding the species range.

*B. lampros* is univoltine in Newfoundland. Overwintering adults are sexually immature. In 1981, the first females with mature eggs were found on April 27. By June 2, all field collected females had laid eggs. The first teneral specimen was collected June 9 and by July 29 the entire population was composed of current year adults.

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Wing dimorphism (the occurrence of both individuals with fully developed wings (macropters, M) and with wings reduced and non-functional (brachypters, B) occurs in a wide variety of insect species. Such dimorphism may be sexual, environmentally induced or under genetic control (Harrison 1980). In ground beetles, non-sexual wing dimorphism is common and where investigated has been found to be under genetic control with the factor determining the brachypterous condition dominant over the macropterous factor (Lindroth 1946; 1963a). Wing dimorphism in a population presumably results in individuals of two differing dispersal abilities. The macropters should be capable of dispersing farther and faster than the brachypters (den Boer 1970) and thus be the principal colonizing form. Therefore, in a colonizing species macropters would be expected to predominate in populations toward the periphery of the range as founders of such populations would likely be homozygous recessive macropters.

To be incorporated into a population, flightlessness must have some advantages. It could be that brachyptery has higher survivalship value because such individuals are not subjected to the hazards of flight dispersal. A differ-

ential dispersal rate from a population would increase the frequency of the allele that dispersed most slowly. Also, brachypters may have a higher reproductive potential because they can put additional energy into reproduction rather than flight muscle formation. These factors could result in an increase in the frequency of brachypterous individuals in established local populations. In a species whose range is expanding, new peripheral populations are most likely to be established by individuals with the greatest dispersal abilities. Thus in a wing dimorphic colonizing species, macropters would be expected to be most numerous towards the periphery of the range and in relatively recently colonized habitat while the proportion of brachypters should be higher in established populations.

However, it must be noted that possession of fully developed wings does not ensure flight dispersal capabilities. Brachypters usually lack flight musculature and in some species macropters have been observed as lacking flight muscles or showing flight muscle histolysis with the advent of reproduction (Carter 1976; Jackson 1952, 1956a, b).

*Bembidion lampros* Herbst, a species which shows wing dimorphism, was accidentally introduced into Newfoundland from Europe and had established a population in St. John's by 1949 (Lindroth 1955, 1963a). Since then its range has expanded (and is probably still expanding), but is still confined to the Avalon Peninsula (Larson & Langor 1982). This species offers a unique field opportunity to investigate the function of a dispersal polymorphism and to test the implication of differing dispersal abilities of these phenotypes on their frequencies and distribution in Newfoundland populations.

#### MATERIALS AND METHODS

To facilitate wing morph identification, wing length measurements, and flight muscle dissections, it was necessary to remove the elytra from each specimen. Individuals possessing large metathoracic wings with reflexed apices were classed macropterous, while those with wings lacking reflexed apices were considered brachypterous. Wing lengths, measured from the apex to the base of the costa, are expressed as a ratio of elytra length (from apex of scutellum to elytral tip). The metanotum of each individual was removed to determine the condition of the flight muscle. Fully muscled individuals possessed large blocks of vertical muscle in the metathorax. The metathorax of muscleless individuals contained part of the crop (and ovaries of females) and a few small wing base muscles.

To test the hypothesized dispersal model, samples of *B. lampros* were collected from sites throughout the known Newfoundland range including the probable site of species establishment, St. John's (Lindroth 1955). All specimens in each sample were examined for wing length and macropters were dissected to determine condition of the flight muscles.

A sample of 30-40 adults was collected weekly from a small field near Long Pond, St. John's, from April 1 to August 8, 1981. These individuals were dissected to determine wing length, condition of flight muscles, condition of testes in males, and number of mature eggs carried by each female.

