Oecologia (Berl.) 40, 125–132 (1979)

Oecologia

Flight Polymorphism in the Field Cricket *Gryllus pennsylvanicus*

R.G. Harrison

Department of Biology, Yale University New Haven, CT. 06520 USA

Summary. Wing length polymorphisms are common in many groups of insects. In the field cricket *Gryllus pennsylvanicus* the long-winged morph occurs in low frequency in most populations but seems not to occur at all in certain areas and to become relatively abundant in others. Laboratory rearing experiments and single-pair crosses suggest that both inter- and intra-population variation can be explained at least in part by genetic differences. A model of genetic variation in threshold response is consistent with all available data. One possible mechanism for maintenance of the flight polymorphism is discussed.

Introduction

Andrewartha and Birch (1954) pointed out that "...because motility is a primary quality of animals, adaptations among them for dispersal are less obvious [than among plants]" (p. 89). In certain groups of insects "trivial movements" (Southwood, 1962), those "restricted to the animal's habitat" and generally associated with feeding, reproduction, predator avoidance, etc., are usually accomplished by walking or swimming. For these insects flight may be primarily an adaptation for dispersal. In many of these same groups wing length and flight muscle development are variable and individual species exhibit distinct morphological polymorphisms that clearly affect flight ability. Crickets (Orthoptera: Gryllidae) provide an excellent example of this phenomenon (Sellier, 1954; Alexander, 1968). Species may be entirely macropterous (long-winged), entirely micropterous (short-winged), or polymorphic.

In this paper I discuss observations and experiments on wing polymorphism in the North American field cricket *Gryllus pennsylvanicus*. Two questions are of particular concern: Do morph frequencies vary among populations? If so, do genetic differences contribute to intra-specific variation in morph frequency?

0029-8549/79/0040/0125/$01.60

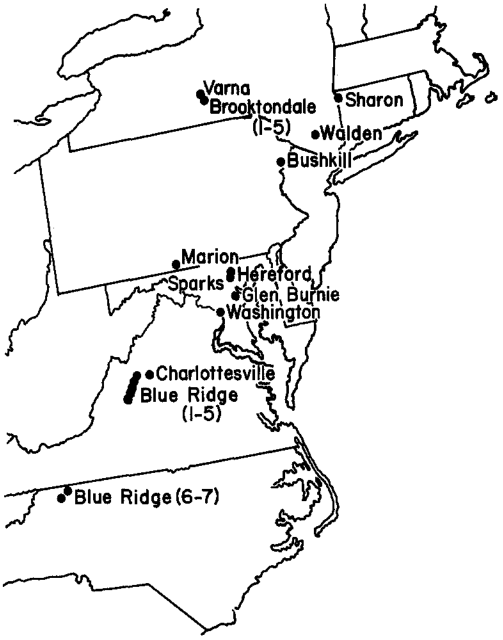

Fig. 1. Collecting localities for *Gryllus pennsylvanicus* populations in the eastern United States

Materials and Methods

I sampled populations of *Gryllus pennsylvanicus* from 21 localities in the eastern United States (Fig. 1). These areas include a variety of disturbed habitats – pastures, fields, and roadsides – all of which are characteristic for this species. Crickets were brought to the laboratory where body length and hind wing length were measured to the nearest 0.5 mm. Additional information on morph frequency was obtained from field censuses of marked individuals of *G. pennsylvanicus* in populations from Brooktondale, New York.

In order to assess the contribution of genetic differences to geographic varation in wing morphology and development, I reared *G. pennsylvanicus* from six populations under constant laboratory conditions. Adult crickets from New York, Connecticut, Maryland, Virginia, and Washington, D.C. were brought into the laboratory between August 26 and September 10. For each population, eggs derived from 10 field collected females were placed in a refrigerator ($T = 4$–7° C) for 108–122 days in order to break diapause. Upon removal from the cold, eggs were allowed to develop at 29° C, with a light:dark regime of 14 h light, 10 h dark. Nymphs were reared under the same conditions in small aquaria (40 nymphs/aquarium) with food (Purina Cat Chow® and lettuce), water, and shelter (paper towel). Adults were removed as they appeared and body length and wing length determined as described above.

Long-winged and short-winged laboratory-reared crickets from one population (Hereford, Maryland) were used as parents in single-pair crosses. Rearing procedures for the offspring of these crosses were identical to those used for the parents.

