Wing Dimorphism in *Gryllus rubens* (Orthoptera: Gryllidae)

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ABSTRACT Long- and short-winged morphs of *Gryllus rubens* Scudder occur at all seasons in north Florida. Percentage of macroptery is apparently relatively high during spring and summer (5–60%) and relatively low during fall and winter (2–30%). When tested, 7–10% of macropters flew. Field-collected females of *G. rubens* differ significantly in proportions of long- and short-winged progeny they produce. Eight generations of 100% selection produced two lines of *G. rubens*, one >90% long-winged and the other <10% long-winged. Genes responsible for interline differences in frequency of the long-winged morph were largely or completely X-linked. Macroptery was less frequent in short photoperiods (11:13 [L:D]) than in long (16:8) and in wild populations than in groups reared in 4-liter jars indoors or out. Macroptery was not significantly influenced by number of adults reared from one jar. Crickets reared alone in 30-ml containers were more frequently long-winged than their siblings reared in groups in the 4-liter containers. Dimorphism depends, in part, on genetic polymorphism, which may be maintained because natural selection is inconsistent. Dimorphism depends, in part, on polyphenism, which may be conditional (dependent on environmental cues that predict which morph will likely be appropriate) or stochastic (dependent on probabilistic determination of morph).

KEY WORDS *Gryllus rubens*, polymorphism, migration, flight, genetics, polyphenism

WING DIMORPHISM is common among insects, but in most instances little is known of its immediate causes or its adaptive significance (Harrison 1980, Dingle 1985, Roff 1986a,b). Because many field cricket species (*Gryllus*) are dimorphic, whereas others are either entirely long-winged or short-winged, and because field crickets are easily reared in the laboratory or in cages outdoors, they are attractive subjects for studying the phenomenon (Walker & Sivinski 1986, Wineriter & Walker 1987).

Two *Gryllus* species common in the southeastern United States produce substantial proportions of long- and short-winged morphs in the field under a variety of circumstances. Roff (1984, 1986a) has studied one of these, *Gryllus firmus* Scudder; this paper concerns the other species, *Gryllus rubens* Scudder, and addresses these questions: 1) What are the proportions of long- and short-winged morphs in wild populations? 2) Do all long-winged morphs fly? 3) What is the genetic basis of the dimorphism? 4) How does environment influence the dimorphism?

Section 1. Proportions of Long- and Short-winged Morphs in Wild Populations

Repeatably estimating the proportions of long- and short-winged morphs in a natural population is difficult both because of phenotypic plasticity (percentage of macroptery is a function of environment as well as genotype and the natural environment is continually changing), and because of sampling problems (e.g., the different behaviors of long- and short-winged morphs make it likely that a field-collected sample of a mixed population will be biased).

These two difficulties can be addressed by rearing cohorts of crickets in a standardized environment, thus holding the environment constant for all crickets, and scoring all crickets that complete development. To overcome the second difficulty, but not the first, one can rear crickets in cages outdoors (ensuring that all individuals that become adults are scored). These solutions create difficulties of their own: crickets are developing under artificial conditions and the results may not be indicative of wild populations.

Methods. For more than 2 yr *G. rubens* were collected weekly or biweekly by looking under boards and other debris at an organic gardening site on the University of Florida campus at Gainesville and sometimes at other nearby sites. Juveniles were transferred to 4-liter jars and reared to adulthood outdoors under a plywood roof that protected jars from direct sun and rain. (See Wineriter & Walker [1987] for details of rearing methods.) Jars were tended weekly, development of individuals recorded, and adults removed and recorded by sex and wing morph. (Long-winged individuals have metathoracic wings longer than the mesothoracic wings [Walker & Sivinski 1986].) Field-collected adults were recorded by sex and wing morph, and some females were put, one per 4-liter jar, under the shelter and allowed to lay eggs. Each egg-laying female was transferred weekly to a new jar. Suc-

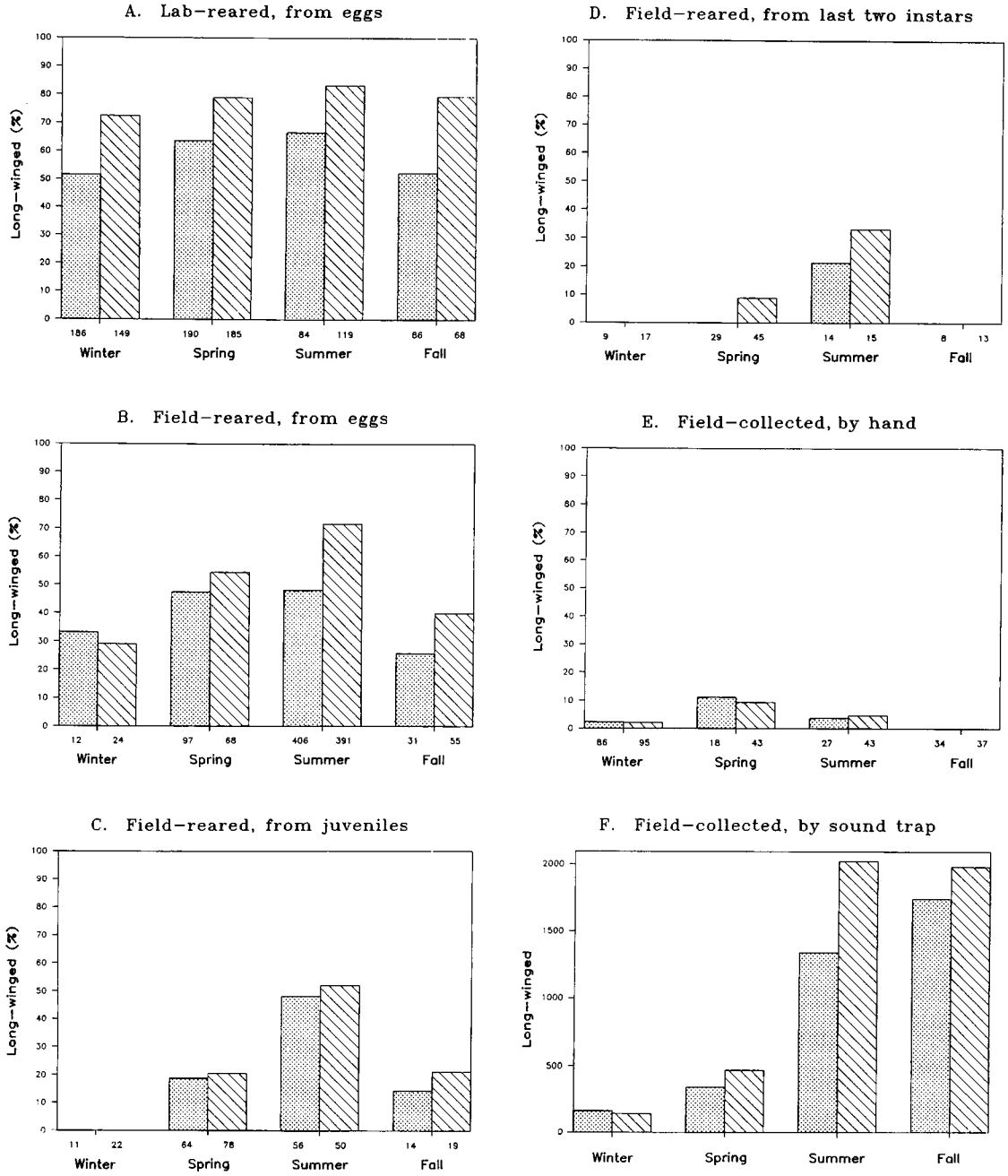

Fig. 1. Seasonal occurrence of long-winged males (stippled) and females (cross-hatched) of *G. rubens* at Gainesville, Fla. (A–D) Percentage of long-winged animals as a function of season of maturation. (Numbers beneath bars show size of sample; winter, 21 December–20 March; spring, 21 March–20 June, etc.) (A–B) Eggs of field-collected, field-held females were collected weekly and alternately reared (A) in the laboratory at 25 ± 1°C and 16:8 photoperiod or (B) outdoors beneath a shelter. (C–D) Field-collected juveniles were reared outdoors beneath a shelter. (E) Percentage of long-winged animals as a function of season of collection. Adults collected under boards and other debris. (F) Average numbers of long-winged individuals flying to trap as a function of season of capture. The trap broadcast *G. rubens* calling song and was operated nightly for 3 yr (Walker 1986b).