A breeding study was performed to determine the genetic mechanism controlling wing length inheritance. Sixteen crosses were carried out (in two non-replicate series of 8) using parents with various combinations of the wing morphs. Individuals used in the crosses were early spring field collected adults. Females were initially isolated for a period of 2-3 weeks to test for prior

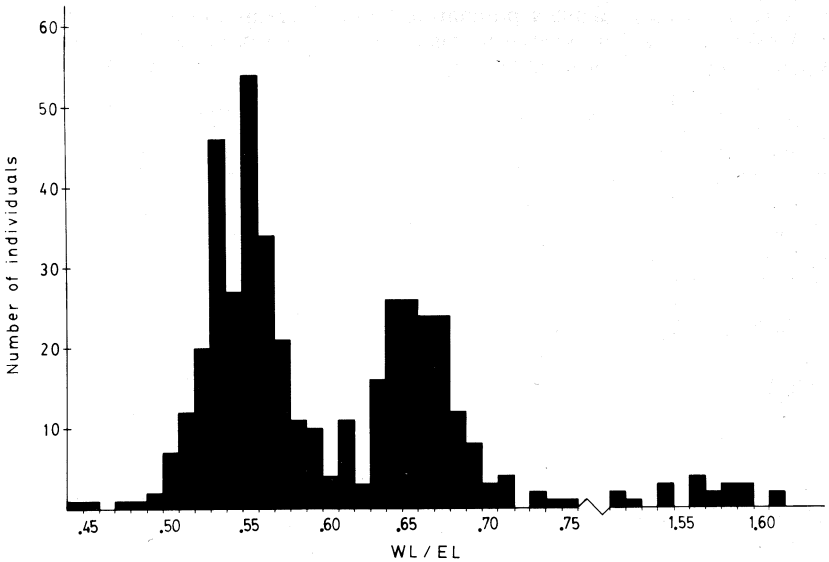


Fig. 1. Wing length (WL)/elytral length (EL) ratios of specimens of *Bembidion lampros* collected near Long Pond, St. John's in 1981.

breeding. None of these individuals produced larvae during the isolation period and it was assumed they were sexually immature and virgin when collected.

The two parental individuals of each cross were kept in a 10 cm diameter finger bowl three-quarters filled with soil sifted through a 0.85 mm mesh sieve. Each container contained a small strip of blotting paper which was kept moist using a dilute (0.4–0.5%) formalin solution, a mould inhibitor. The bowls were stacked in an incubator at 23–25°C.

Adults were fed small pieces of dry dog food containing at least 21% protein. Each day food was changed and a search made for larvae. Eggs were not collected because the sieving required may have resulted in their damage. Larvae were usually found beneath the food, perhaps feeding on it. Larvae were reared individually in screw-top vials (2 × 5 cm) ¼–½ filled with sifted soil and containing a small strip of blotting paper moistened with 0.5% solution of formalin. Vials were kept in an incubator at 23–25°C.

Larvae were fed on *Drosophila* larvae or punctured *Tribolium* larvae, which were changed as they were consumed or became mouldy. Newly emerged adults were kept for 2–3 days until their exoskeleton hardened, then preserved in 70% ethanol. They were dissected later to determine wing length and condition of flight musculature.

## RESULTS

**Variation in wing length and morphology:** Data on the wing length (WL)/elytra length (EL) ratio for 433 specimens of *B. lampros* is presented in Fig. 1. Three phenotypes were recognized: a macropterous (M) form with WL/EL—1.51 to 1.61 (wing length—2.82 mm to 3.48 mm); a brachypterous I (BI) form with WL/EL—0.44 to 0.60 (wing length—1.0 mm to 1.4 mm); and a brachyp-

Table 1. Wing phenotypes of parents and progeny obtained in laboratory breeding studies of *Bembidion lampros* (M—macropterous; BI—brachypterous short winged; BII—brachypterous, intermediate; B(?)—brachypterous, subgroup not determined).

Cross Number	Parental Phenotypes		Total Progeny	Phenotypes of progeny			
	♂	♀		BI	BII	B(?)	M
1	M	M	5	—	—	—	5
2	M	M	5	—	—	—	5
3	M	M	1	—	—	—	1
4	B(?)	M	5	—	—	2	3
5	B(?)	M	4	—	—	3	1
6	M	B(?)	5	—	—	2	3
7	M	B(?)	3	—	1	—	2
8	M	BI	1	1	—	—	—
9	M	BII	2	1	—	—	1
10	B(?)	B(?)	2	—	—	2	—
11	B(?)	B(?)	1	—	—	1	—
12	BI	BI	1	—	1	—	—
13	BI	BI	1	1	—	—	—
14	BI	BI	1	—	1	—	—
15	BII	BII	1	1	—	—	—
16	BII	BI	4	4	—	—	—
	Totals		42	8	3	10	21

terous II (BII) form with WL/EL—0.61 to 0.75 (wing length—1.25 mm to 1.70 mm). There is a zone of overlap (WL/EL—0.58 to 0.62) between the two B phenotypes.