Results

Variation in wing length in *G. pennsylvanicus* is clearly discontinuous. Figure 2 shows that the frequency distribution is bimodal. Both field collected and laboratory-reared crickets can readily be divided into two distinct classes (micropters and macropters).

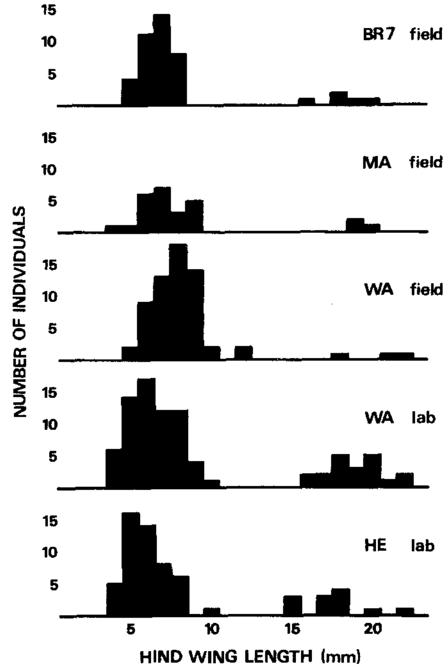

Fig. 2. Frequency distribution of hind-wing length in field-collected and laboratory-reared *Gryllus pennsylvanicus* from Lowland and Blue Ridge populations

Table 1 presents frequencies of long-winged and short-winged individuals in natural populations of *G. pennsylvanicus* with collecting localities grouped according to geographic area. Three areas have been distinguished: Northern, Lowland, and Blue Ridge. Electrophoretic surveys of genetic variation in *G. pennsylvanicus* provide support for grouping populations in this way. Electromorph frequencies are relatively constant among populations within a geographic area, but differ significantly between areas (Harrison, 1977, manuscript in preparation). There are also consistent differences in morphology and development. However, the BR2 population at the northern end of the Blue Ridge Parkway in Virginia is exceptional. Crickets from this site appear intermediate between Lowland and Blue Ridge forms in morphology, development, and electromorph frequency (Harrison, 1977).

The frequency of long-winged *G. pennsylvanicus* is low everywhere these crickets have been sampled, but populations from Lowland areas generally have higher frequencies of macropterous individuals (Table 1). Long-winged males have only been found in these Lowland populations and in the southernmost Blue Ridge population (BR7), which also contains a high proportion of long-winged females. The BR2 collection has a relatively high frequency of macropters, consistent with its known genetic affinities with Lowland populations. Although the frequency of long wings is greater among females than males (Table 2), this cannot account for differences between geographic areas, since Lowland collections contain a smaller proportion of females than Northern or Blue Ridge collections.

Table 1. Frequency of long-winged and short-winged crickets in populations of *Gryllus pennsylvanicus* from the eastern United States. Some populations were sampled once, others more than once, during the summers of 1974–1977. See Fig. 1 and Harrison (1977) for additional information on collecting localities

Population		*n*	Short	Long
Northern				
Brooktondale, N.Y.	BD1	450[a]	0.989	0.011
	BD2	91	0.989	0.011
	BD3	41	0.976	0.024
	BD4	422[a]	0.993	0.007
	BD5	107	1.00	0.000
Varna, N.Y.	VA	17	1.00	0.000
Walden, N.Y.	WL	39	1.00	0.000
Sharon, Ct.	SH	49	1.00	0.000
Bushkill, Pa.	BU	7	1.00	0.000
Blue Ridge				
Blue Ridge Parkway	BR1	100	0.990	0.010
	BR2	51	0.941	0.059
	BR4	70	1.00	0.000
	BR5	35	1.00	0.000
	BR6	53	0.981	0.019
	BR7	41	0.878	0.122
Lowland				
Marion, Pa.	MA	22	0.864	0.136
Hereford, Md.	HE	28	0.929	0.071
Sparks, Md.	SP	27	0.889	0.111
Glen Burnie, Md.	GB	21	0.952	0.048
Washington, D.C.	WA	89	0.966	0.034
Charlottesville, Va.	CH	21	0.952	0.048

[a] Sample size include data from field censuses of marked crickets

Table 2. Numbers of long-winged and short-winged males and females of *G. pennsylvanicus*. Data from all years and all collecting localities

	Long	Short
males	6	987
females	27	761
$X^2 = 19.24$	$p < 0.001$	

Table 3 shows that even when eggs and nymphs develop in a uniform environment Lowland *G. pennsylvanicus* (HE and WA populations) have a significantly higher proportion of macropterous individuals. Indeed, the differences are far more striking in laboratory populations than in the field. The frequency of long-winged adults is also high among laboratory-reared crickets from BR2.

