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Differential Mating Success of Male Wing Morphs of the Cricket, Gryllus rubens

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ABSTRACT.—Genetically marked individuals were used to study differential mating success between male wing morphs of the cricket, *Gryllus rubens*. Previous studies of *Gryllus rubens* and other wing-dimorphic insects have documented that flightless short-winged or wingless females typically attain reproductive maturity earlier and oviposit more eggs relative to their long-winged counterparts. This study was done to determine if flightless males also exhibit enhanced reproductive characteristics. Segregation analyses documented the genetic basis of allozymes used to infer paternity in subsequent experiments. Control experiments documented the absence of effects on mating success independent of wing morph due to (1) the genetic stock from which males were taken; (2) male size; or (3) female wing morph. Mating trials involving a long-winged male, a short-winged male and a female of either wing morph documented no significant differences in the number of progeny sired by male wing morphs. This pattern was true for both the first group of offspring and for the entire set of offspring produced during a 20-day period. Thus, in contrast to females, we observed no increase in reproductive output in males resulting from the loss of the flight apparatus. However, substantial variance in mating success was observed between males independent of wing morph. This result was likely due to the existence of a dominance hierarchy and the increased mating success of the dominant male.

INTRODUCTION

Wing polymorphism is a common feature of many insects (Harrison, 1980; Pener, 1985; Roff, 1986). The polymorphism involves discontinuous variation in a variety of characteristics resulting in morphs that are adapted for dispersal at the expense of reproduction and vice versa. For example, the cricket, *Gryllus rubens,* consists of a flightless morph with shortened wings and rudimentary flight muscles and a flight-capable morph with fully developed (long) wings and functional flight muscles (Veazy *et al.,* 1976; Walker, 1987; Zera and Rankin, 1989; Mole and Zera, 1992). Short-winged females produce ca. 25% more eggs than their long-winged counterparts during the 1st 3 wk of adulthood (Zera and Rankin, 1989).

Wing polymorphism is a useful experimental system to investigate the evolution of flightlessness (or its converse, dispersal). Numerous studies have compared various fitness components between dispersive and flightless morphs to identify the factors that influence the evolution of flightlessness (Harrison, 1980; Pener, 1985; Dingle, 1985; Roff, 1986). Of special interest has been the search for enhanced aspects of fitness in the flightless morph that would indicate an evolutionary advantage for the loss of the flight apparatus. A general observation, derived from many studies, is the earlier onset of oviposition and enhanced reproductive output of flightless females (summarized in Harrison, 1980; Zera, 1984; Zera and Rankin, 1989; Roff, 1984, 1986). These results implicate a cost in the production/maintenance of the flight apparatus itself that results in decreased female fecundity. The evolution of flightlessness, at least in females, appears to be driven in large part by selection favoring the flightless morph because of its enhanced fecundity.

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In contrast to the extensive information available on females, there are only very limited data on fitness differences between male wing morphs (Utida, 1972; Crespi, 1988; Fujisaki, 1992; Roff and Fairbairn, 1993). Thus the factors that influence the evolution of flightlessness in males are poorly understood and indeed may be very different from those in females. Sex-specific differences in the evolution of flightlessness might result from variation in the cost of reproduction which is thought to be considerably lower in males than in females (Trivers, 1972; Burk, 1983). If males make only a small energetic investment in reproduction, a reallocation of nutrients from the flight apparatus to reproductive output might result in no significant additional increase in fecundity. Thus the energetic basis for an evolutionary trade-off between flight capability and dispersal would not exist in males, in contrast to the situation in females (Zera and Rankin, 1989; Mole and Zera, 1992). On the other hand, since the cost of reproduction has been much less studied in male insects, it may be higher in males than previously thought. For example, the cost of producing spermatophores or attracting females by calling may be high in male crickets (Sakaluk and Cade, 1983; Stevens and Josephson, 1977; Prestwich and Walker, 1981; Burk, 1988). According to this scenario, the evolution of flightlessness in both sexes would primarily be due to the same factor: the enhanced reproductive output of the flightless morph.

In this study we investigated whether short-winged males exhibited enhanced mating success over their long-winged counterparts in the cricket *Gryllus rubens*. This was done as a first step in determining whether the loss of flight capability is associated with enhanced fecundity in this sex.