There was no significant difference in the distribution of phenotypes between sexes ( $\chi^2$ ,  $P = 0.05$ ) indicating no sex linkage pattern. Comparisons of WL and EL between male and female M and between M with full flight muscles and those lacking flight muscles resulted in no significant difference (one way analysis of variance,  $P = 0.05$ ). The mean EL of M was slightly larger than that of B individuals (significant at  $P = 0.05$ ) but it is unknown whether this difference was due to body size differences or degree of wing development (in some wing dimorphic species the B form is known to have shorter and more strongly curved elytra (Lindroth 1963b)).

**Breeding study:** Sixteen crosses, that included all possible combinations of the 3 parental phenotypes in at least one cross, were conducted. Reciprocal crosses of some, but not all, phenotypic combinations were made. Parental phenotypes and the number and phenotypes of offspring are indicated in Table 1.

The number of progeny produced and reared to the adult stage was low, but at least one adult offspring was obtained from each cross. The results were: M × M—all offspring M; BI × BI—BI and BII offspring; BII × BII—BI offspring; BI × BII—BI offspring; M × BI—BI offspring; M × BII—BI and M offspring. In 6 crosses, phenotypes of B parents and B progeny were unknown due to loss of specimens before wing measurements could be made. However, M × B(?) produced B(?) and M offspring, and B(?) × B(?) produced B(?) offspring.

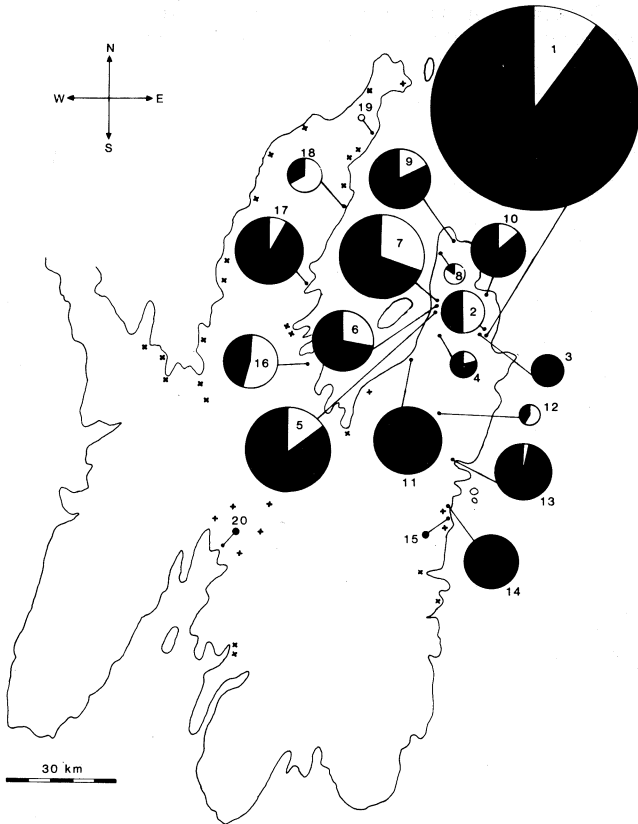


Fig. 2. Distribution of macropterous and brachypterous specimens of *Bembidion lampros* on the Avalon Peninsula, Newfoundland. The areas of the circles are proportional to the number of individuals examined. Open circles and sectors = macropterous individuals; black circles and sectors = brachypterous specimens. Numbers denote site numbers (Table 3) and X indicates sites which were carefully searched but no specimens discovered.

**Distributional study:** *B. lampros* specimens were collected from 20 localities on the Avalon Peninsula. Collection sites, number of specimens, and percentage of macropters in each sample are indicated in Fig. 2. Samples from localities in the southern portion of the range contained higher percentages of brachypters, while macropters were relatively more numerous in collections from northern and western localities. The species was most abundant on the northeastern Avalon Peninsula where at least a few specimens were found in every locality (with suitable habitat) searched. However, many localities with apparently suitable habitat near the apparent range limits yielded few or no specimens.

Wing morph frequencies in the weekly samples taken from Long Pond, St. John's, in 1981 are recorded in Table 2. Macropters comprised 9.9% of the

Table 2. Frequencies of macropterous (M) and brachypterous (B) adults of *Bembidion lampros* and the percentage of macropters with flight muscles in weekly collections taken near Long Pond, St. John's (Site 1) during 1981.

