Wing Dimorphism in Field Crickets
(Orthoptera: Gryllidae: *Gryllus*)

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ABSTRACT   Adult *Gryllus* are either short-winged (hind wings [HW] shorter than fore wings [FW]: HW/FW < 1) or long-winged (HW/FW > 1). Short-winged individuals are flightless, whereas long-winged individuals generally can fly. Hind wings are not shed after flight. Of five species occurring in peninsular Florida, *G. ovisopis* Walker is always short-winged (mean value of HW/FW ratio = 0.5), *G. fultoni* (Alexander) is virtually so (for short-winged morph, mean HW/FW = 0.6), *G. assimilis* F. is always long-winged (mean = 1.5), and *G. firmus* Scudder and *G. rubens* Scudder are dimorphic (mean = 0.8 and 1.6 for short- and long-winged morphs, respectively). In the four Florida species that have short-winged morphs, short-winged males had HW/FW ratios 5–15% less than short-winged females. In long-winged *G. firmus* and *G. rubens*, HW/FW ratios differed according to female parentage. In short-winged *G. rubens*, HW/FW ratios increased with body size (as measured by length of pronotum and hind femur).

WING POLYMORPHISM in insects is of interest to those concerned with dispersal, investment patterns, sexual tactics, and genetics (e.g., Matsuda 1979, Harrison 1980, Roff 1984). Crickets of the genus *Gryllus* are attractive subjects for studying this phenomenon because they not only vary in the occurrence of long- and short-winged morphs (within and between species) but are also large, widely distributed insects that are easily collected and reared.

Studies of wing dimorphism in *Gryllus* have been few. Sellier (1954) intensively studied *Gryllus campestris* L. (<1% long-winged) and reported measurements of *G. bimaculatus* DeGeer (100% long-winged). Fuzeau-Braesch (1961), investigating the effects of individual and group rearing, reported three South American *Gryllus* to be dimorphic and one monomorphic: *G. capitatus* Saussure (ca. 10% long-winged), *G. argentinus* Saussure (ca. 20%), *G. peruviensis* Saussure (ca. 50%), and *G. assimilis* F. (100%). Alexander (1968), in a review of cricket life cycles, reported the following as approximate percentages of long-winged individuals, in the field, for six U.S. species of *Gryllus*: *G. vernalis* Blatchley, 0%; *G. fultoni* (Alexander), 0%; *G. veletis* (Alexander & Bigelow), 4%; *G. pennsylvanicus* Burmeister, 4%; *G. rubens* Scudder, 8% (overwintering as juveniles) and 75% (directly maturing); *G. firmus* Scudder, 14% (spring), and 18% (fall). He did not report the geographical origins of his samples nor the method(s) of collecting. Veazey et al. (1976) analyzed three *Gryllus* species collected in pitfalls during a 3-year study in north Florida: *G. ovisopis* Walker (0% long-winged), *G. rubens* (0–52% long-winged,

varying seasonally), and *G. firmus* (0–28% long-winged, varying seasonally). Harrison (1979) studied wing dimorphism in "*G. pennsylvanicus*," including populations of both *G. pennsylvanicus* and *G. firmus* (Harrison and Arnold 1982). His field samples of verified (i.e., "Northern") *G. pennsylvanicus* were <3% long-winged; those of verified *G. firmus* (i.e., "Lowland *G. pennsylvanicus*") were 3–14% long-winged. Roff (1984), studying a laboratory colony of *G. firmus*, found that the progeny of long-winged parents were significantly more likely to develop long wings than were progeny of short-winged parents and that short-winged females were more fecund than long-winged ones.

This report deals with wing length in five *Gryllus* species occurring in peninsular Florida. It includes two species that are never long-winged in the field (*G. ovisopis* and *G. fultoni*), one that is always long-winged (*G. assimilis*), and two that are the most extensively dimorphic *Gryllus* known (*G. rubens* and *G. firmus*). We made detailed measurements of wing length and body size and investigated the following factors as sources of individual variation in relative length of the hind wings within a morph: species, sex, female parentage, rearing conditions, and season.