MATERIALS AND METHODS

Experimental animals and rearing conditions.—Crickets used in this study were derived from a long-winged (LW) and a short-winged (SW) laboratory stock of the cricket *Gryllus rubens*. The LW stock is nearly pure-breeding for the LW phenotype (>85%) while the SW stock is nearly pure-breeding for short wings (>95%). Stocks have been maintained in the laboratory for several years and are the same as those used in endocrine studies of wing morph determination (Zera and Tobe, 1990; Zera and Holtmeier, 1992, and references therein). All crickets were reared and all mating trials were conducted at 28 ± 1 C under a 16 h light : 8 h dark photoregime. Crickets were fed a modified *Manduca* diet (Zera and Tiebel, 1988).

Electrophoresis.—Starch gel electrophoresis was performed on homogenates of a single hind leg of adults or whole juvenile crickets. These samples were homogenized in 0.1 M potassium phosphate buffer pH 7.1 with 0.1% (v/v) β-mercaptoethanol. The electrode buffer was 0.135 M Tris-citrate pH 7.4 and the gel buffer was a 1:10 dilution of the electrode buffer. Gels were run until the bromphenol blue marker had migrated approximately 11 cm from the origin. Gels were stained for isocitrate dehydrogenase (IDH, E.C. 1.1.1.42) and phosphoglucose isomerase (PGI, E.C. 3.5.1.9) as described in Zera (1981).

Verification of the genetic basis of electromorphs.—Segregation analyses of PGI and IDH electromorphs were performed to verify the genetic basis of enzyme forms which were used to infer paternity. Analyses were performed on the two common PGI electromorphs (designated F and S) and the three common IDH electromorphs (F, S and S′). F, S and S′ denote electromorphs of decreasing mobility from the origin, respectively.

The PGI and IDH phenotypes of adult males and females of both morphs were determined by electrophoresing a hind leg of each individual. Single pair crosses were then set up and eggs were collected. Fourteen days after hatching, juveniles were either homogenized live and subjected to electrophoresis or were stored frozen at −76 C for subsequent homoge-

nization. Freezing did not affect electrophoretic mobility of either PGI or IDH electromorphs. Phenotypic ratios of progeny were compared to those expected due to segregation of codominant alleles at a single autosomal locus using a G-test for homogeneity employing Yates's correction (Sokal and Rohlf, 1981).

Male mating success experiments. (A) Experimental design.—Mating trials were performed to determine if mating success differed between LW and SW males. Trials consisted of an LW virgin male, an SW virgin male and a virgin female of either morph. To obtain virgin adults of known age and genotype, males during the penultimate stadium and females during the last stadium were removed from aquaria in which crickets had been reared and were housed separately in 600-cm^3 containers. The PGI and IDH genotypes of these juveniles were then determined by electrophoresing a hind leg. Crickets often lose a hind leg and this procedure had no apparent detrimental effect on mating. Individuals were then checked daily for adult molt.

Where possible, test mating trials were conducted with males that were homozygous for different electromorphs and females that were homozygous for one of the two electromorphs. This allowed the paternity of all progeny to be definitively ascertained. For example, in one case, the SW male was PGI-FF, the LW male was PGI-SS and the female was PGI-SS. All progeny with a PGI-FS phenotype must have been sired by the SW male while all progeny with a PGI-SS phenotype must have been sired by the LW male. This type of a mating trial was called a "definitive trial." An adequate number of definitive mating trials could not be conducted since we often did not have crickets with the appropriate homozygous genotypes. Therefore, other trials, termed "nondefinitive trials," were also conducted. In these trials, one of the males was heterozygous at one of the loci. The paternity of each progeny could not be determined in the trials but the proportion of progeny sired by each male could still be estimated. For example, in one case, the SW male was PGI-FS, the LW male was PGI-SS and the female was PGI-SS. All progeny with a PGI-FS phenotype must have been sired by the SW male, but progeny with a PGI-SS phenotype could have been sired by either male. The method used to estimate the proportion of progeny sired by each male morph in these nondefinitive trials is given below.

Two virgin adult males emerging during a 24-h period and a virgin female were put in a 2-liter (15 cm diam) container with an oviposition cup with moist sand and a piece of the standard diet. Adult females do not begin oviposition until ca. 4–5 days after adult emergence. In order that male mating success was not confounded by the reproductive competence of the female, 9–15-day-old females were used. Oviposition cups were changed every 4 days for a 20-day period to determine whether the proportion of progeny sired by a particular morph changed through time. In eight of 26 trials, hatchlings were only collected from one oviposition period.