Results from single pair matings of laboratory-reared crickets (Table 4) show that crosses of macropter × macropter give rise to significantly more macropterous offspring than micropter × micropter crosses. However, both types of crosses produce long-winged and short-winged progeny, and there is no reason to assume that the polymorphism is determined by a single gene. All individuals

Table 3. Proportions of long-winged individuals in laboratory-reared *G. pennsylvanicus* from six localities

	Males	Females
BD1	0/20 (0.00)	0/23 (0.00)
BD5	0/13 (0.00)	1/11 (0.09)
SH1	0/26 (0.00)	0/13 (0.00)
BR2	5/17 (0.29)	7/17 (0.41)
HE	5/32 (0.16)	11/34 (0.32)
WA	5/53 (0.09)	18/41 (0.44)

Table 4. Results of single pair crosses involving short-winged (S) and long-winged (L) *G. pennsylvanicus*. Parents were reared in the laboratory at 29° C, 14 h light: 10 h dark. Their offspring were reared under identical conditions

Cross	Parental phenotypes	Numbers of offspring of given phenotypes			
		males		females	
		L	S	L	S
1	L × L	1	2	1	2
2	L × L	8	3	2	0
3	L × L	3	2	6	1
4	S × L	0	2	5	4
5	S × S	2	17	4	9
6	S × S	0	4	0	6
All L × L crosses		12	7	9	3
All S × S crosses		2	21	4	15

Comparison of results of all L × L and S × S crosses: for males $X^2 = 13.89$ ($p < 0.001$), for females $X^2 = 8.79$ ($p < 0.005$)

used in these crosses were derived from one Lowland population (Hereford, Maryland). Genetic variation affecting wing development must, therefore, exist within as well as between populations.

Discussion

The observed frequencies of macropters in *G. pennsylvanicus* populations sampled here are consistent with the mean value of 4% reported by Alexander (1968) for this species. Information on wing morph frequencies can also be derived from earlier observations of *G. pennsylvanicus*. Walker (1904) reported long-winged female *G. abbreviatus* (=*pennsylvanicus*) "common" in Ontario, although far less so than the short-winged form. In August, 1901 he observed a "considerable number" of long-winged females floating in Lake Huron, suggesting that these individuals do indeed fly. Although long-winged females were frequently seen in Ontario, Piers (1918) wrote that "only the short-winged form...has been met with in...[Nova Scotia]". Cantrall (1943) found no macropterous *G. pennsylvanicus* among 33 males and 77 females collected at the

George Reserve in Michigan. Lutz (1908) examined specimens from populations along the east coast of the United States. Among *G. pennsylvanicus* from Perkins Cove, Maine, 3% of males and 11% of females were long-winged. At other localities in northern New England no macropters were found (among a total sample of 205 females). Piers, Cantrall, and Lutz do not refer to the species as *G. pennsylvanicus*, but it is evident from the localities and dates of collection that this is the species involved.

Thus, although most populations of *G. pennsylvanicus* have the long-winged morph in low frequency, this form appears to be absent (or extremely rare) in certain areas and to become locally abundant in others. In general, the data suggest that southern populations (Lowland and southern Blue Ridge) have higher frequencies of the long-winged morph. However, this observation can be explained either in terms of environmetal differences (e.g. warmer temperatures during development in Lowland areas) or in terms of genetic differences (which would be consistent with patterns of variation in soluble enzymes).

Environmental factors have frequently been implicated in the control of flight polymorphisms in insects (for example, Brinkhurst, 1959; Young, 1965; Lees, 1966, 1967; Vepsalainen, 1974). In the family Gryllidae, changes in temperature (Ghouri and McFarlane, 1958; McFarlane, 1962), photoperiod (Masaki and Oyama, 1963; Saeki, 1966b; Alexander, 1968; Mathad and McFarlane, 1968; Tanaka et al., 1976), density (Fuzeau-Braesch, 1961; Saeki, 1966a) and diet (McFarlane, 1962) have all been shown to affect the proportion of long-winged individuals in laboratory populations.