We use the term "short-winged" to denote crickets that have hind wings completely concealed by the overlying fore wings (Fig. 1). Such crickets cannot fly. Crickets that have hind wings extending (at rest) beyond the fore wings can generally fly and are here termed "long-winged." Alexander (1968) used the same criterion for distinguishing *micropterous* and *macropterous* crickets. Sellier (1954) and other French workers writing of wing polymorphism in crickets have divided our short-winged category into *brachyptère* (hind wings with veins; fore wings normal or reduced)
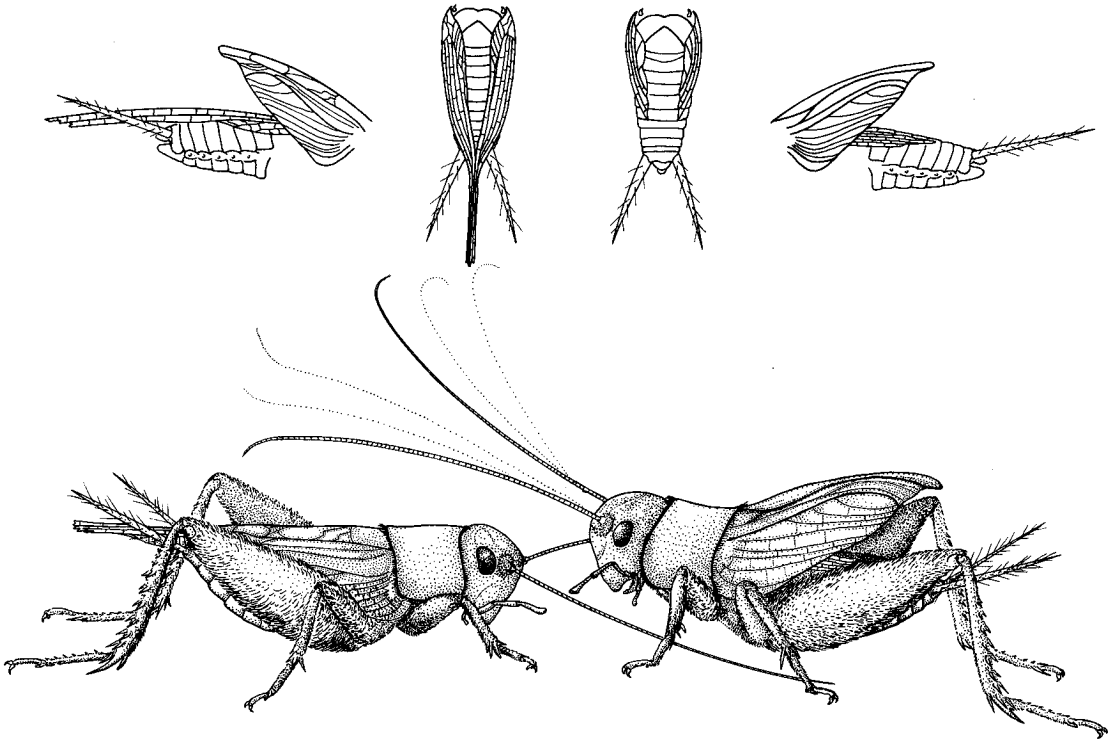
Fig. 1. *G. rubens.* (Bottom) Short-winged male (right) attacking long-winged male (left). (Top) Dorsal and lateral views of wings of respective males. In dorsal views tegmina are removed; in lateral views tegmina are in calling position (drawings by Amy Petty).

and *microptère* (hind wings without veins; fore wings reduced). By these criteria all short-winged *Gryllus* are *brachyptères* and all long-winged ones are *macroptères.*

Some long-winged crickets shed their hind wings after flight, becoming *dealated.* Dealated and short-winged crickets can be confused, since in neither do the hind wings extend beyond the fore wings (Walker 1972, 1977). However, dealated crickets have wing stumps rather than miniature hind wings beneath the fore wings. Long-winged *Gryllus* do not normally shed their wings, but if they are seized by the hind wings, the wings sometimes part just distal to the axillary sclerites. On rare occasions field-collected or laboratory-maintained *Gryllus* are found to have lost one or both hind wings.