In most of the mating trials the SW male came from the SW stock and the LW male came from the LW stock. However, the LW and SW stocks are not pure-breeding; the LW stock produces ca. 15% short-winged adults while the SW stock produces about 5% long-winged individuals. The production of both morphs in each stock allowed mating trials to be set up where the LW and SW males were derived from the same or different stocks. This, in turn, allowed control matings to be set up where the effect of various factors on mating success could be tested. For example, mating trials were set up where the different morphs came from the same stock (*e.g.,* LW and SW males from the LW stock). This allowed us to determine if wing morph, *per se,* independent of stock, was responsible for any differences in mating success. To further determine whether mating success was influenced by genetic stock independent of wing morph, control matings were set up with SW males derived from the different stocks. Control matings using LW males derived from the

TABLE 1.—Segregation analysis of isocitrate dehydrogenase and phosphoglucose isomerase alleles in *Gryllus rubens*. F, S and S′ denote electromorphs with decreasing mobility from the origin, respectively

Isocitrate dehydrogenase								
Parental phenotypes			Progeny phenotypes					
♀		♂	SS	FS	FS′	SS′	n[a]	G-values[b]
S′S′	×	FS	—	—	10	11	21	0.02, n.s.
SS	×	FS	72	66	—	—	138[c]	0.06, n.s.
SS′	×	SS	52	—	—	27	79	3.45, n.s.
SS′	×	SS	25	—	—	30	55	0.08, n.s.
Phosphoglucose isomerase								
Parental phenotypes			Progeny phenotypes					
♀		♂	FF	FS	SS		n[a]	G-values[b]
FS	×	SS	—	56	48		104[c]	0.17, n.s.
FF	×	FS	40	42	—		82[c]	0.00, n.s.
SS	×	SS	—	—	74		74[c]	—

[a] n = Number of progeny electrophoresed

[b] G-tests involved 1 df in all cases

[c] Progeny ratios of several pooled crosses; in each of these cases, progeny ratios did not differ significantly among crosses

LW and SW stocks were not set up, because the SW stock only rarely (typically <6%) produces LW individuals.

Males were also weighed to investigate if the size of the male, independent of wing morph, contributed to mating success. To determine if female morph influenced mating success, mating trials were set up with each female morph. Females that died during the mating trial were replaced with a new female of known electrophoretic genotype. In a subset of trials, the percent survivorship of hatchlings was determined from egg hatch to sampling for electrophoresis (10–20 days posthatch).

(B) Data analysis.—Differential mating success in the definitive trials was assessed by comparing the observed number of progeny sired by each morph with that expected from the null model of 50% progeny sired by each morph. Contingency tests employing the G-statistic with Yates's correction were used to determine the statistical significance of deviations from the null model. These tests were performed separately on (a) the first set of progeny and (b) on the pooled frequency of progeny sired by a particular morph in the temporal collections (*i.e.*, all offspring).

For the nondefinitive trials, which consisted of a heterozygous male and a male and female that were homozygous for the same genotype, the frequency of progeny sired by the heterozygous male is estimated as [2(freq. of heterozygous progeny)]. Under a null model of no morph-specific mating success, the expected frequency of heterozygous progeny is 0.25, and if all or no progeny are derived from the heterozygous male, the frequency of heterozygous progeny will be 0.5 and 0.0, respectively. Statistical significance of deviations from the null model was determined by contingency tests using the G-statistic.

To determine whether there was an overall influence of wing morph on mating success, a sign test was used to compare the number of trials in which there was an excess of progeny sired by the SW male. This was done for both the first set of progeny and for the entire set of progeny collected over the five time periods. A Kruskal-Wallis test was used to compare the magnitude of deviations from equal mating success in trials where there was an excess

TABLE 2.—Proportion of progeny sired by the short-winged (SW) male parent in control and test mating trials. Control matings involved an SW male from the SW stock and an SW male from the LW stock.[a] Test matings involved an SW and a long-winged (LW) male from various stocks. G-values refer to the goodness-of-fit to the null model of 50% progeny sired by each male and not to an excess of progeny sired by the SW morph