Attempts to define a genetic basis for flight polymorphisms have often produced ambiguous results. Only in the weevil *Sitona hispidula* does wing length clearly appear to behave as a simple Mendelian trait (Jackson, 1928), although Lindroth (1946) has scanty evidence that the same is true in the Carabid beetle *Pterostichus anthracinus*. In both cases the short-winged condition appears to be dominant. Single-locus genetic models have also been proposed to explain observations on wing polymorphisms in water-striders (Poisson, 1924; Ekblom, 1941; Brinkhurst, 1959) and in the field cricket *Gryllus desertus* (Sellier, 1954), but in none of these cases are the results convincing. Multi-locus models are equally satisfactory.

The results presented here suggest that genotype makes a significant contribution to determination of wing length and flight muscle development in field crickets. Differences in morph frequency between laboratory-reared F_1 crickets could be attributed to matérnal influence rather than genetic variation, but this seems less likely in view of the clear-cut results from single-pair crosses of these F_1 individuals. Thus, both inter- and intra-population variation in *G. pennsylvanicus* can be explained at least in part by genetic differences. In the genus *Gryllus* the frequency of long-winged and short-winged morphs varies significantly among species (Alexander, 1968). These differences no doubt also reflect genetic differentiation.

The observations reported here, together with earlier work on the importance of environmental factors, are consistent with a model of genetic variation in threshold response. Individuals are assumed to have a threshold (perhaps determined by hormone concentrations (Southwood, 1961)) above (or below) which they become long-winged. They also have defined sensitivities to particular environmental cues (e.g. temperature, photoperiod, food quality, etc.). These characteristics are most likely determined by a large number of loci. Within a given population individuals may become short-winged or long-winged depending on (1) the series of environments (including other biota) encountered during development and (2) their genetically determined threshold and sensitivities. Inter-population variation must be explained in terms of genotype-environment interactions. Differences in macropter frequency between males and females within the same population will result if the two sexes have different thresholds or different sensitivities. Individuals may be sensitive to particular environmental factors only during a limited period of their life cycle.

Elsewhere (Harrison, 1977) I have shown that short-winged *G. pennsylvanicus* always lack fully developed flight muscles, whereas these are usually present in long-winged crickets. Reduced flight musculature in adult insects is known to occur in a variety of groups including many species of Hemiptera, Homoptera, Coleoptera, and Orthoptera, In certain species individuals with reduced flight muscles may have greater survival and/or fecundity (Young, 1965; Byers, 1969; Tanaka, 1976). In flightless aquatic beetles, the part of the thorax that normally houses the flight muscles is occupied by the fat body and, in mature beetles, by part of the reproductive system (Jackson, 1952). Thus, in relatively permanent habitats (those that persist for a long time at the same location), reduction of flight musculature may confer a distinct selective advantage on the flightless morph. On the other hand, colonization of new habitat patches may depend on dispersal by flight. If this is true for *G. pennsylvanicus*, then maintenance of flight polymorphism in this species might be viewed as the result of a balance between the superior survivorship and fecundity of the short-winged crickets and the superior dispersal ability of their long-winged siblings.

Acknowledgements. I am indebted to Peter Brussard and Ron Hoy for advice and support throughout the course of this work. I am grateful to the National Park Service for allowing me to collect along the Blue Ridge Parkway in Virginia and North Carolina. This research was supported by grants from the Theodore Roosevelt Memorial Fund of the American Museum of Natural History and the E.I. DuPont de Nemours Co. (to the Section of Ecology and Systematics, Cornell University). Much of the work is based on one chapter of a thesis submitted to Cornell University in partial fulfillment of the requirements for a Ph.D. degree.

References

Alexander, R.D.: Life cycle origins, speciation, and related phenomena in crickets. Quart. Rev. Biol. **43**, 1–41 (1968)

Andrewartha, H.G., Birch, L.C.: The Distribution and Abundance of Animals. Chicago: University of Chicago Press 1954

Brinkhurst, R.O.: Alary polymorphism in the Gerroidea (Hemiptera-Heteroptera). J. Anim. Ecol. **28**, 211–230 (1959)

Byers, G.W.: Evolution of wing reduction in crane flies (Diptera:Tipulidae). Evol. **23**, 346–354 (1969)

Cantrall, I.J.: The ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan. Univ. Mich. Mus. Zool. Misc. Publ. **54**, 1–182 (1943)

Ekblom, T.: Untersuchungen über der Flugopolymorphism der *Gerris asper*. Notul. Ent. Helsingf. **29**, 1–15 (1941)