Date	N	% of each phenotypes		Number (%) of macropters with flight muscles
		B	M	
April 1-10	319	90.9	9.1	4 (13.8)
April 27	40	90.0	10.0	1 (25.0)
May 6	41	95.1	4.9	0
May 12	39	92.3	7.7	0
May 19	46	91.3	8.7	0
May 27	34	94.1	5.9	0
June 2	40	85.0	15.0	2 (33.3)
June 9	25	96.0	4.0	0
June 16	40	85.0	15.0	1 (16.7)
June 23	37	78.4	21.6	1 (12.5)
June 30	38	94.7	5.3	0
July 8	30	93.3	6.7	0
July 15	39	84.6	15.4	0
July 22	29	96.6	3.4	0
July 29	30	96.7	3.3	0
August 8	40	80.0	20.0	0
September 2	10	80.0	20.0	0
October 29	11	90.9	9.1	0
Totals	888	90.1 (ave.)	9.9 (ave.)	9 (10.2)

total number. The proportions of macropters and brachypters varied considerably throughout the sampling period and no trends were shown.

**Flight muscle development:** All individuals dissected possessed either fully developed flight muscles or no flight muscles—there were no intermediate forms. Flight muscles were not observed in any brachypters dissected while only 5.9% of macropters possessed flight muscles. All macropters with flight muscles were collected within an 8 mile radius of St. John's, between April 1 and June 23 (Tables 2, 3). None of the teneral macropters examined (including 21 lab reared specimens) possessed flight muscles.

#### Life History

*B. lampros* inhabits cultivated fields, gardens, waste-places, and other kinds of open, sun-exposed clay and gravelly ground. Since this type of habitat in Newfoundland is created principally by human activity, *B. lampros* is synanthropic.

The crops of 25 adults were dissected to determine feeding habits. All contained fine particulate material and liquids which were impossible to identify. However, small amounts of plant material were found in crops of two individuals. No material was found in the crops of individuals collected from early autumn to early spring.

Data on gonad development of females are presented in Table 4. Eggs were first found April 27 and by May 19 over 90% of the females contained eggs. Mature eggs were pale yellow and oblong, 0.51 mm × 0.31 mm (as measured

Table 3. Percentage of macropters with fully developed flight muscles in samples of *Bembidion lampros* collected from 20 localities on the Avalon Peninsula in 1981. Site numbers correspond to those of Fig. 2.

Site	Date	Location	n	# of macropters	# (%) of macropters with flight muscles
1	April 1–Oct. 29	Long Pond (St. John's)	888	88	9 (10.2)
2	September 8	Pippy Park (St. John's)	34	17	0
3	May 8	Oxen Pd. (St. John's)	18	0	—
4	April 30	Tolt Rd. (St. Phillip's)	14	3	0
5	April 29	Murray's Pd., Portugal Cove	125	18	3 (16.7)
6	August 7	Indian Meal Line, Portugal Cove	70	20	0
7	April 29	Western Island Pd., Torbay	114	35	2 (5.7)
8	May 11	Bauline	7	6	0
9	May 11	Pouch Cove	63	11	0
10	May 11	Outer Cove	49	6	4 (66.7)
11	May 22	Chamberlains	76	0	—
12	June 13	Cockrane Pond	9	5	0
13	June 15	Bay Bulls	56	21	0
14	June 15	Tors Cove	48	0	—
15	June 15	Burnt Cove	1	0	—
16	June 19	South River	51	27	0
17	June 19	Harbour Grace	88	5	0
18	June 19	Blackhead	23	15	0
19	June 24	Lower Island Cove	2	2	0
20	September 19	Haricot	1	0	—
Totals			1737	279	18 (6.5)

*in situ*). Oviposition had begun by May 19 (as indicated by the presence of corpora lutea) and by June 2, all females had laid eggs. The number of mature eggs per female was at a maximum between May 19 and June 30 then decreased rapidly. The number of mature eggs carried per female did not differ significantly between macropters and brachypters (AOV,  $P = 0.05$ ). Fully developed testes were possessed by 50% of all males by May 12 and this value had increased to 100% by May 27. No copulation was observed in the field or laboratory.