	First oviposition period		All oviposition periods combined	
Trial no.	Proportion sired by SW-parent	Results of G-tests	Proportion sired by SW-parent[b]	Results of G-tests
Control trials involving an $SW_{(SW)}$[c] and an $SW_{(LW)}$ male				
20[d]	1.00 (57)[e]	$P < 0.005$	1.00 (114)	$P < 0.005$
26	1.06 (34)	$P < 0.005$	1.06 (34)[f]	$P < 0.005$
22	1.22 (54)	$P < 0.005$	1.22 (54)[f]	$P < 0.005$
39D	0.95 (22)	$P < 0.005$	0.59 (44)	n.a.[g]
38	0.92 (63)	$P < 0.025$	0.92 (63)[f]	$P < 0.005$
25	0.32 (50)	$P > 0.1$, n.s.	0.37 (107)	$P > 0.1$, n.s.
21	0.21 (58)	$P > 0.1$, n.s.	0.27 (118)	$P > 0.1$, n.s.
37	0.10 (78)	$P < 0.005$	0.10 (78)[f]	$P < 0.005$
Test trials involving an $LW_{(LW)}$ and an $SW_{(SW)}$ male				
3D	1.00 (28)	$P < 0.005$	1.00 (142)	$P < 0.005$
7D	1.00 (28)	$P < 0.005$	1.00 (14)	$P < 0.005$
13D	1.00 (40)	$P < 0.005$	1.00 (57)	$P < 0.005$
18D	1.00 (17)	$P < 0.005$	1.00 (35)	$P < 0.005$
8D	0.93 (48)	$P < 0.005$	0.81 (141)	$P < 0.005$
16	0.76 (55)	$P > 0.1$, n.s.	0.63 (85)	$P > 0.1$, n.s.
4	0.63 (96)	$P > 0.1$, n.s.	0.57 (261)	$P > 0.1$, n.s.
35	0.00 (64)	$P < 0.005$	0.02 (128)	$P < 0.005$
28	0.00 (59)	$P < 0.005$	0.42 (111)	n.a.[g]
Test trials involving an $LW_{(LW)}$ and an $SW_{(LW)}$ male				
36D	1.00 (20)	$P < 0.005$	1.00 (20)[f]	$P < 0.005$
6D	1.00 (47)	$P < 0.005$	0.78 (134)	n.a.[g]
33	1.00 (48)	$P < 0.005$	0.63 (113)	n.a.[g]
31	0.14 (72)	$P > 0.1$, n.s.	0.14 (72)[f]	$P > 0.1$, n.s.
30	0.00 (26)	$P > 0.1$, n.s.	0.02 (141)	$P < 0.005$
34	0.00 (23)	$P < 0.005$	0.00 (23)[f]	$P < 0.005$
32D	0.00 (17)	$P < 0.005$	0.00 (17)[f]	$P < 0.005$
9D	0.00 (47)	$P < 0.005$	0.00 (47)[f]	$P < 0.005$
Test trials involving an $SW_{(LW)}$ and an $LW_{(SW)}$ male				
14D	0.30 (46)	$P > 0.1$, n.s.	0.51 (113)	n.a.[g]

[a] For control trials involving two SW males, proportion of progeny sired by the male from the SW stock is given

[b] Weighted mean frequency of progeny sired by SW male over all oviposition periods

[c] Designation before the parentheses indicates wing morph, designation within the parentheses indicates the stock; *e.g.*, $SW_{(LW)}$ = a short-winged morph from the long-winged stock

[d] Trials without a letter are nondefinitive, while those with a letter are definitive (*see* Methods)

[e] Number of progeny subjected to electrophoresis

[f] Samples were taken from only one time period

[g] N.A. = not applicable; because of temporal heterogeneity in the frequency of progeny sired by a particular male, a G-test on the entire set of progeny could not be performed

TABLE 3.—Proportion of progeny sired by the short-winged (SW) morph during sequential 4-day oviposition periods. Mating trials involved an SW and a long-winged (LW) male while control trials involved two SW males