Fuzeau-Braesch, S.: Variations dans la longeur des ailes en fonction de l'effet de groupes chez quelques especes de Gryllides. Bull. Soc. Zool. Fr. **86**, 785–788 (1961)

Ghouri, A.S.K., McFarlane, J.E.: Occurrence of a macropterous form of *Gryllodes sigillatus* (Walker) (Orthoptera: Gryllidae) in laboratory culture. Can. J. Zool. **36**, 837–838 (1958)

Harrison, R.G.: Patterns of variation and genetic differentiation in closely related species: the field crickets of eastern North America. Ph.D. Thesis, Cornell University (1977)

Jackson, D.J.: The inheritance of long and short wings in the weevil (*Sitona hispidula*) with a discussion of wing reduction among beetles. Trans. Roy. Soc. Edinburgh **55**, 665–735 (1928)

Jackson, D.J.: Observations on the capacity for flight of water beetles. Proc. Roy. Ent. Soc. A **27**, 57–70 (1952)

Lees, A.D.: The control of polymorphism in aphids. Adv. Ins. Phys. **3**, 207–277 (1966)

Lees, A.D.: The production of the apterous and alate forms in the aphid *Megoura viciae* Buckton with special reference to the role of crowding. J. Ins. Phys. **13**, 289–318 (1967)

Lindroth, C.H.: Inheritance of wing dimorphism in *Pterostichus anthracinus* Ill. Hereditas **32**, 37–40 (1946)

Lutz, F.E.: The variation and correlations of certain taxonomic characters of *Gryllus*. Carnegie Inst. Wash. Publ. No. **101**, 3–63 (1908)

Masaki, S., Oyama, N.: Photoperiodic control of growth and wing form in *Nemobius yezoensis* Shiraki. Kontyu **31**, 16–26 (1963)

Mathad, S.B., McFarlane, J.E.: Two effects of photoperiod on wing development in *Gryllodes sigillatus* (Walk.). Can. J. Zool. **46**, 57–60

McFarlane, J.E.: Effect of diet and temperature on wing development of *Gryllodes sigillatus* (Walk.) (Orthoptera: Gryllidae). Ann. Soc. Ent. Quebec **7**, 28–33 (1962)

Piers, H.: The Orthoptera (cockroaches, locusts, grasshoppers and crickets) of Nova Scotia. Trans. Nova Scotia Inst. Sci. **14**, 201–356 (1918)

Poisson, R.: Contribution a l'etude des Hemipteres aquatiques. Bull. Biol. **58**, 49–305 (1924)

Saeki, H.: The effect of population density on the occurrence of the macropterous form in a cricket, *Scapsipedus aspersus* Walker (Orthoptera: Gryllidae). Jap. J. Ecol. **16**, 1–4 (1966) (in Japanese, English abstract)

Saeki, H.: The effect of day-lenght on the occurrence of the macropterous form in a cricket, *Scapsipedus aspersus* Walker (Orthoptera: Gryllidae). Jap. J. Ecol. **16**, 49–52 (1966) (in Japanese, English abstract)

Sellier, R.: Recherches sur la morphogenese et le polymorphisme alaires chez les Orthopteres Gryllides. Ann. Sci. Nat., 11th Ser. **16**, 595–740 (1954)

Southwood, T.R.E.: A hormonal theory of the mechanism of wing polymorphism in Heteroptera. Proc. Roy. Ent. Soc. Lond. A **36**, 63–66 (1961)

Southwood, T.R.E.: Migration of terrestrial arthropods in relation to habitat. Biol.Rev. **37**, 171–214 (1962)

Tanaka, S.: Wing polymorphism, egg production and adult longevity in *Pteronemobius taprobanenis* Walker (Orthoptera: Gryllidae). Kontyu **44**, 327–33 (1976)

Tanaka, S., Matsuka, M., Sakai, T.: Effect of change in photoperiod on wing form in *Pteronemobius taprobanensis* Walker (Orthoptera: Gryllidae). Appl. Ent. Zool. **11**, 27–32 (1976)

Vepsalainen, K.: Determination of wing length and diapause in water striders (*Gerris* Fabr., Heteroptera). Hereditas **77**, 163–177 (1974)

Walker, E.M.: The crickets of Ontario. Can. Ent. **36**, 249–255 (1904)

Young, E.C.: Flight muscle polymorphism in British Corixidae: ecological observations. J. Anim. Ecol. **34**, 353–389 (1965)

Received August 30, 1978