Fig. 3 shows the proportions of old and new generation adults in the samples collected from Long Pond, St. John's, in 1981. Teneral specimens first appeared June 9 and by July 29 they comprised 100% of the weekly samples. Towards the end of summer most new generation adults were well sclerotized, but could be recognized by the lack of eggs and corpora lutea in the females and by the small, immature testes in the males. Small numbers of new generation adults were active in the field until early November.

There are 3 larval instars. Frontale widths did not differ significantly from those recorded by Mitchell (1963). When fully grown, each third instar larva formed an oblong chamber beneath the soil surface within which it pupated. After the teneral adult emerged from the pupa, it remained in the chamber for a short period while tanning of the cuticle occurred, then made its way to the surface.

Table 4. Data on the gonad development of macropterous (M) and brachypterous (B) females collected near Long Pond, St. John's (site 1) in 1981.

Date	Number dissected		% with eggs		$\bar{x}$ mature eggs/♀		% females with corpora lutea	
	M	B	M	B	M	B	M	B
1-10.IV	19	19	0	0	—	—	—	—
27.IV	4	19	25	10.5	0	0	0	0
6.V	2	20	0	15	0	0.4	—	0
12.V	3	17	100	59	1.33	0.44	0	0
19.V	2	19	50	95	0	3.00	0	53
27.V	2	17	100	88	4.0	2.53	100	82
2.VI	1	14	100	100	5.0	4.64	100	100
9.VI	1	13	100	92	3.0	3.08	100	100
16.VI	3	16	100	94	2.0	1.69	100	100
23.VI	4	16	100	100	4.0	3.0	100	100
30.VI	0	18	—	94	—	2.28	—	100
8.VII	2	15	100	87	2.0	2.47	100	100
15.VII	4	18	100	78	1.5	2.06	100	100
22.VII	1	17	100	12	3.0	0.29	100	100
29.VII	0	22	—	0	—	—	—	—
8.VIII	4	22	0	0	—	—	—	—
2.IX	0	2	—	0	—	—	—	—
29.X	1	4	0	0	—	—	—	—

The length of development from egg to adult in the field was estimated at 21 days using the difference in time between the first evidence of oviposition, May 19 (Table 4), and the appearance of the first teneral adult, June 9 (Fig. 3). Among lab reared specimens, the time of development from egg to adult was considerably longer than the above estimate. The mean development time from first instar larva to adult for the first series of lab reared specimens was 34 days and for the second series, 21 days. Mortality rates were 61% and 48%, respectively. The lower mortality rate for the second series of rearings may indicate more favorable conditions and thus the 21 day development period may be a more valid estimate.

#### DISCUSSION

**Wing and flight muscle inheritance:** Previous studies on wing length inheritance in beetles (Lindroth 1946, 1963a; Jackson 1928; Stein 1973) have shown wing length to be controlled by a factor acting in a simple Mendelian manner with the B condition dominant. However, breeding experiments with *B. lampros* indicate that wing length, although genetically determined, is not a single simple Mendelian trait. Too few data were obtained to determine the genetic mechanism controlling wing length inheritance. However, the phenotypic ratios among the progeny do not support the M condition being recessive.

The M phenotype is apparently homozygous, for all M × M crosses produced only M offspring (n = 11). Similarly, all crosses between parents of the B (I or II) phenotypes, produced only B offspring (n = 11). Crosses between M and B parents produced mixed progeny (n = 20, ratio 1:1). The simplest system that could be hypothesized for controlling wing length would be: M phenotype—



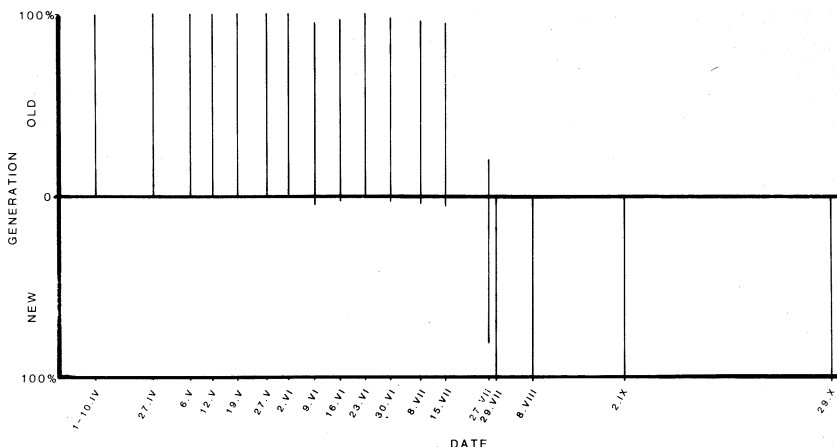


Fig. 3. Percentage of old and new generation adult *Bembidion lampros* in collections made near Long Pond, St. John's, 1981.