Cross no.	Oviposition period[a] 1	2	3	4	5	Results of G-tests[b]
$LW_{(LW)}$ vs. $SW_{(SW)}$[c] trials						
8D	0.94 (48)[d]	0.91 (24)	0.65 (23)	0.63 (22)	0.75 (24)	$P < 0.005$
20	1.00 (57)	1.00 (57)	—	—	—	n.s.[e]
3D	1.00 (28)	1.00 (28)	1.00 (28)	1.00 (28)	1.00 (28)	n.s.
7D	1.00 (28)	1.00 (28)	1.00 (28)	1.00 (28)	1.00 (28)	n.s.
18D	—	—	—	1.00 (17)	1.00 (18)	n.s.
4	0.63 (96)	0.33 (24)	0.83 (48)	0.46 (48)	0.44 (45)	n.s.
28	0.00 (59)	—	0.42 (52)	—	—	$P < 0.005$
35	0.00 (64)	—	0.30 (64)	—	—	n.s.
$LW_{(LW)}$ vs. $SW_{(LW)}$ trials						
6	1.00 (47)	1.00 (24)	0.72 (22)	0.58 (24)	0.23 (17)	$P < 0.005$
33	1.00 (48)	—	0.35 (65)	—	—	$P < 0.005$
30	0.00 (26)	0.04 (73)	—	0.00 (30)	—	n.s.
16	0.76 (55)	—	—	0.40 (30)	—	n.s.
$LW_{(SW)}$ vs. $SW_{(LW)}$ trial						
14D	—	0.30 (46)	0.48 (21)	0.48 (21)	0.95 (22)	$P < 0.005$
$SW_{(LW)}$ vs. $SW_{(SW)}$ controls[f]						
20	1.00 (57)	1.00 (57)	—	—	—	n.s.
21	—	0.21 (58)	—	0.33 (60)	—	n.s.
25	0.32 (50)	—	0.42 (57)	—	—	n.s.
37	0.10 (78)	—	0.01 (56)	—	—	n.s.
39D	0.95 (22)	—	—	—	0.23 (22)	$P < 0.005$

[a] Duration of each oviposition period was 4 days beginning on the day the mating trial commenced

[b] G-test of homogeneity; H_0: Proportion of progeny sired by the SW male does not differ among oviposition periods

[c] Abbreviation (LW or SW) before the parentheses refers to the phenotype (long winged or short winged) and that within the parentheses refers to the stock from which the cricket was taken (*see* Methods)

[d] Number outside the parentheses denotes the proportion of progeny sired by the SW male; number within the parentheses denotes the number of progeny surveyed

[e] $P > 0.1$

[f] For control trials, values represent the proportion of progeny sired by $SW_{(SW)}$ males

of progeny sired by the SW male vs. trials where there was an excess of progeny sired by the LW male.

RESULTS AND DISCUSSION

Segregation analyses.—Staining for phosphoglucose isomerase (PGI) or isocitrate dehydrogenase (IDH) produced either single-banded or triple-banded phenotypes which were inferred to be homozygotes or heterozygotes, respectively (Table 1). In all crosses, electromorph inheritance was consistent with that expected due to segregation of codominant alleles at a single locus. This result verifies that the electromorphs could be used as single-locus genetic markers to infer paternity.

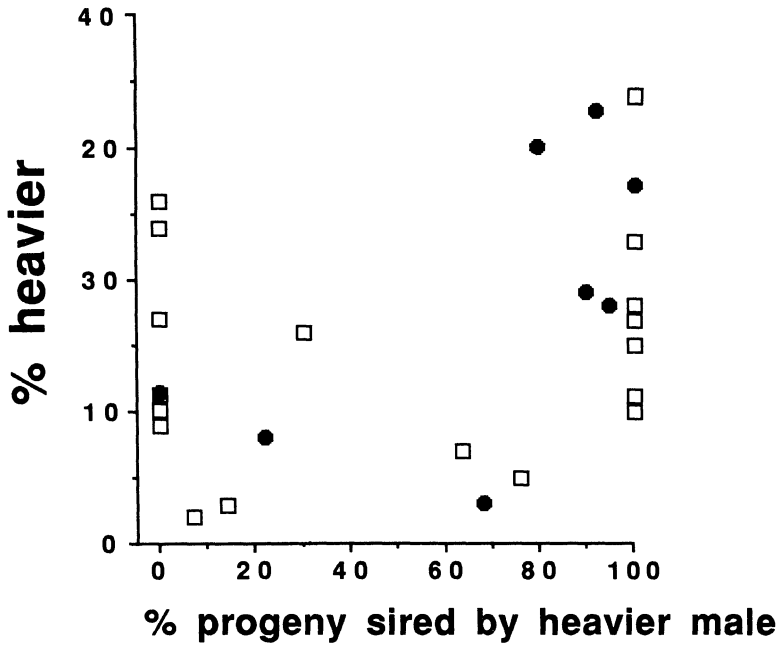

FIG. 1.—Relationship between weight and % progeny sired in individual mating trials. (□) represents trials involving a long-winged and a short-winged male while (●) represents control trials involving two short-winged males. Results of statistical analyses of these data are given in the text