Materials and Methods

Crickets used in this study came from Homestead (*G. assimilis*) and Gainesville, Fla. (*G. ovisopis, G. fultoni, G. firmus,* and *G. rubens*). Of 1,076 individuals measured, 855 were reared progeny of wild-fertilized, field-collected females. These females had been held individually outdoors in screen-capped 4-liter jars with sand for oviposition. A plywood roof protected the jars from rain and direct sunlight. Each week each female was transferred to a new jar. For each female, succes-

sive jars containing 1 week's eggs were alternatively left outdoors under the open shelter or held in a rearing room at 25 ± 1°C and 16:8 (L:D) photoperiod. These jars, each containing a 1-week group of sibs or half-sibs (a *cohort*), were tended weekly. Fresh food (Purina Dog Chow) was added, moisture was replenished, and crickets that had become adult were removed and preserved, by cohort, in isopropanol for later measurement. The remaining measured crickets (46 *G. firmus* and 175 *G. rubens*) were from the field rather than reared.

Selection of reared crickets to be measured was a two-step process. First, cohorts were selected to maximize diversity in season of oviposition, parentage (i.e., which field-fertilized female laid the eggs), and site of rearing. Then specimens within a cohort were selected to give diversity in sex and state of wings. The latter process was accomplished by taking, without bias, crickets from the preserved cohort until a predetermined number (usually six) of each category (short-winged males, long-winged females, etc.) was reached. For cohorts of *G. rubens* and *G. firmus,* numbers taken of long- and short-winged morphs were made equal even if numbers taken of males and females had to be made discrepant in the process.

Each cricket was viewed through a stereomicroscope as four measurements were made to the

Table 1. HW (mm) in *Gryllus* spp.

Species	Short-winged morph[a]				Long-winged morph[b]			
	n	*x̄*	SD	Range	*n*	*x̄*	SD	Range
ovisopis	19	5	1	4–6	—	—	—	—
fultoni	120	7	1	5–10	1	17	—	—
firmus	214	11	2	6–16	118	24	2	19–29
rubens	233	9	1	6–14	258	21	2	13–26
campestris[c]	200	11	—	9–14	19	22	—	17–26
bimaculatus[c]	—	—	—	—	400	26	—	20–32
assimilis	—	—	—	—	112	22	2	15–25

[a] Hind wings shorter than fore wings.
[b] Hind wings longer than fore wings.
[c] Data from Sellier (1954).

nearest 0.1 mm with dial calipers. Right fore wing length (FW) was measured dorsally while the pronotum was pushed downward to expose the wing base. The length of the folded right hind wing (HW) was measured from the anterior face of the tegula to the wing tip with the fore wing held fully elevated. Length of right hind femur (FM) was measured parallel to its dorsal surface from the femur's proximal end to its dorsal distal extreme. Pronotal length (PN) was measured medially. Measurements were subjected to linear correlation and regression, analysis of variance, and Duncan's (1955) multiple range test.

Results and Discussion

The occurrence of long- and short-winged morphs in Florida *Gryllus* agreed with previous observations of field-collected specimens, except for a single long-winged *G. fultoni* female. *G. ovisopis* (19 specimens from 3 cohorts produced by 3 females) were monomorphic for short wings. *G. assimilis* (112 specimens, 11 cohorts, 3 females) were monomorphic for long wings. All but one *G. fultoni* (121, 15, 4) were short-winged. *G. firmus* (286, 21, 5; plus 46 field-collected specimens) and *G. rubens* (316, 13, 11; plus 175 field-collected specimens) were dimorphic (see Tables 1 and 3, Fig. 2).

The discovery of long-winged morphs among reared individuals of a species otherwise known only from short-winged morphs has previously been reported in *Gryllodes supplicans* (Ghouri and McFarlane 1958, but see Vickery and Kevan 1983) and *Velarifictorus micado* (Saeki 1966). During 4 years of studies, T.J.W. recorded four additional long-winged *G. fultoni* (all females) among 253 reared adults. In no case were hind wings as long as is usual for long-winged *G. firmus* and *G. rubens* (Fig. 2 B, D, and E). The long-winged morph of *G. campestris* also has relatively short hind wings (Fig. 2F), and we know of no records of its flying.