homozygous for macropterous condition; BI—homozygous for brachypterous condition; and BII—heterozygous. However, both a  $M \times BII$  cross and a  $M \times BI$  cross each produced a BI offspring, and neither  $BI \times BI$  nor  $BII \times BII$  bred true. Thus the results do not support a two allele system.

Three alleles at one locus could be involved, but the observation that neither BI nor BII phenotypes are necessarily homozygous rules against this possibility. Two genes may be involved, one determining macroptery or brachyptery and the other modifying the brachypterous phenotype. The large amount of variation within each phenotype suggests the action of modifying genes upon the primary alleles. Clearly, wing development is under the control of a system more complex than a single gene with two or three alleles and a more extensive breeding program than is presented here will be required to elucidate the mechanism.

It was not determined if flight muscle development was controlled by a genetic mechanism or by environmental features. If flight muscle development is determined genetically, the absence of flight muscles in brachypters indicates the absence or suppression of the alleles controlling flight muscle inheritance in BI and BII individuals. Conversely, the presence of flight muscles in some macropters indicates the presence or enhancement of these alleles in that phenotype. The low frequency of muscled individuals among macropters and the lack of evidence that flight muscles are either formed or histolyzed during adult life suggests that flight muscle condition is inherited independently of wing length. In *Amara lunicollis* Schiodte, where there is evidence that flight muscles are built up and broken down in at least some adult individuals, specimens with partly developed muscles have been discovered (Van Huizen 1979). An examination of 56 specimens of *B. lampros* collected by C. H. Lindroth, W. J. Brown, and E. Palmén from St. John's in 1949 (Canadian National Collection, Ottawa; Zoological Institute, Lund) yielded only one macropter, which also lacked flight muscles. The frequency of the allele(s) controlling these traits in the founding population was low.

**Distribution, dispersal, and significance of dispersal polymorphisms:** Most suitable habitat for *B. lampros* in Newfoundland is limited to areas in and around human habitation. Towns on the Avalon Peninsula are generally separated by several kilometers of habitat unsuitable for *B. lampros* (e.g., forest, heath, bog). Since established in St. John's, the species has spread from town to town along the coast in both directions as well as inland. Distances between towns are probably small enough to allow rapid dispersal by flight (den Boer 1970) or slower dispersal by surface locomotion across fields or cultivated land or along the gravel sides of roads connecting towns. In time, the distribution of the phenotypes would be expected to follow a centrifugal cline with the frequency of the faster dispersing macropters increasing towards the limits of the range. Established populations would be expected to become predominantly brachypterous as the frequency of the allele(s) determining macroptery decreased due to the relatively more rapid emigration of the macropters, provided immigration was not compensating. The actual distribution of *B. lampros* does not follow this pattern. Although there is a general increase in macropter frequency towards the northern and western limit of the range, the reverse is true towards the south. The distribution pattern is further complicated by the presence of populations with low macropter frequencies in regions of the range where macropter frequencies are relatively high. This may be due to mutation and subsequent loss of the macropterous morph in these populations. More likely, the dispersal of this species has been aided by human activities such as transport of topsoil, potted plants, or agricultural products. At the margins of the range, the distribution of the species is very patchy in relation to the distribution of suitable habitat, i.e., there are many areas of apparently suitable habitat which have no populations of *B. lampros* (Fig. 2). Since areas of suitable habitat nearest the point of dispersal are likely to be colonized first (especially by surface dispersers), the patchy distribution of *B. lampros* in peripheral parts of its range may be further evidence of human assisted dispersal. The prevailing winds in Newfoundland are from the southwest in summer. Since flight direction of carabids is highly influenced by wind (Lindroth 1949), flight dispersal of *B. lampros* would likely be in a northeastern direction, away from land. Thus there is likely strong selection against flight dispersal.