cessive jars, containing 1 wk's eggs of a female, were alternately left outdoors under the shelter or transferred to a rearing room at 25 ± 1°C and 16:8 (L:D) photoperiod. These "sibling-cohort" jars were tended weekly in the same manner as those with field-collected juveniles.

Results. Offspring of 28 field-collected females, when reared from egg to adult at 25 ± 1°C and 16:8 photoperiod, were 68% long-winged (n = 1,067) (Fig. 1A). A significantly greater proportion of females was long-winged (78%; n = 521) than males (58%; n = 546) (χ^2 = 47; df = 1; $P < 0.001$). Seasonal differences in proportions of long- and short-winged individuals were moderate (males, χ^2 = 9.4; df = 3; $0.05 > P > 0.01$; females, χ^2 = 4.7; df = 3; $P > 0.10$).

When siblings of the laboratory-reared crickets were reared outdoors, only 55% developed long wings (n = 1,084) and seasonal differences were more pronounced (males, χ^2 = 6.6; df = 3; $0.10 > P > 0.05$; females, χ^2 = 39; df = 3; $P < 0.001$) (Fig. 1B).

When field-collected juveniles were reared outdoors, total macroptery dropped to 28% (n = 314), and males and females no longer differed in the proportion that were long-winged ($P > 0.90$). Seasonal differences were further increased (males, χ^2 = 20; df = 3; $P < 0.001$; females, χ^2 = 26; df = 3; $P < 0.001$) (Fig. 1C).

When juveniles that were collected earlier than the last two juvenile stadia were excluded from the data set, the percentage of long-winged crickets dropped still further (to 8%; n = 150) (Fig. 1D).

When adults were field-collected by hand (i.e., when possible effects of rearing were eliminated), the overall percentage of long-winged crickets became 3% (n = 383) and differences among seasons were no longer significant for either males or females (males, χ^2 = 5.6; df = 3; $P > 0.05$; females, χ^2 = 2.6; df = 3; $P > 0.05$) (Fig. 1E).

Discussion. On the basis of hand-collected adults, long-winged morphs are only 3% of the natural *G. rubens* population at Gainesville (12 of 383 crickets in Fig. 1E). Nevertheless, hundreds of long-winged *G. rubens* were collected each winter and spring and thousands each summer and fall by a single sound-baited trap (Fig. 1F; Walker 1986b). Why hand-collecting yielded so few long-winged morphs is not known, but outdoor rearing confirms that long-winged individuals can mature outdoors at any season (Fig. 1B). The fact that the proportion of long-winged morphs produced outdoors increases each time the duration of confinement in a jar increases (Fig. 1 B–D) suggests that effects of confinement (abundant food? crowding?) are cumulative. More hand collecting and at a greater variety of sites should give a more representative sample of long-wingedness in natural populations. Veazey et al. (1976) used pitfall traps to collect *G. rubens* in fields 200 km northwest of Gainesville and caught much higher proportions of long-winged morphs than I found in Gainesville: winter, 1%; spring, 12%; summer, 36%; fall, 30%.

That females exceed males in proportions of long-winged individuals is consistent with females' being capable of colonizing new habitats without males accompanying them. No sexual differences in long-wingedness in field-collected adults were apparent in this study (Fig. 1E), but Veazey et al. (1976) reported that female *G. rubens* trapped in pitfalls were significantly more likely to be long-winged than were males (36 versus 26% in samples of ca. 2,086 males and 2,892 females trapped 17 June–27 October 1969–73). Roff (1986a; personal communication) compared percentage of macroptery for males and females in five species of crickets and in >45 other species of insects. In the crickets, values for females exceeded those for males, but in the other species no pattern was apparent.

Section 2. Flight in Long-winged Morphs

Long-winged morphs have the external equipment required for flight and large numbers do fly (Fig. 1F). However, what proportion ever fly, how long or how far they fly, how often they fly, and during what period or periods of their adult lives they fly are unknown for *G. rubens* and for other species of *Gryllus* having long-winged morphs (Walker & Sivinski 1986).

A technique for addressing some of these questions, and results of preliminary tests, are described below.

Methods. In each of four tests, crickets were placed in four cages built to monitor flight (Fig. 2) and provided pieces of egg carton for shelter, vials of water, and food and oviposition dishes. In some treatments the dishes were left empty and in some they were kept filled with food (Purina Cricket Chow) and damp sand, respectively. The sex ratio of the crickets in each container was 1:1. Cages were checked daily. Individuals at the bottom of the outer can were recorded as having flown the previous night and were returned to the inner container.

For the first and fourth tests, progeny of field-collected females were reared in the laboratory. When the crickets were nearly mature, the rearing jars were checked daily. Adults were removed, marked with dots of Tech-pen ink on the pronotum for individual recognition (Wineriter & Walker 1984), and placed in one of the flight-test cages. The crickets were monitored for flight until dead or until none had flown for 3 wk.

In the initial test, beginning 5 October 1985, 4, 16, and 64 long-winged individuals and 64 short-winged individuals were transferred to the four cages, and food and damp sand were supplied to all. The cages were kept in an open shed that protected them from sun and rain, yet provided near-natural light and temperature. In this test none of the short-winged crickets made it to the outer con-

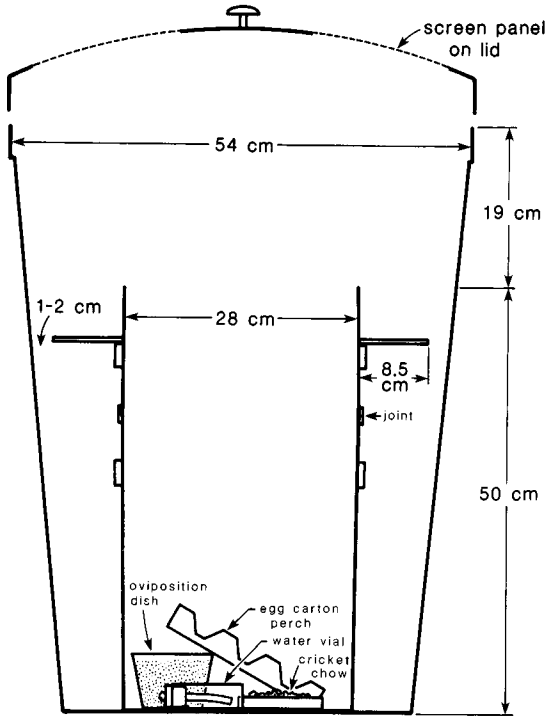

Fig. 2. Cross-section of flight-test cage. Inner cylinder is a 19-liter plastic bucket with a partial, bottomless second bucket inverted and taped to it (at "joint"). The outer container is a plastic garbage can. Crickets that flew could reach the bottom of the garbage can but were prevented from flying back to the top (and possibly returning to the inner container) by a plastic ring that projected 8.5 cm from the circumference of the inner container.

tainer, confirming that crickets could not leap or crawl from the inner container and justifying the elimination of short-winged crickets, as controls, from subsequent tests. Because only 7% of the long-winged crickets flew, all from the 64-cricket cage, the lowest density was dropped in subsequent tests and treatments were added in which neither food nor ovipositional medium was supplied. For the final three tests, the four treatments were 16 and 64 long-winged crickets with and without food and damp sand.