Since larger crickets of a given morph would be expected to have longer hind wings, HW should be scaled to some measure of body size to make data from large and small individuals more directly comparable. We therefore tried expressing

HW in terms of FW, PN, and FM. HW as a proportion of FW (i.e., HW/FW) gave the lowest coefficients of variation (Table 2), but we were concerned that the decreased variance might result from correlated hind- and fore-wing development and that PN or FM might be a superior indicator of body size. Consequently, we studied the relationships of HW, FW, PN, FM, HW/FW, HW/PN, and HW/FM by calculating their correlations. We did these calculations separately for long- and short-winged individuals of *G. firmus* and *G. rubens* and yet again using the means of specimens having the same female parent. The latter procedure was added after we found significant differences among groups according to female parent.

FW, PN, and FM were highly correlated with one another ($r = 0.70$–0.90 for individuals and 0.75–0.99 for means of groups according to female parent). No candidate measure of size consistently showed significant correlation with any ratio—including the ratio for which the measure itself was the denominator and regardless of whether the analysis was of individuals or of means. Our correlation analysis did not show FM or PN to be substantially different from FW as a measure of size.

We adopted HW/FW as the standard for further comparisons not only because of its lower coefficient of variation but also because Sellier (1954) reported FW and HW, and not FM or PN, and because other authors (e.g., Alexander 1968) have defined long-winged morphs as having HW/FW > 1.

For the species having short-winged morphs (five, including *G. campestris*), short-winged males had HW/FW ratios 5–15% less than short-winged females. Sexual differences in HW/FW for long-winged morphs were less (1–6%) and were significant only in *G. rubens* (male > female) and *G. assimilis* (male < female) (Table 3). Since male fore wings are specialized for calling and female fore wings are not, sexual differences in HW/FW could be construed to result from sexual differences in FW rather than in HW. However, we refuted this hypothesis by determining that sexual differences for HW/PN and HW/FM were similar in magnitude and direction to those for HW/FW (Table 4).

Perhaps the reason that short-winged morphs, in which hind wings have no function, have more consistent (five of five species) and more substantial sexual differences in HW/FW values than do long-winged morphs is that hind wing length (and hence HW/FW value) is free to respond in nonadaptive ways in short-winged morphs but is narrowly selected for optimal function in long-winged morphs. In other words, sex-related differences in (nonwing) development may have incidental effects on hind wing length that are expressed only in the absence of selection for efficient flight.