If dispersal by flight does occur, it is not known at what time of year this phenomenon takes place as no specimens were collected in flight. If flight dispersal occurs after copulation but before oviposition, it would be possible for the progeny of founders to be heterozygous (MB) for wing development even if macropters are homozygous. Van Huizen (1979) has found that mated or gravid females of species with life histories similar to that of *B. lampros* may fly, although the phenomenon is relatively uncommon.

Flight muscle development may be controlled by genetic and/or environmental factors. At one extreme, different muscle morphs may represent different genotypes with no environmental effects on the phenotype (Ford 1961). Alternatively, the morphs may be maintained by a threshold response, i.e., the phenotype produced is dependent upon whether the concentration of an effector (perhaps a hormone) is above or below a threshold level with the concentration of the effector changing in response to environmental stimuli (Brinkhurst 1969; Harrison 1979; Vepsäläinen 1974b).

If flight plays a significant role in dispersal, the majority of macropters would be expected to possess fully developed muscles during some part of their adult life. However, a very low percentage of macropters were found to have fully developed flight muscles. There was no evidence of flight muscle histolysis and

the distribution of the wing morphs did not conform to the centrifugal cline in frequency postulated if macropters possessed greater dispersal abilities than brachypters. On the basis of these considerations it appears that flight, although it is known to occur in *B. lampros* (Lindroth 1963b), is an infrequent event which plays a limited role in dispersal of the species.

Flightlessness should have an adaptive significance to be incorporated into a population or species (Darlington 1936; 1943). The ability to fly allows insects to disperse over long distances and establish new populations, but as the costs associated with flight dispersal increase (decreased survivorship and fecundity), selective advantage of the flight dispersal morph decreases. Also, in established populations, the more rapid dispersal of flying individuals would result in a differential loss of alleles from the population with the alleles controlling flight incurring the relatively greater losses. It is believed that the survivorship of the flight dispersal morph is lower because these individuals are subjected to the hazards of flight. Although a few attempts have been made to document this, mainly among Hemiptera and Homoptera (Ammar 1973; Guthrie 1959; Vepsalainen 1974a; Young 1965), the data are inconclusive. Also, the flight dispersal morph may have a lower fecundity. The observation that flight muscle histolysis often precedes ovarian growth and egg development (Andersen 1973; Atkins and Farris 1962; Carter 1976; Chapman 1956; Hocking 1952; Reid 1958; Tanaka 1976; Van Huizen 1979) suggests a trade-off between dispersal and reproduction. Since flight dispersal in carabids usually occurs prior to egg laying (Dingle 1972; Van Huizen 1979), the flight dispersal morph has less energy and material to put into reproduction because of the investment in flight. Too few M females were collected to present an adequate comparison of the fecundities of B and M females (using the number of mature eggs per female as the index of fecundity), but differences between the morphs were not significant. This does not preclude differences in total number of eggs produced.

The lack of flight muscles may provide additional space for organ systems involved in reproduction. In flightless Hemiptera (Andersen 1973; Larsen 1970; Lowe and Taylor 1964) and Coleoptera (Chapman 1956; Jackson 1933, 1952, 1956b) the space otherwise taken up by flight muscles is occupied by ovaries and fat body. The metathorax of flightless *B. lampros* specimens contains part of the crop and ovaries (females). The energy and materials tied up in flight muscles is probably greater and more readily available to an insect than the energy invested in wings, which are essentially thin cuticular flaps. Thus, incorporation of flightlessness into a population or species would likely result first in loss of flight muscles followed by a reduction in wing length.

Flightless individuals may have greater reproductive success but are at a disadvantage and susceptible to extinction if the local habitat becomes unsuitable. The habitat for *B. lampros* in Newfoundland is relatively stable but patchy, the climate is usually unsuitable for flight (frequent wind, cold, rain, fog), and the prevailing winds would tend to sweep flying individuals out over the ocean thus reducing the advantage of flight dispersal. Therefore, the low proportion of flight dispersers in Newfoundland populations may reflect a balance between the advantage of flight dispersal to new sites and the costs (increased mortality and lower fecundity) associated with flight.

Many earlier studies on dispersal polymorphisms in insects did not involve flight muscle dissections of the species studied. It may be that the frequency of flight dispersal is much lower than previously thought and, therefore, as in *B. lampros*, does not play as significant a role in the dispersal of those species as the presence of full wings might indicate.

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