The second and third tests, beginning 5 and 14 September 1986, used crickets that had been captured as they flew to synthesized calling song in a pasture (Walker 1986b). Unlike the reared crickets, these crickets were of unknown age but proven fliers. Daily monitoring was ended after the seventh night of confinement.

The third test was moved indoors to determine if results at 25°C and 16:8 photoperiod would be similar to those in the shed. They were; and the final test, beginning 2 December 1986 and using reared progeny of field-collected females, was indoors.

Table 1. Pooled results of three tests for flight in long-winged *G. rubens*

Comparison	*n*	% that flew
Source of crickets[a]		
Reared	160	10
Captured in flight	320	44
Sex[a]		
♂	240	25
♀	240	41
Food and damp sand[a]		
Yes	240	25
No	240	40
Density (NS)		
16/flight cage	96	32
64/flight cage	384	33

[a] $P < 0.001$; NS, not significant; χ^2.

Results. The percentages of long-winged crickets that flew in the four tests were 7, 42, 47, and 10, respectively.

Reared crickets first flew as early as age 5 d and as late as age 14 d; mean first flight was at 8 d. Reared crickets that flew, often did so on more than one night (range, 1–6; mean = 2.2 d) and over a period as long as 19 d. The oldest flier was 28 d old; mean last flight was at age 12 d. Median survival of reared crickets with food was 7–9 wk; without food, ca. 3 wk.

Crickets trapped in flight that flew again when put in the flight-test cages did so an average of 2.1 nights during the seven nights of observations. Of 142 first flights, 55 (39%) were on the first night.

During the outdoor tests, at least 95% of the nights were suitable for flight, as shown by catches of flying *G. rubens* in nearby traps (Walker 1986b). Table 1 summarizes the results of the three tests that included comparisons of crickets held with and without food and damp sand.

Discussion. The comparison of reared and captured crickets in Table 1 is weak because the tests were not run simultaneously. However, if all tests are considered, the two using reared crickets had much lower percentages flying (7 and 10%) than the two using captured crickets (42 and 47%).

That long-winged females are significantly more likely to fly than long-winged males (Table 1) can be viewed as extending the finding that females are more likely to be long-winged (Fig. 1). That flight is more likely in the absence of food and ovipositional medium is clearly adaptive. That no significant difference in the percentage flying occurred between 16 and 64 animals per test cage suggests that both densities are high enough to promote flight or that flight in long-winged crickets is not sensitive to density.

The low percentage of flight in reared long-winged *G. rubens* was surprising. Perhaps it is pertinent that most reared crickets would not have been long-winged had they not developed in con-

tainers (Fig. 1). Dingle (1985) summarized a variety of instances in which a portion of macropters never fly. For example, Shaw (1970) found that 1–4% of alate bean aphids did not fly from the laboratory host plants on which they matured, and Dingle et al. (1980) reported that 30% of (macropterous) *Oncopeltus fasciatus* (Dallas) from Guadeloupe did not perform in laboratory flight tests.

Long-winged morphs in *Gryllus* generally bear their metathoracic wings throughout their adult lives, but in many other crickets the wings are shed after the period when flight occurs (Masaki & Walker 1987). After dealation wing muscles may be histolyzed, reducing the cost of maintenance and making the material available for other uses. This implies that long-winged individuals that do not fly may lack the needed flight muscles and that the ontogeny of flight behavior might have morphological correlates detectable by dissection. D. Roff (personal communication), in investigating the effects of artificial dealation, dissected 10 intact long-winged *G. firmus* females of each of three ages. He found 10 with well-developed flight muscles at age 0, 6 at age 4 d, and 4 at age 7 d.

Section 3. Genetic Basis of Dimorphism

In some species of *Gryllus* all individuals are short-winged, whereas in others all are long-winged. When such species are reared in the laboratory under standardized conditions or in the field under a shelter, they maintain their distinctive wing lengths, demonstrating that in these cases genetic differences rather than environmental differences are responsible for the development of long or short wings (Walker & Sivinski 1986). Furthermore, Harrison (1979) and Roff (1984, 1986a) have experimentally established that genetic differences are partly responsible for development of long- or short-winged morphs in the dimorphic species *G. firmus*. (Harrison's "lowland *pennsylvanicus*" was *firmus* [Harrison & Arnold 1982].)

The studies reported here demonstrate that genetic differences also contribute to wing dimorphism in *G. rubens*.

Methods. To determine if females of *G. rubens* differ in the proportions of long- and short-winged progeny they produce, I reared progeny of 28 field-collected females in the laboratory at 25 ± 1°C and 16:8 photoperiod as described in section 1. Spearman's rank correlation procedure (Zar 1984) was used to test whether propensities of a female to produce long-winged sons and long-winged daughters were correlated.

To investigate the effects of selection on the proportion of long-winged morphs in *G. rubens*, I established two laboratory lines from crickets collected at Gainesville, Fla., on 8 March 1983. A long-wing-selected line (designated L × L) was started with five males and nine females that had flown to a sound trap (Walker 1986b). A short-wing-selected line (S × S) was started with eight short-winged individuals, four of each sex, collected at an organic gardening site on the University of Florida campus.

All rearing was in a controlled-environment room set at 25°C, 65% RH, and 16:8 photoperiod. Two rearing methods were used. (For details, see Wineriter & Walker 1987.) In group rearing, a group of 10–110 hatchlings (usually 50) was transferred to a 4-liter glass jar containing 900 ml of moist sand. Each jar had a food dish, a water vial, and a roost, and was covered by a screen lid. Four to 17 (mean = 8) group-rearing jars were set up for each line in each generation. During the first three generations, group-reared crickets were fed ground Purina Dog Chow; for the final five generations, they were fed Purina Cricket Chow. Jars were tended weekly, and adults were removed as they matured. In single rearing, a hatchling cricket was transferred to a 30-ml plastic container one-third to one-half full of pinto-bean diet and secured with a cardboard lid. When the diet became dry or moldy, the cricket was transferred to a new container. Four to six transfers were required before the cricket matured. Containers were checked weekly during the maturation period. For most generations, 75 hatchlings from each strain were used to initiate the individual rearing. Only once were fewer than 40 used (F_7, L × L, because of shortage of hatchlings). Each succeeding generation was generally started from a single group of group-reared parents. Exceptions were the use of singly reared parents to found the F_3 and F_4 generations and the use of both types to found the F_5. The number of parents used to establish a generation was 4–14 during the first three generations and 31–54 for the last four generations. Sex ratio was generally 50:50. Selection was 100% in each generation: long-winged L × L males and virgin long-winged L × L females were mated to continue the L × L line, and similarly for the S × S line.

Beginning with generation F_3, reciprocal crosses were made between the two selected lines using long-winged individuals from the L × L line and short-winged individuals from the S × S line. From 1 to 25 of each sex were used for a cross. I attempted to rear singly 25–75 hatchlings from the (L × L male) × (S × S female) cross (= LL × SS cross) and similar numbers from the reciprocal (SS × LL) cross.