More detailed analysis of HW/FW in *G. firmus*
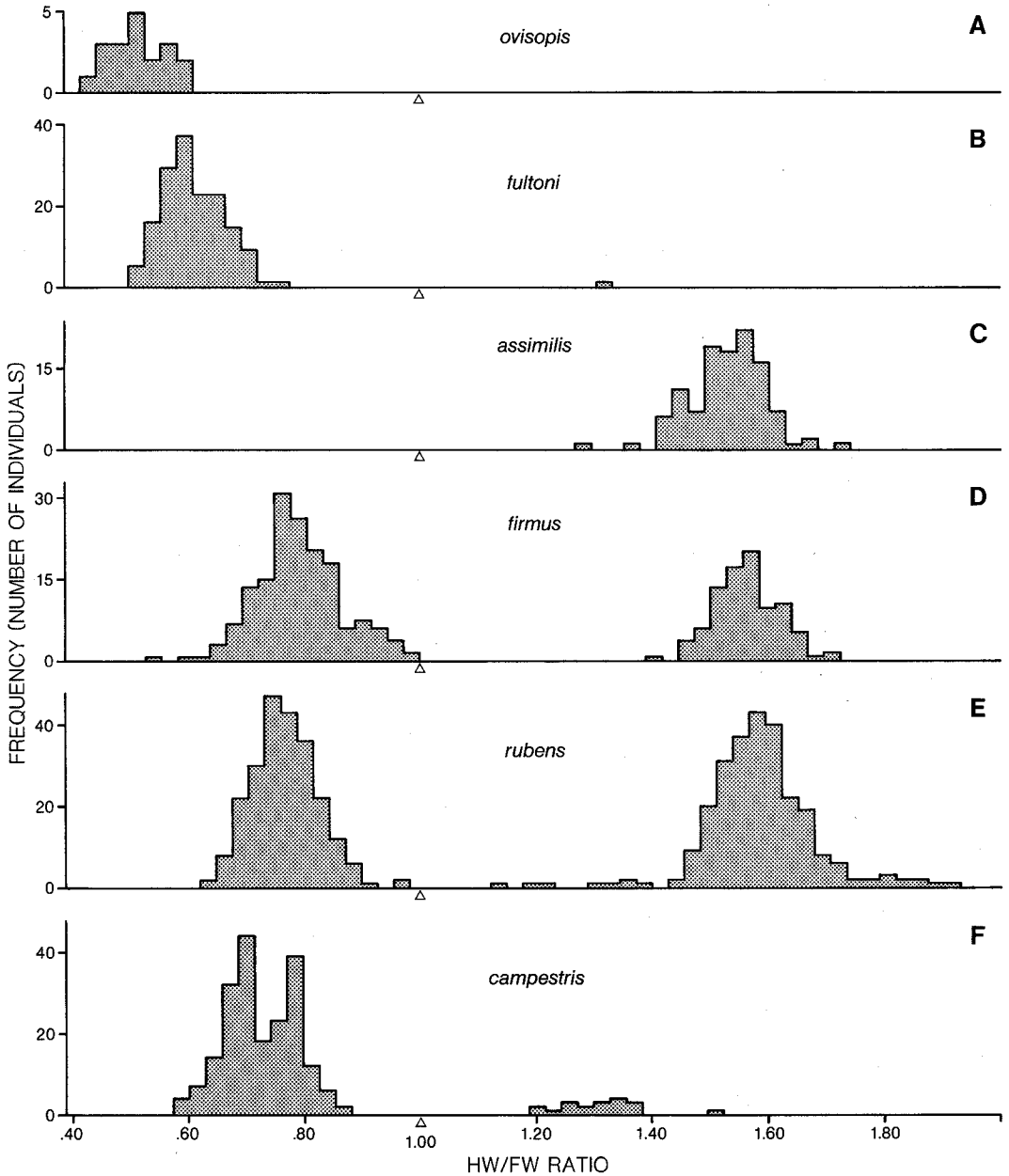
Fig. 2.   Frequency distributions of HW expressed as a proportion of FW for six species of *Gryllus*. (Relative numbers of short- and long-winged morphs of dimorphic species are not meant to be representative of field populations.) (A) *G. ovisopis*, Gainesville, Fla. ($n = 19$, $\bar{x} = 0.50$). (B) *G. fultoni*, Gainesville ($n = 121$, $\bar{x} = 0.60$). (C) *G. assimilis*, Homestead, Fla. ($n = 112$, $\bar{x} = 1.53$). (D) *G. firmus*, Gainesville (short-winged, $n = 214$, $\bar{x} = 0.80$; long-winged, $n = 118$, $\bar{x} = 1.56$). (E) *G. rubens*, Gainesville (short-winged, $n = 233$, $\bar{x} = 0.76$; long-winged, $n = 258$, $\bar{x} = 1.58$). (F) *G. campestris* (data from Sellier [1954]), Main-et-Loire, France (short-winged, $n = 200$, $\bar{x} = 0.73$; long-winged, $n = 19$, $\bar{x} = 1.31$).

and *G. rubens* showed that female parentage and rearing site (i.e., wild, outdoor reared, or laboratory reared) but not month of oviposition sometimes had significant effects (Table 5). Mean HW/FW values for long-winged morphs of the same female parent ranged from 1.54–1.59 in *G. firmus* and 1.51–1.62 in *G. rubens*. The fact that long-winged morphs, but not short-winged morphs, were involved in the female-parentage effects weakens our hypothesis that long wings are narrowly selected for function and suggests that considerable genetic variation in HW/FW ratio remains in the population. Outdoor-reared, short-winged *G. firmus* and *G. rubens* had HW/FW values of 0.78