Effect of genetic stock, male weight and female phenotype on male mating success.—Eight control mating trials involved an SW male from the LW stock [$SW_{(LW)}$] and an SW male from the SW stock [$SW_{(SW)}$] (Table 2). In five of these trials the SW male sired more progeny than the LW male. This outcome did not differ significantly from the null expectation of half (4) the crosses exhibiting an excess of progeny sired by the SW male parent [sign test on the first set of progeny ($G = 0.00$; $P > 0.1$) or on the entire set of progeny ($G = 0.07$; $P > 0.1$)]. A Kruskal-Wallis test also failed to demonstrate differences in the degree of deviation from 50-50 mating success for $SW_{(LW)}$ vs. $SW_{(SW)}$ males ($P > 0.1$ for both the first set of progeny and for the entire set of progeny). In five of the eight control mating trials, two or more successive batches of progeny were sampled at 4-day intervals. In four of five cases there was no significant change in the proportion of progeny sired by a particular male over time (Table 3). These results collectively provide no evidence for an inherent mating advantage of males from a particular genetic stock.

Enhanced mating success of heavier males has been observed in some mate competition experiments (Dixon and Cade, 1986; Simmons, 1986; however, *see* Alexander, 1961, and Zuk, 1987). However, in the present study, we found no case (all trials, test matings alone, control matings alone) where male weight and % progeny sired was significantly correlated [Fig. 1; correlation coefficients and 95% confidence limits of arcsine transformed data are as follows: all trials ($n = 26$), $r = 0.317$, $L_1 = -0.779$, $L_2 = 0.6276$, $P > 0.1$; test trials only ($n = 18$), $r = 0.209$, $L_1 = -0.285$, $L_2 = 0.612$, $P > 0.1$; control trials alone ($n = 8$), $r = 0.568$, $L_1 = -0.229$, $L_2 = 0.909$, $P > 0.1$]. Thus, in the present study, mating success was not confounded by weight differences between competing males.

Wing phenotype of the female also did not influence mating success of male wing morphs.

The frequency of the female wing morph did not differ significantly between trials where the SW male sired greater than 50% of the first group of progeny (10 trials; 70% LW females) vs. trials in which the LW male sired more than 50% of the progeny (eight trials; 50% LW females; $G = 0.143$; $P > 0.1$). A similar lack of association was found between female wing morph and mating success of the male wing morph when all progeny produced in a mating trial were considered (data not shown). In each of eight trials studied, mean hatchling survival was very high (>91%). This result eliminates the possibility of erroneous paternity estimates due to differential survivorship among progeny with different electrophoretic phenotypes.

Test mating trials.—Considerable variability was observed with respect to the number of progeny sired by the SW vs. the LW male in individual mating trials (Table 2). In some cases (*e.g.,* trials 18D and 13D), the SW male sired all the progeny while in other cases (*e.g.,* trials 35 and 28) the SW male sired none of the progeny. Overall, the SW male sired an excess (>50%) of progeny in 10 of 18 trials (first set of progeny) and in 11 of 18 cases (all progeny) (Table 2). These results did not differ significantly from the null expectation that half the crosses would exhibit an excess of progeny sired by the SW male ($G = 0.03$, $P > 0.1$, first set of progeny; $G = 0.00$, $P > 0.1$, all progeny). In addition, a Kruskal-Wallis test of the magnitude of deviations from 50% paternity in crosses where there was an excess of progeny sired by the SW vs. the LW male was also nonsignificant for both the first set of progeny ($H = 0.05$; $P > 0.1$) and the entire set of progeny ($H = 0.34$; $P > 0.1$). In addition, there was no evidence for a consistent temporal change in the proportion of progeny sired by a particular male morph (Table 3). Thus, we observed no significant difference in male mating success between the morphs. Moreover, short-winged males did not attain reproductive maturity and begin mating earlier than their long-winged counterparts.