Adults from the sixth generation of selection were preserved in isopropanol and later measured as described by Walker & Sivinski (1986).

Results and Discussion. For 13 of the 28-field-collected females, at least 10 male and 10 female progeny were reared under standard conditions in the laboratory, and macroptery ranged from 54 to 93% (Table 2). For male progeny the range was 36–82%, and for females, 61–100%. Of the 923 laboratory-reared progeny of the 13 females, 68% were long-winged; males and females were 57 and

Table 2. Percentage of long-winged crickets among laboratory-reared progeny of 13 field-collected females

Female code[a]	No. progeny		% long-winged		
	♂♂	♀♀	♂♂	♀♀	All
73-8 (SW)	30	46	43	61	54
75-8 (SW)	42	27	43	70	54
72-7 (LW)	29	19	48	79	60
75-5 (LW)	90	55	52	75	61
75-6 (SW)	39	45	36	84	62
75-3 (SW)	50	51	64	65	64
72-1	34	35	68	69	68
72-2	23	26	61	81	71
71-5	41	46	61	89	76
72-18 (SW)	45	49	73	94	84
71-15	20	27	75	93	85
71-6	15	12	80	100	89
74-1 (SW)	11	16	82	100	93
All	469	454	57	79	68

[a] Year, number, morph. (Morph of mother was not recorded in earliest rearing experiments. Morphs of fathers were not known because females mated before collection.)

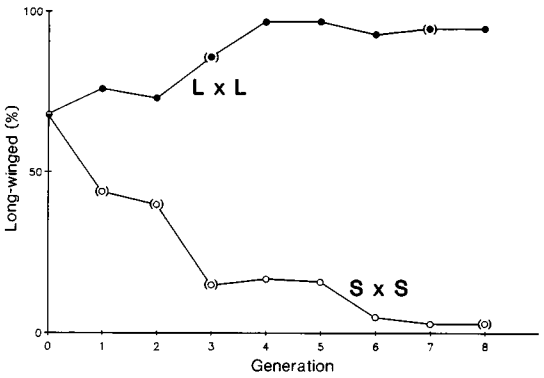

Fig. 3. Result of 100% selection for long- and short-winged morphs of *G. rubens* for eight generations. Values are averages of single- and group-rearing results (Table 3). (Points in parentheses include one estimated value.) Generation 0 (68%) is based on the crickets reported in Fig. 1A.

79% macropterous, respectively. χ^2 tests showed that the females differed significantly in the proportions of their sons, daughters, and total progeny that were long-winged (χ^2 = 31, 40, 53; df = 12; $P < 0.005$, 0.001, 0.001). Furthermore, the ranks of females in their propensity to produce long-winged sons were significantly correlated with their propensity to produce long-winged daughters ($r_s = 0.614$; $0.05 > P > 0.02$; Spearman rank correlation test).

These data suggest that genetic differences are important in determining morph frequencies within *G. rubens* sibling cohorts. The fact that the morph of the mother was of no value in predicting the rank of her progeny in the percentage of long-winged crickets (Table 2) is not surprising in view of the small sample and lack of knowledge about the morphs of the fathers.

After eight generations of selection the L × L line was ca. 95% long-winged, and the S × S line 98% short-winged (Fig. 3; Table 3). No progress was evident in the L × L line after generation 4, nor in the S × S line after generation 7.

Reciprocal crosses between lines showed that genetic control of macroptery was primarily or solely on the X chromosome (Table 4). In the SS × LL crosses, males were nearly always (>99%) long-winged like their mothers. In the LL × SS crosses, males were usually (89%) short-winged, like their mothers. In both crosses females were nearly equally divided between long- and short-winged morphs. The proportion of males that were long-winged in the SS × LL crosses did not differ significantly from the proportion of males that were long-winged in the singly reared component of the last four generations of L × L crosses, when compared generation by generation or by summing the generations. Likewise, the proportion of males that were long-winged in the LL × SS crosses was similar to the proportion of males that were long-winged in the singly reared component of S × S generations 5–8. For LL × SS males the proportion of long-winged crickets for generations 5–8 summed was 0.11 (9/82); for singly reared S × S males it was 0.09 (10/115) ($\chi^2 = 0.084$; df = 1; $P > 0.75$).

The fact that the number of long-winged female progeny of LL × SS and SS × LL crosses did not differ significantly from 0.50 (Table 4) refutes the hypothesis that long wings are determined by X-linked dominant alleles, which could have accounted for females being long-winged more frequently than males. Without additional crossing data, further speculation about detailed genetic mechanisms is unprofitable.

A. Zera (personal communication) crossed independently selected L × L lines of *G. rubens* from Gainesville, Fla., with my S × S line. He too concluded that X-linkage contributed strongly to the interline genetic differences, but his results were interestingly different from mine. In crosses with an L × L line that he had started from a single female, the differences behaved as though determined by two alleles at a single X-linked locus, with the allele for short wings dominant to the one for long. (Specifically, LL male × SS female gave all short-winged progeny; SS male × LL female gave males all long-winged and females all short-winged; [SS × LL] or [LL × SS] female × LL male gave both males and females ca. 50% long-winged and 50% short-winged.) When he made crosses using parents from a mass-selected L × L line, the results were intermediate between my results and his initial results.

Dingle (1985) summarized previous studies of the genetics of wing polymorphisms in insects. Few species had been investigated and in no case had the genetics of dimorphism within a naturally dimorphic population been well worked out. Dingle

Table 3. Percentage of macroptery (and number of individuals scored) for eight generations of 100% selection for long-winged morphs (L × L) and for short-winged morphs (S × S) in *G. rubens* reared both singly and in groups

Generation	L × L line		S × S line	
	Single % (*n*)	Group % (*n*)	Single % (*n*)	Group % (*n*)
1	84 (25)	67 (48)	*50* [—(0)][a]	38 (45)
2	91 (55)	55 (53)	50 (26)	*29* [20 (5)]
3	98 (64)	*74* [21 (14)]	10 (42)	*19* [0 (10)]
4	100 (54)	93 (361)	23 (26)	10 (206)
5	100 (39)	94 (154)	29 (35)	3 (157)
6	98 (47)	88 (165)	7 (60)	3 (170)
7	*98* [80 (5)]	91 (132)	2 (60)	3 (74)
8	99 (68)	91 (65)	2 (60)	3 [0 (16)]

[a] When $n < 20$, values were estimated by linear interpolation or extrapolation from adjacent generations. Actual percentages and (*n*) are in brackets.

concluded that gene/environment interactions should be evaluated more carefully in future genetic analyses. In Roff's (1986a) and my studies of the genetics of wing dimorphism in *Gryllus*, we tried to minimize the effect of gene/environment interactions by working under controlled, constant temperature and photoperiod, except when an environmental variable itself was being studied.

Roff (1986a) concentrated on estimating the heritability of long or short wings in an unselected stock of *G. firmus* under conditions that favored dimorphism (and maximal heritability). At 30°C and a 17:7 photoperiod, he found heritability of 0.62 for males and 0.68 for females. He looked for maternal effects but found none. In crosses between wing morphs the percentage of macroptery among offspring was similar whether the male or the female parent had the long wings. These results suggest that *G. firmus* does not share with *G. rubens* the X-linkage of morph-determining alleles. However, as Roff was not crossing crickets from nearly pure-breeding long- and short-winged lines, X-linkage might have been masked by other determinants of macroptery. (Indeed, A. Zera [personal communication] made reciprocal crosses of the long- and short-winged progeny of field-collected *G. rubens* and, like Roff, found no evidence of X-linkage.)