Table 2. Effect of expressing HW as a function of FW, PN, and FM in two dimorphic *Gryllus*

Morph, species, sex	n	HW $\bar{x}$	HW CV	HW/FW $\bar{x}$	HW/FW CV	HW/PN $\bar{x}$	HW/PN CV	HW/FM $\bar{x}$	HW/FM CV
Short-winged									
firmus	214								
♂♂	118	10.1	0.14	0.76	*0.09*	2.49	0.10	0.87	0.10
♀♀	96	11.1	0.14	0.84	*0.07*	2.58	0.09	0.92	0.08
rubens	233								
♂♂	102	8.11	0.13	0.74	*0.08*	2.33	0.10	0.08	0.10
♀♀	131	9.34	0.12	0.78	*0.06*	2.47	0.09	0.83	0.09
Long-winged									
firmus	118								
♂♂	43	23.7	0.07	1.57	*0.03*	5.52	0.05	1.94	0.04
♀♀	75	23.5	0.08	1.57	*0.04*	5.31	0.05	1.89	0.05
rubens	258								
♂♂	109	20.4	0.08	1.61	*0.06*	5.67	0.07	1.92	0.07
♀♀	149	21.5	0.09	1.57	*0.06*	5.60	*0.06*	1.92	0.07

In each line, the lowest coefficient of variation is italicized.

and 0.75 compared with 0.81 and 0.78 for wild short-winged individuals.

HW/FW ratio was positively correlated with size (FM and PN) in short-winged *G. rubens* but not in *G. firmus* or in long-winged *G. rubens* ($P_\alpha = 0.0001$). Regressing HW/FW on FM and PN gave r^2 values of 0.17 and 0.12 and slopes (b) of 0.002 and 0.006.

Table 3. HW/FW for seven *Gryllus* spp.

Species, sex	Short-winged n	Short-winged $\bar{x}$	Short-winged SD	Long-winged n	Long-winged $\bar{x}$	Long-winged SD
ovisopis[a]						
♂♂	9	0.46	0.03	—	—	—
♀♀	10	0.54	0.03	—	—	—
fultoni[a]						
♂♂	65	0.57	0.04	—	—	—
♀♀	55	0.64	0.04	1	1.32	—
firmus[a]						
♂♂	118	0.76	0.06	43	1.55	0.11
♀♀	96	0.84	0.09	75	1.57	0.06
rubens[ab]						
♂♂	102	0.74	0.06	109	1.60	0.13
♀♀	131	0.78	0.05	149	1.57	0.10
campestris[ac]						
♂♂	100	0.68	0.04	2	1.24	—
♀♀	100	0.76	0.04	17	1.32	0.08
bimaculatus[c]						
♂♂	—	—	—	200	1.40	—
♀♀	—	—	—	200	1.51	—
assimilis[b]						
♂♂	—	—	—	59	1.52	0.07
♀♀	—	—	—	53	1.55	0.06

[a] HW/FW of short-winged morph significantly different between sexes ($P = 0.05$; ANOVA).
[b] HW/FW of long-winged morph significantly different between sexes ($P = 0.05$; ANOVA).
[c] Data from Sellier (1954).

The most important conclusion from this study is that hind wing length in *Gryllus* is ontogenetically channeled into either of two contrasting states. Although variation in each state occurs both within and between species, no specimen we encountered closed the gap between the two morphs (Fig. 2). Even a species classed as monomorphic in the wild demonstrated a bifurcate hind-wing-development program (Fig. 2B).