At this point a caveat should be made concerning the resolving power of the present study. The large amount of labor required to screen (1) males and females to obtain appropriate genotypes for the mating trials and (2) progeny genotypes (over 2000 individual progeny alone) for the paternity estimates, limited the number of test matings that could be performed. Consequently, the power to detect reproductive differences between male wing morphs was low. The present study should therefore be viewed as only the first step in determining whether morph-specific reproductive differences exist between male morphs. On the other hand, our results at least suggest that the large reproductive differences that have been typically documented between female wing morphs do not exist between male wing morphs of *Gryllus rubens.*

The observation of no strong difference in mating success between male morphs of *Gryllus rubens* is similar to a recent similar observation in the congeneric cricket *G. firmus* (Roff and Fairbairn, 1993). While it is premature to draw any strong generalizations, these data do collectively suggest that the absence of a reproductive gain attained by the loss of the flight apparatus in flightless males may be a feature of field crickets. This result would fit with the notion that male reproductive investment is low in this group (Burk, 1983) and thus fecundity is not significantly enhanced in flightless males due to a reallocation of energy from growth and maintenance of the flight apparatus.

If flightless males do not exhibit a gain in reproductive output, what factors might be responsible for the evolution of flightlessness in that sex? There are several possibilities. Calling is important in attracting females at a distance in the field (Hedrick, 1986; Zuk, 1987) and is energetically expensive (Stevens and Josephson, 1977; Prestwich and Walker, 1981; Burk, 1988). It is conceivable that the short-winged morph might utilize nutrients not required for construction and maintenance of the flight apparatus to begin calling earlier

or to call for a longer duration. This could lead to enhanced success over the long-winged morph in attracting females in the field. In our experiments, females were always in close proximity to both males and thus morph-specific differences in calling, if present, probably would have had little effect. There is currently no comparative information on calling characteristics of male wing morphs in any cricket species.

Roff and Fairbairn (1993) have documented a strong genetic correlation ($r = 0.7–0.8$) for wing phenotype between the sexes in the cricket *Gryllus firmus*. That is, genetically related males and females exhibit a similar wing phenotype to a greater degree than unrelated males and females. Because of this genetic correlation, flightlessness could evolve in males simply because of indirect selection favoring this trait in females rather than because of any direct advantage in males. Although we have no information concerning the genetic correlation of wing phenotype in male and female *G. rubens*, it is conceivable that flightlessness in male *G. rubens* could be the consequence of indirect selection.

Differential mating success independent of wing morph.—Although we observed no consistent difference in mating success between male wing morphs when all mating trials were considered, we often observed significant deviations from equal mating success between males in individual trials (*see* G-values in Table 2). There was a highly significant deviation from equal mating success by the two males in 19 of 26 trials (first set of progeny) and in 14 of 21 trials (pooled progeny) ($P < 0.005$ in individual G-tests; Table 2). For five mating trials, percent paternity varied significantly temporally and thus pooled progeny ratios could only be tested in 21 of 26 trials. Overall G-tests, performed by summing the individual G-values over trials (first set of progeny), were highly significant for (1) all 18 test matings involving an LW and an SW male ($G = 361$, 17 df; $P < 0.005$); (2) all control trials involving two SW males ($G = 136$, 7 df; $P < 0.005$); and (3) the entire set of 26 trials ($G = 497$, 25 df; $P < 0.005$). Similar results were obtained when deviations from equal paternity were tested on the entire set of progeny. This documents that overall there was a highly significant deviation from equal mating success between competing males.

Mating success was not related to male size (Fig. 1), as has been documented in several studies of field crickets (Dixon and Cade, 1986; Simmons, 1986; however, *see* Alexander, 1961, and Zuk, 1987). Also, since this was observed for both the first batch of progeny and for the entire set of several groups of progeny (Table 2), it is unlikely due to the earlier maturation of one of the males. In previous studies of mate competition in field crickets, one male was often observed to be dominant over the other and to obtain a higher frequency of matings (Burk, 1983). This is the likely explanation for the variation in mating success in the present study. Importantly, this result indicates that our experiments were capable of documenting the existence of differential mating success. It strengthens our conclusion that strong differential mating success did not occur between male wing morphs of *Gryllus rubens* under our experimental conditions.

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