Sex linkage has been found in the genetic basis of migration or dispersal in several other insects (reviewed by Dingle [1985]). Both male and female heterogametic species are involved, and no theoretical reason for sex linkage is apparent.

I evaluated the possibility that selection for 100% long- and short-winged crickets would change the relative length of the metathoracic wings within a morph by measuring 332 F_6 individuals and comparing the measurements with those of 316 reared progeny of field-collected females. The F_6 crickets included subgroups reared singly and in groups and under 16-h and 11-h photophases. Before combining measurements for the same morph reared under different conditions, I tested for differences in mean hindwing/forewing ratios but found none (*t* test; $\alpha = 0.05$). Hindwing/forewing ratios, which scale the length of the hindwing against the length of the forewing, were similar for all groups of long-winged crickets measured and for all groups of short-winged crickets measured (Table 5). Specifically, the measured morphs of the L × L line did not differ significantly from the corresponding morphs of unselected crickets. On the other hand, short-winged males and females, the only morphs measured from the S × S line, had modestly but significantly greater mean ratios (and significantly longer hindwings) than the unselected crickets.

Section 4. Environmental Influences on Dimorphism

Environmental factors, such as density of conspecifics (crowding) and photoperiod, are often important in determining the proportions of long- and short-winged morphs in wing-dimorphic crickets, including *Gryllus* spp. (Masaki & Walker 1987). Consequently, I tried to maintain the same environment throughout the selection experiments. One reason for rearing a portion of the crickets singly was to control crowding. In group-reared crickets

Table 4. Proportion of long-winged crickets in reciprocal crosses between L × L and S × S selected lines, F_5 through F_8, singly reared (no. long-winged/total)

	(L × L ♂) × (S × S ♀)		(S × S ♂) × (L × L ♀)	
	♂♂	♀♀	♂♂	♀♀
F_5	2/9	10/14	42/42	12/24
F_6	1/30	12/26	17/18	4/7
F_7	4/12	4/9	30/30	16/31
F_8	2/31	9/25	38/38	14/28
F_{5-8}	9/82[a] (11%)	35/74[b] (47%)	127/128[a] (99%)	46/90[b] (51%)

[a] Males significantly different from females in proportion long-winged and significantly different from 0.50 long-winged ($\alpha = 0.05$; χ^2).

[b] Females not significantly different from 0.50 long-winged ($\alpha = 0.05$; χ^2).

Table 5. Hindwing/forewing ratios and (*n*) of morphs of *G. rubens*

Line or cross	Generation	Long-winged[a]		Short-winged[a]	
		♂	♀	♂	♀
Unselected	F_1[b]	1.60a (80)	1.55a (118)	0.74a (63)	0.77a (55)
L × L	F_6	1.60a (70)	1.57a (55)	0.73a (39)	0.77a (24)
S × S	F_6	—[c]	—[c]	0.78b (74)	0.82b (70)

[a] Means in the same column followed by the same letter are not significantly different (t test; $\alpha = 0.05$).
[b] Same specimens as reported by Walker & Sivinski (1986), except that field-collected specimens are excluded.
[c] —, <10 specimens available.

different numbers of adults matured per jar, even though the number of hatchlings started per jar was standardized at 50 by generation 4. These variations make crowding potentially important for interpreting the results of group rearing.

The original intent of the selection program was to develop lines that were 100% long-winged and 100% short-winged (at 25°C, 16:8 photoperiod) and then to test the lines under varied indoor and outdoor conditions to determine if the selected genotypes would produce the alternative phenotypes. By generation 6 it was evident that 100% would not soon be reached in either line, and tests were begun to see if short days would modify the proportions of the two morphs.

Crowding

I did no direct tests on the effects of crowding on wing dimorphism in *G. rubens*, but I had the opportunity to observe such effects during studies that incidentally resulted in varied densities. These observations suggest to me that crowding in the field and in rearing cages is so different in quantity or quality that increases in density in the two situations may produce effects of opposite sign.

Evidence that field densities are generally associated with low percentages of macropters is reported in section 1. Outdoor rearing in 4-liter jars (surely more crowded than field conditions, but also different in food amount and kind, etc.) significantly increased the proportions of long-winged individuals (Fig. 1), suggesting that increases in usual field densities would also increase the proportions of long-winged individuals.

Among crickets reared in confinement, the greatest contrast in exposure to other crickets was between singly and group-reared crickets in the selection study: the former were reared in solitude, whereas the latter crickets, from the same parents, were exposed to other crickets throughout their development. When samples of 20 or more were available for comparison, singly reared crickets generally exceeded group-reared crickets in the proportion that were long-winged (9 of 10 cases in Table 3). This effect was not necessarily due to extent of exposure to other crickets, because both diet and container size were also different between group- and singly reared crickets. The effect of diet was controlled in an experiment with the SS × LL cross of generation 7. Pinto-bean diet was dried, ground, and substituted for cricket chow in five jars of 50 hatchlings. Of the 97 males and 61 females that matured, 68 and 43% were long-winged. Of the 30 males and 31 females reared singly from the same cross, 100 and 52% were long-winged. For males and for males and females combined, singly reared crickets were significantly more frequently long-winged than were genetically comparable group-reared crickets ($\chi^2 = 11.0$ and 4.9; df = 1; $P < 0.05$). These results demonstrate that exposure to other crickets is not required to produce higher than usual proportions of long-winged individuals.

The only extensive crowding-relevant results for which container size and food (as well as temperature and photoperiod) were kept constant are from laboratory-reared progeny of field-collected females. The eggs laid by one female in 1 wk were hatched and reared in a 4-liter jar. The number of adults reared per jar is a measure of crowding and varied from 1 to 66. (Number reared per jar was not experimentally varied and depended chiefly on number of eggs laid and early juvenile mortality.) Arcsine-transformed proportions were regressed against number of adults maturing per rearing jar to reveal what effect this measure of crowding had on the proportion of males and of females that were long-winged. In neither case did the regression coefficient differ significantly from zero. A third regression was made in which the data for males and females were combined: (arcsine$\sqrt{p_m}$ + arcsine $\sqrt{p_f}$)/2. It too showed no significant effect of crowding (Fig. 4).

In the absence of proven effects of crowding within the range of densities encountered by my group-reared crickets, I made no corrections for density in interpreting the results reported in this paper. However, in tests using his mass-selected L × L line of *G. rubens*, Zera (personal communication) found that crowding greatly affected wing dimorphism. When he reared 60 per 38-liter aquarium (the density maintained during selection), >90% were long-winged. When he reared five per 470-ml cup, 20% were long-winged. When he reared one per 235-ml cup, 95% were long-winged. Food, photoperiod, and temperature were held constant.