The adaptive significance of wing dimorphism is a complex issue. Roff (1975) used a simulation model to investigate the effects of four measures of environmental stability on the frequency of dispersers. Alexander (1968) discussed the subject with an emphasis on crickets, and Harrison (1980) reviewed all types of insect dispersal polymorphisms. Alexander and Harrison each noted that larger proportions of flight capable morphs are associated with less permanent, more heterogeneous habitats and that greater risks associated with dispersal may be balanced by higher payoffs (to successful dispersers). The ultimate in countering high risk with high payoff was proposed by Hamilton

Table 4. Sexual differences in HW when alternate scalers are used

Wings Species	Measure of hind wing length HW/FW	HW/PN	HW/FM
Short-winged			
G. firmus	1.10[a]	1.05[a]	1.05[a]
G. rubens	1.06[a]	1.06[a]	1.04[a]
Long-winged			
G. firmus	1.00	0.96[a]	0.97[a]
G. rubens	0.98[a]	0.99	1.00

Each value is the mean female ratio divided by the mean male ratio. (If value > 1.00, females have the higher mean ratio.)
[a] Ratios for sexes significantly different at $P_\alpha \leq 0.01$. (Other ratios not significantly different—i.e., $P_\alpha > 0.05$.)

Table 5. Analysis of variance in HW/FW within morphs of G. firmus and G. rubens

	firmus		rubens	
	Short-winged	Long-winged	Short-winged	Long-winged
Female parent	NS	0.012	NS	0.002
Rearing site	0.004[a]	NS	0.001[b]	NS
Month	NS	NS	NS	NS

Numbers are probabilities of larger F values. NS, not significant.

[a] Outdoor-reared individuals have significantly lower HW/FW than wild or laboratory-reared individuals.

[b] Outdoor-reared individuals have significantly lower HW/FW than wild individuals.

and May (1977), who noted that even if all habitats suited to a species are entirely permanent and fully occupied only those genotypes that produce some dispersers have a chance (however small) to take over sites occupied by other genotypes. If "genes" that do not produce dispersers are eventually replaced by genes that do, the payoff for genes producing dispersers is the avoidance of extinction.

Species of *Gryllus* show the predicted correlation between proportion of long-winged morphs and habitat impermanence. *Gryllus ovisopis, G. vernalis,* and *G. fultoni* live in woods, the most permanent type of habitat in the eastern United States (ignoring recent human activities). They are 100% short-winged. Other species live in open areas (e.g., fields, rock slides) that in the natural course of events are eventually invaded by trees (i.e., the open areas are successional stages that lead toward woodland). Other factors being the same, open areas at higher latitudes are more permanent (trees take longer to invade) than those in the tropics. Of the species occupying open habitats, the most northern species, *G. pennsylvanicus, G. veletis,* and *G. campestris,* have the lowest percentages of long-winged morphs (<5%), whereas the most tropical species, *G. assimilis* and *G. bimaculatus,* have the highest percentage (100%). Species intermediate geographically, *G. rubens* and *G. firmus,* are also intermediate in the prevalence of long-winged morphs.

The proximate causes of dimorphism (i.e., the circumstances that cause one individual to develop long wings while another individual in the same deme develops short wings) should reflect the contexts in which the dimorphism evolved and is maintained. One major category of proximate causation is genetic polymorphism. Here genetic differences are responsible for switching development to one morph or the other. Selection experiments (Harrison 1979, Roff 1984; T. J. Walker and S. A. Wineriter, unpublished data) have revealed that genetic differences make a significant contribution to wing dimorphism in *G. firmus* and *G. rubens.* A second major category of proximate causation is polyphenism. Here environmental differences account for the developmental switching.

Experiments with *Gryllus* spp. (e.g., Fuzeau-Braesch 1961, Alexander 1968) and other crickets (e.g., Masaki and Oyama 1963, Tanaka 1978) have frequently shown significant effects of environmental cues, especially photoperiod and population density, on the proportions of long- and short-winged morphs.

Although some proximate causes of wing dimorphism in *Gryllus* have been identified, we cannot presently predict or control satisfactorily the proportions of the morphs in any dimorphic species. For example, cohorts of Gainesville *G. firmus* and *G. rubens* include substantial but widely varying proportions of long- and short-winged morphs at all seasons, whether they develop outdoors under natural temperatures and photoperiods or indoors at 25 ± 2°C and 16:8. In the case of *G. rubens,* dimorphism persists (at 25 ± 1°C, 16:8) in both long-wing-selected and short-wing-selected strains after six generations of 100% selection. Thus far, neither genetic selection nor environmental uniformity has suppressed dimorphism (T. J. Walker and S. A. Wineriter, unpublished data).

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