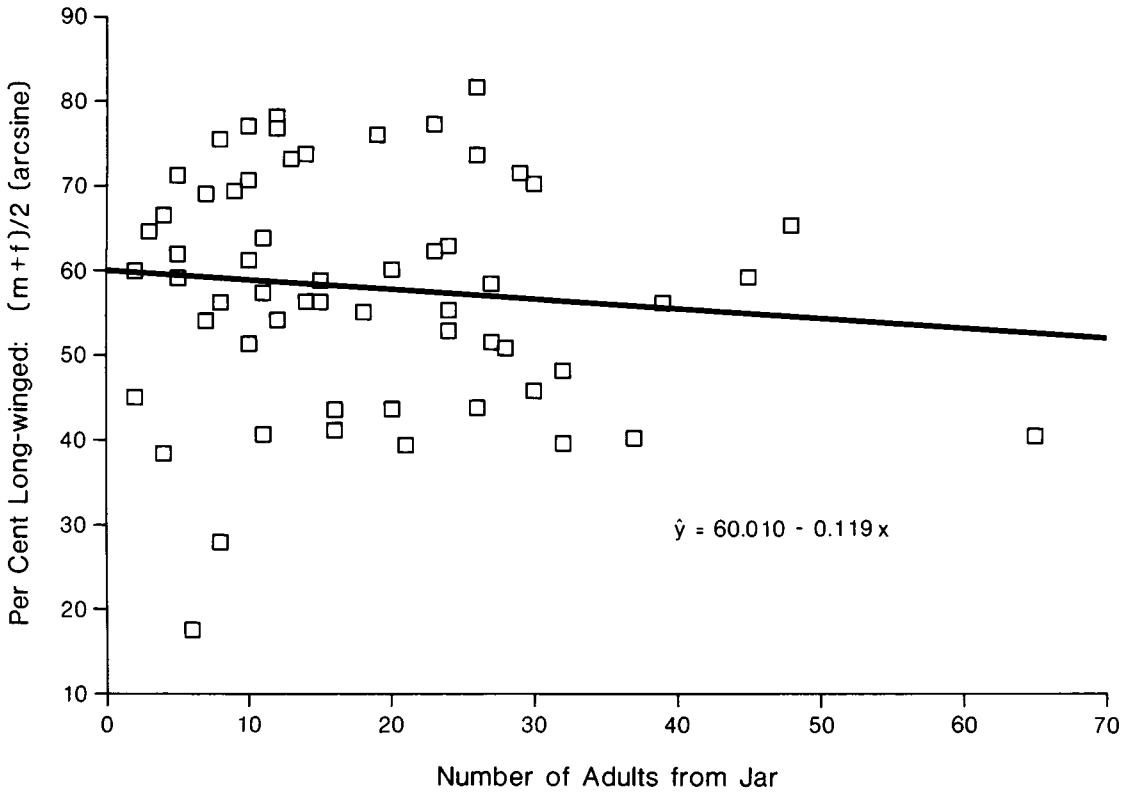

Fig. 4. Regression of average proportion of long-winged crickets $[(p_m + p_f)/2]$ against number of adults maturing from jar. (Proportions were arcsine-transformed before averaging.) Regression was not significant ($P > 0.05$).

Photoperiod

Methods. In generations 6–8, crickets from both selected lines were reared in short (11:13) and long (16:8) photophases. Short-day treatments were in a photoperiod chamber and long-day treatments were in a matching chamber (F_{6-7}) and in the main rearing area (F_{6-8}). The crickets were exposed to the treatment photoperiods during their entire development, except that eggs were as old as 7 d when transferred to the chambers from the main rearing area, and that in generations 7 and 8 a portion of the juveniles were transferred during the last three stadia from short-day to long-day conditions, to determine when during development short days had their effect. Crickets in the photoperiod tests were group-reared (F_{6-8}) and singly reared (F_8).

The photoperiod chambers were in the main rearing room and the temperatures within were kept at 25 ± 1°C by fans drawing air from the room through the chambers. Heating by the fluorescent lights was minimized by housing them behind glass in blower-ventilated compartments.

Results. Long-day crickets reared in the long-day photoperiod chamber and crickets reared simultaneously in the main rearing area (which had the same long-day photoperiod) showed no differences in proportions of long-winged crickets, and rearing data from the two places were combined.

Short days produced a significant decrease in the proportion of long-winged individuals in the L × L line (Table 6). For males the mean percentage dropped from 86 to 45 for group rearing, and from 98 to 73 for single rearing. Corresponding values for L × L females were 95 to 55 and 100 to 57. In tests of S × S crickets, short-day-reared males and females were less frequently long-winged, but the differences between treatments were not significant (Table 6).

When juveniles were transferred from short to long days, those transferred as penultimate and antepenultimate instars did not differ significantly in the percentage becoming long-winged from those reared entirely under long days (Table 7). On the other hand, those transferred as penultimate and final instars did not differ significantly from those that completed their entire development under short days. The last two or three instars are apparently the ones most sensitive to photoperiod. Any earlier effects of short days are largely negated by a transfer to long days before the final few stadia. Transfers during these stadia become less

Table 6. Effect of long days (16:8) and short days (11:13) on two lines of *G. rubens* selected for five or more generations under long days

Category	Long days		Short days	
	% long-winged	(*n*)	% long-winged	(*n*)
L × L ♂♂				
GR,[a] F_{6-8}[b]	86	(207)	45*	(119)
SR, F_8	98	(44)	73*	(22)
L × L ♀♀				
GR, F_{6-8}[b]	95	(155)	55*	(88)
SR, F_8	100	(24)	57*	(7)
S × S ♂♂ (all)	1	(174)	0	(105)
S × S ♀♀ (all)	6	(146)	5	(109)

*, $P < 0.05$; χ^2; proportion long-winged when reared under short days significantly different from proportion long-winged when reared under long days.

[a] GR, group reared; SR, singly reared.

[b] χ^2 tests for heterogeneity showed no significant differences in generations 6–8.

Table 7. Effect of transferring group-reared L × L, F_7 and F_8, *G. rubens* from short days (SD) to long days (LD)

Instar transferred[a]	♂♂ % long-winged (*n*)	♀♀ % long-winged (*n*)	(M% + F%)/2[b]
Egg (LD-reared)	87 (124)	97 (73)	92
Antepenultimate[c]	94 (17)	79 (14)	86
Penultimate[c,d]	43 (14)	94 (16)	68
Ultimate[d]	62 (8)	58 (12)	60
Adult (SD-reared)	47 (66)	59 (44)	53

[a] The number of juvenile instars in *Gryllus* is indeterminate but is usually between 8 and 12. The terminal instars are easiest to distinguish because the degree of development of the wing pads changes with each molt. The penultimate instar is usually the earliest instar with conspicuous wing pads, and the ultimate instar has pads as long as the pronotum.

[b] M%, males percentage long-winged; F%, females percentage long-winged.

[c] If data for the antepenultimate and penultimate instars are combined to make the sample large enough for χ^2 analysis, neither males nor females are different ($P > 0.05$) from LD-reared crickets (of the same sex) in the proportion of long-winged crickets, but both are different from SD-reared crickets.

[d] If data for penultimate and ultimate instars are combined to make the sample large enough for χ^2 analysis, both males and females are different ($P < 0.05$) from LD-reared crickets (of the same sex) but neither are different from SD-reared crickets.

and less effective as the crickets approach maturity (Table 7, last column).

Discussion. Short days have been demonstrated to inhibit development of long wings in a variety of wing-dimorphic crickets (Masaki & Walker 1987). The only other tests with *Gryllus* were by Alexander (1968) on *Gryllus "integer,"* a close relative of *G. rubens*, and by Roff (1986a) on *G. firmus*. Because Alexander incorporated stepwise changes of photoperiod and temperature in his treatments, the results cannot be unequivocally attributed to photoperiod. His "short day" crickets were 0% long-winged (reared at photophases decreasing from 12 to ca. 9 h light), whereas his "long day" crickets were 95% long-wnged (reared, after 18 d, at photophases increasing from 14 to ca. 16 h light). Roff (1986a) divided 14 sibling cohorts of *G. firmus* between 17:7 and 12:12 photoperiods. The animals reared under 12-h days had substantially lower proportions of long-winged individuals than those reared under 17-h days. Under 12:12, males from 12 of the cohorts and females from 5 of the cohorts were 100% short-winged.

Other Environmental Influences

Two other environmental factors, temperature and food, probably influence the ontogeny of wings in *G. rubens*. Their influence, as well as that of crowding and photoperiod, might be partly by means of an influence on the developmental rate.

Temperature. Although I have no data for *G. rubens*, high temperatures probably increase the proportion that are long-winged. In studies of photoperiodic effects it is usual that high temperatures enhance long-day effects (in this case macroptery) and low temperatures enhance short-day effects (see Beck 1980). Such an effect has been demonstrated for two grylline crickets: *Gryllodes supplicans* (Walker) [="*sigillatus*"] (Ghouri & McFarlane 1958) and *G. firmus* (Roff 1986a). In the latter species, males were 0 and 21% long-winged at 25 and 30°C, respectively, and females were 16 and 57% long-winged at the same two temperatures ($n \geq 57$).

Food. Ghouri & McFarlane (1958) suggested that a poor diet inhibited the development of macroptery in a laboratory colony of *G. supplicans*. In generations 2 and 3 of my selecting for long- and short-winged *G. rubens*, rearing success for group-reared crickets plummeted (Table 3). Wineriter & Walker (1987) attributed this to inadequate food, because a change in diet solved the problem and subsequent tests supported this conclusion. In Table 3, there is a perfect correlation between abnormally low survival in group-reared crickets and a lower percentage of macroptery than estimated from adjacent values. If diet is investigated experimentally, it is important to determine to what extent the effects of diet on macroptery are through differential mortality of juveniles that are presumptively long- and short-winged.

Development Rate. High temperature and adequate diet generally increase rate of development and apparently increase the likelihood that a cricket will develop long wings. Alexander (1961, 1968) noted this correlation and ventured that accelerated development might be a crucial factor in the development of long wings. This notion can be tested by comparing maturation times of long- and short-winged crickets that were reared in the various component projects of this study.

The most relevant data are from rearing progeny of 28 field-collected females at 25 ± 1°C and 16:8

Table 8. Maturation periods (days; oviposition to final molt) for progeny of 28 field-collected *G. rubens* females reared in the laboratory at 25 ± 1°C and 16:8 photoperiod, or outdoors

	Laboratory[a]		Outdoors[b]			
			No developmental delay		Developmental delay	
	n	Maturation period ($\bar{x}$ ± SEM)	*n*	Maturation period ($\bar{x}$ ± SD)	*n*	Maturation period ($\bar{x}$ ± SD)
Male						
Long-winged	305	110 ± 1	178	136 ± 33	53	263 ± 13
Short-winged	211	117 ± 2	210	119 ± 26	60	258 ± 18
Female						
Long-winged	376	108 ± 1	270	131 ± 31	43	257 ± 16
Short-winged	99	115 ± 3	137	137 ± 30	44	259 ± 21

[a] Maturation times for long-winged and short-winged morphs of the same sex are significantly different ($P < 0.001$); between sexes they are not significantly different ($P > 0.05$; t test). ($F = 10.96$; df = 3,988; $P < .001$; ANOVA.)

[b] Temperatures strongly affect development rates and vary so much outdoors that maturation times outdoors were not statistically analyzed beyond determining means and standard deviations.

photoperiod (see section 1). Maturation time, in days, averaged 110 for long-winged males, 117 for short-winged males, 108 for long-winged females, and 115 for short-winged females (Table 8). Although the differences are not great, they are significant and in the direction predicted by Alexander's thesis. The distributions of maturation times in the laboratory (Fig. 5) reveal that some of the longer mean development times for short-winged crickets resulted from three individuals that took >30 wk to develop, a duration indicative of diapause. However, outdoor rearing of siblings of the crickets in Fig. 5 demonstrated that crickets that diapause are not necessarily short-winged. Development times of outdoor-reared crickets were much more heterogeneous than those of their laboratory-reared siblings, as would be expected with temperatures seasonally exceeding or falling far below 25°C. Nevertheless, the 995 maturation times were discretely bimodal, with 80% being ≤29 wk and the remainder ≥31 wk. The quick maturers were crickets that became adult in summer or fall, whereas the slow maturers were generally those that overwintered as juveniles and became adult the following spring. Even though crickets maturing in spring had taken, on average, nearly twice as long as summer or fall adults to develop, many were long-winged (Table 8; Fig. 1B). In fact, delayed development did not substantially reduce the proportion of long-winged adults. With delay, males were 47% long-winged and females 49%. Without developmental delay, males and females were 46 and 66% long-winged, respectively.

Another prediction following from Alexander's hypothesis that fast development leads to more macroptery is that the L × L line would have a faster rate of development than the S × S line. However, long-winged L × L crickets matured, on average, 5 d more slowly than short-winged S × S ones. A t test comparing mean maturation time showed that the differences were significant for both males and females ($P < 0.001$).

To summarize, fast development and macroptery are, at best, weakly correlated, and selection for and against macroptery had an effect on development opposite of that predicted by the correlation. Experimental intervention in the hormonal control of development should help clarify the relationship between rate of development and wing length.

Section 5. Overview

The first two sections of this paper addressed questions about the natural occurrence of flight dimorphism in *G. rubens:* what proportion of the natural population (at Gainesville) is macropterous, and what proportion of those that have the external equipment for flight actually fly? The data permit no confidence in estimates of the proportion of macropterous crickets but demonstrate that the proportion varies greatly with environmental circumstances. The proportion of reared long-winged individuals that fly during their lifetimes was examined in two experiments. Surprisingly, only 7 and 10% flew. On the other hand, in tests of wild long-winged individuals collected in flight, 44% flew again during the next seven nights.

The third section concerned the genetic basis of the dimorphism. At 25 ± 1°C and 16:8 photoperiod, with individuals crowded in jars or isolated in small cups, eight generations of 100% selection demonstrated that genetic differences contribute substantially to the polymorphism, that these differences are on the X chromosome, and that the wild genome is buffered against selection for either all long- or all short-winged individuals (both lines remained polymorphic).

The fourth section dealt with how the developing cricket's environment affects its adult wing length. Although it is easy to prove that environment influences wing ontogeny, it is difficult to relate laboratory findings to field conditions. For instance, photoperiod is evidently important, but

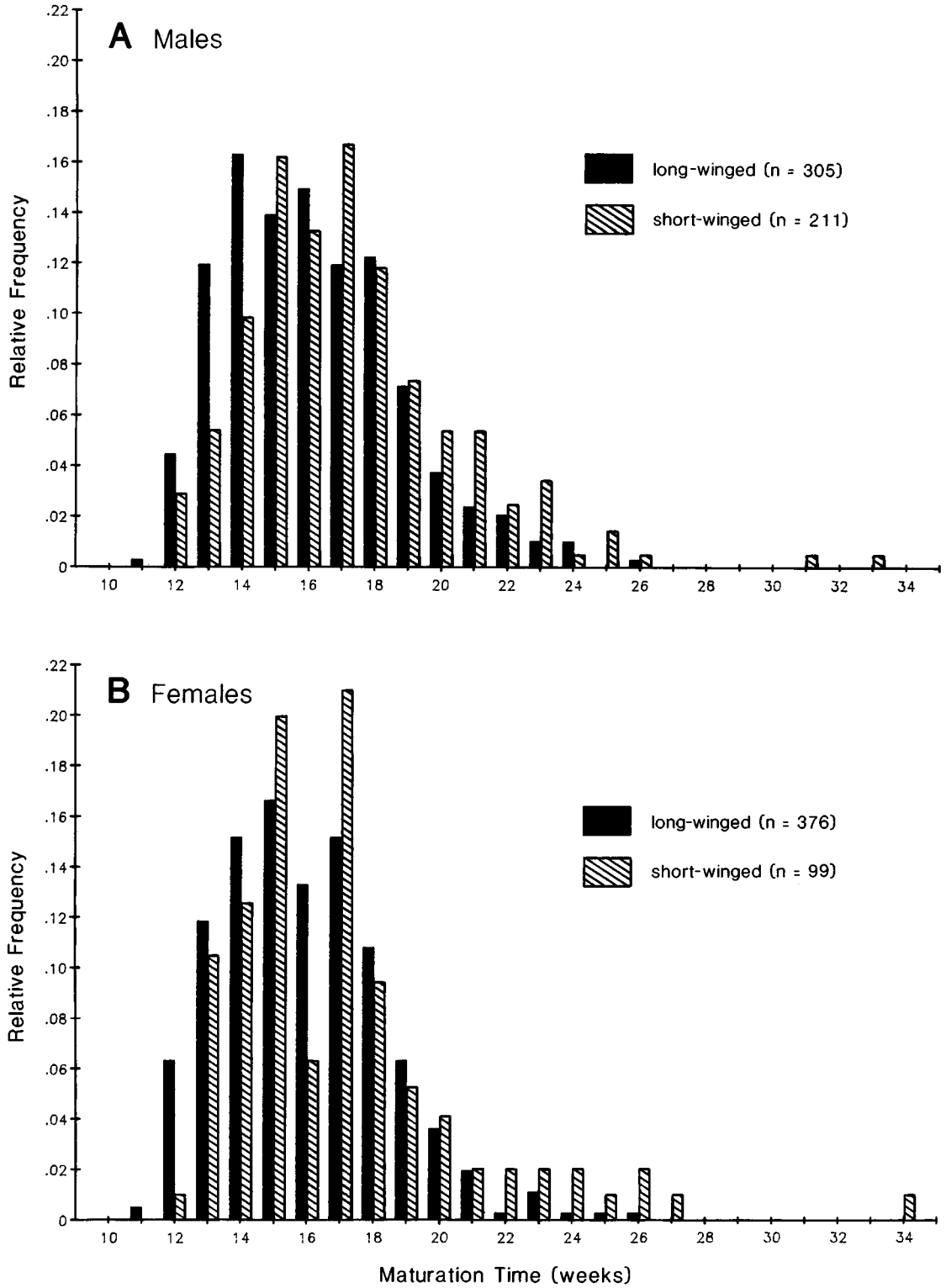

Fig. 5. Maturation times of progeny of 28 field-collected *G. rubens* females reared in the laboratory at 25 ± 1°C and 16:8 photoperiod. (A) Males. (B) Females.

the fact that wing development responds to differences in two-phase, unvarying photoperiods with no correlated temperature changes (when the cricket is confined to a rearing container) does not permit the responses of crickets in nature to be easily or safely predicted. The fact that stimuli associated with crowding are apparently important to developing and using long wings makes understanding field determination of macroptery and flight especially difficult to investigate under controlled conditions. Cages distort density-dependent interactions, and natural environmental causes of dimorphism may prove as elusive as natural percentages of macroptery.

Roff (1984, 1986a,b) and Dingle (1980, 1985) have recently addressed the adaptiveness of wing and flight polymorphism in insects. They point out that ability to fly is patently beneficial, although flying may not be. The benefits of being unable to fly are less obvious. Both authors noted that developing the machinery of flight may lead to decreased fecundity or delayed reproduction, or both, and they cite literature to illustrate that flightless morphs may outreproduce ones that can fly. Roff (1984) compared fecundity of the wing morphs within two species of crickets [*G. firmus* and *Allonembius fasciatus* (De Geer)] and found that egg production was delayed in macropterous females and that short-winged females of *G. firmus* had greater cumulative fecundity (even without permitting ecological mortality to penalize reproductive delay). A. Zera (personal communication) found that long-winged *G. rubens* females lay an average of 25% fewer eggs than short-winged females during their first 20 d. Both Roff and Dingle noted that macropters are able to colonize newly suitable sites and to leave deteriorating sites, and that the mobility of species generally correlates with the impermanence of their habitats. Walker & Sivinski (1986) remarked that species of *Gryllus* that occupy early successional stages are dimorphic or fully macropterous, whereas those that live in more permanent habitats have few, if any, macropterous morphs.

If wing dimorphism is viewed as a risk-spreading or bet-hedging adaptation to uncertain or heterogeneous environments, how can genetic systems evolve to effect it? One possibility is that dimorphism is not an adaptation but merely a consequence of inconsistent natural selection. At some times and places genes that determine long wings (and flight) are favored and at other times and places genes that determine short wings are favored. The population remains dimorphic because selection never eliminates the genetic determiners of either morph. A more stable sort of genetic polymorphism would exist if selection were frequency-dependent, with each morph being favored as it becomes rare. It is difficult to see how frequency dependence would work within a local population if macropters leave and short-winged individuals stay. On the other hand, in an aggregation of local populations the average success of macropters could increase as their frequency diminishes. Whatever the means by which genetic differences are maintained that cause alternative wing morphs to develop in Gainesville *G. rubens*, they are only a part of the causation of the dimorphism.

The other part of morph determination depends not on genetic differences between individuals but on a given set of genes responding to nongenetic differences to produce the different morphs (polyphenism [Mayr 1963]). Some polyphenism is "predictive" (Cooper & Kaplan 1982) or "conditional" (Walker 1986a) in that the appropriate morph is produced in response to different environmental conditions that correlate with future circumstances that will favor one morph or the other. For example, long days may signal the coming of good flying weather and much newly available suitable habitat, and short days may signal cold nights and contracting suitable habitat, thereby selecting for genotypes that develop long wings in long days and short wings in short days. In the absence of environmental correlates of future conditions (when the future of the present habitat patch is truly uncertain or when the future state of other habitat patches cannot be predicted by conditions in the present habitat patch), another type of polyphenism is adaptive.

Cooper & Kaplan (1982) and Walker (1986a) showed that when future environments are uncertain, genotypes that probabilistically determine phenotype may be superior. They termed such a phenomenon "adaptive coin-flipping" or "stochastic polyphenism" and addressed the important issue of how a genotype could be stochastic in effect. There is noteworthy empirical evidence for stochastic genotypes in aphids, and the data here presented are compatible with these genotypes' contributing significantly to wing-morph determination in *G. rubens* (Walker 1986a). Specifically, cricket genotypes that produce a mixture of wing morphs should have a greater probability of representation in future generations than those that produce all long- or short-winged individuals. A consequence of stochastic polyphenism is that selection for pure breeding strains is thwarted. All stochastic alleles must be eliminated, and that is difficult because they are carried by both morphs.

The refractory nature of the wing dimorphism in *G. rubens* can also be attributed to a complex genetic polymorphism, in which many loci contribute to determining the level of some continuous variable that must reach a threshold before one morph develops rather than the other (Falconer 1981). If the polygenes involved include some that are closely linked and of opposite effect, selection could not quickly move the system away from the threshold range (Walker 1986a). I am not sure how to distinguish such a system of closely linked polygenes from a supergene of stochastic effect. How-

ever, there is a possibility of proving whether genetic variation is essential to wing dimorphism in *G. rubens*. In some animals, including mice and guinea pigs, inbreeding has been used to establish homozygous strains (e.g., Wright & Chase 1936). If such strains were developed in *G. rubens* and remained wing dimorphic, genetic polymorphism would be demonstrated as unnecessary to produce the phenomenon. (I established four brother/sister-mated lines but lost all by the sixth generation. All were dimorphic when lost.)

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