

Positive Relationship between Signalling Time and Flight Capability in the Texas Field Cricket, *Gryllus texensis*

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Abstract

A trade-off between dispersal ability and reproduction is generally thought to explain the persistence of wing dimorphism in insects, although this trade-off has received minimal attention in male insects. Research on male sand cricket, *Gryllus firmus*, supports the trade-off hypothesis insofar as flight capable cricket's spend significantly less time signalling for potential mates than their flightless counterparts. By contrast, here I show that this expected trade-off between signalling time and wing dimorphism does not exist in a male congener, the Texas field cricket (*Gryllus texensis*). In *G. texensis*, flight capable males signal twice as often as flightless males. Thus, unless male *G. texensis* express trade-offs between dispersal ability and other, presently unmeasured components of reproduction, the trade-off hypothesis may not explain the persistence of wing dimorphism in all male insects.

Introduction

Wing dimorphism, where one morph has long wings and is capable of flight (macropterous) and the other morph has short wings and cannot fly (brachypterous or micropterous), occurs in numerous insect orders (Darlington 1936; Alexander 1968; Harrison 1980; Dingle 1985; Pener 1985; Roff 1986; Zera & Denno 1997). Insects capable of flight have an advantage because they can more readily disperse to new environments when food or mates are scarce (Alexander 1968; Harrison 1980; Dingle 1985; Walker & Sivinski 1986). It has been hypothesized that wing dimorphism is maintained through a trade-off between dispersal ability and reproduction (Roff 1984; Crespi 1988). Substantial empirical evidence supports this hypothesis in females: flightless females tend to have higher fecundity than those capable of flight (reviewed by Roff 1986; Langellotto et al. 2000).

Research on males has received considerably less attention. To date, only a limited number of studies have examined the dispersal and reproduction trade-off, and most of these support the trade-off hypothesis. Flightless plant hopper males (*Prokelisia dolus*

Hemiptera: Delphacidae), for example, mate three times as often and sire twice the number of offspring as males capable of flight (Langellotto et al. 2000). In another plant hopper species (*Nilaparvata lugens*), flightless males also develop faster and experience higher mating success than fliers (Novotný 1995). Wingless (apterous) male water striders (*Aquarius remigis*) mate more often than long-winged males (Kaitala & Dingle 1993), and sexual selection appears to favour wingless males (Fairbairn & Preziosi 1996). In the field cricket, *Gryllus firmus*, flightless males spend significantly more time calling (producing long distance mate attraction signals) and have greater success at attracting females than males capable of flight (Crnokrak & Roff 1995; Crnokrak & Roff 2000; Roff et al. 2003). These studies suggest that wing dimorphism in male insects may be maintained through a trade-off with reproduction.

However, a handful of studies have failed to detect this trade-off. In a third species of plant hoppers, *Laodelphax striatellus*, flightless and flight capable males do not differ in their mating success (Mishiro et al. 1994). In *Gryllus firmus* (the same cricket species mentioned above), flightless and flight

capable males do not differ in their pulses per chirp, chirp rate, chirp length, chirp frequency or in the number of progeny they sire (Webb & Roff 1992; Roff & Fairbairn 1994). Likewise, in a different cricket species (*Gryllus rubens*) flightless and flight capable males also do not differ in the number of progeny they sire, either in the first set of offspring they produce, or in the entire set of offspring they produce over the twenty day period (Holtmeier & Zera 1993). These studies highlight the need for the trade-off hypothesis to be further examined in wing dimorphic male insects.

Here I examine whether a trade-off exists in the male Texas field cricket, *Gryllus texensis*. Both macropterous individuals who are flight capable [fully developed (long) wings with functional flight muscles] and micropterous individuals who are incapable of flight (shortened wings with rudimentary flight muscles) are common in the Texas field cricket (Walker & Sivinski 1986; Souroukis et al. 1992). I examine whether a wing-morph trade-off occurs by investigating the relationship between dispersal ability and the production of long-distance mate attraction signals.

Texas field crickets exhibit two alternative mating behaviours (Alexander 1961). Callers rub their forewings wings together to produce pulses of sound which they append together into trills, and they concatenate these trills to produce long trilling bouts (Alexander 1961). Male callers use these long trilling bouts to attract females from a distance – once a female is nearby they switch to a different courtship song (Alexander 1961). Conversely, satellite males wait silently near callers and attempt to intercept females once they are attracted to the area (Alexander 1961; Cade 1979). Callers exhibit extensive variation in their long distance mate attraction signals: individuals vary in their number of pulses per trill (Souroukis et al. 1992; Gray & Cade 1999), pulse rate (Walker 1974; Souroukis et al. 1992), inter-trill interval (Souroukis et al. 1992; Higgins & Waugaman 2004), trill length (Higgins & Waugaman 2004), average trilling bout duration (time spent trilling without taking at least a 1-min break) (Bertram & Warren 2005), hourly trilling bout number (Bertram & Warren 2005; Bertram and Bowen 2006), and how much time they spend signalling through the course of the night (Cade 1981; Bertram & Johnson 1998; Bertram 2000).

Contrary to the trade-off hypothesis, previous research on the Texas field cricket suggests cricket wing morph does not influence number of pulses per trill or pulse rate (Souroukis et al. 1992). Both these trilling parameters are known to influence

female mating preference (Wagner et al. 1995), and so one might have suspected that a trade-off would have occurred between them and male dispersal ability. It is conceivable, however, that a trade-off between reproduction and dispersal would be more evident if nightly signalling time had been examined, because nightly signalling time is known to directly influence mating success in the Texas field cricket (Cade & Cade 1992). Further, because signalling is energetically demanding in Orthoptera (Bailey et al. 1993; Simmons 1994; Hoback & Wagner 1997), the energetic resources required to maintain flight capability may constrain the resources required for mate signalling (Crnokrak & Roff 1995).

Previous research examining the trade-off between dispersal ability and signalling effort in *G. texensis* revealed no difference between long-winged and short-winged males in their total nightly signalling time (Bertram 2000). This result was confirmed in a subsequent study on *G. texensis* and its closely related sister species, *G. rubens* (Bertram & Bowen 2006). However, both studies were problematic in that they quantified flight ability using the presence of the long or short wing morph. While short winged individuals are incapable of flight, long winged individuals cannot always fly. Absorption of the dorso-lateral flight muscles is common in long-winged *Gryllus* species, rendering them incapable of flight (Zera 2005). Thus, a formal evaluation of the reproduction and dispersal trade-off hypothesis requires confirmation that the crickets are capable of flight. Here I compare the signalling effort of field captured adult male crickets who are flight capable to male crickets who are incapable of flight. Specifically, I determine whether the proportion of the population that signals acoustically differs across these two wing morphs. I also test the prediction stemming from the trade-off hypothesis that males capable of flight will signal less often than flightless males.

Methods

Adult Texas field crickets were collected in late Sep. and early Oct. 2005 in Austin, Texas. Forty flight-capable male crickets were collected after being observed flying around bright lights at a golf course driving range in northern Austin. Each male was collected after it landed on the short grass or the asphalt parking lot surrounding the bright driving range lights. Thirty-five flightless male crickets were collected using pit-fall traps in a grassy field in eastern Austin. All flightless male crickets were short-winged (micropterous); flight capable crickets could

easily escape the pitfall traps and were therefore not collected in this manner.

Within 20 h of being collected, each male cricket was housed individually in a 500 ml wax coated paper container with moistened soil for a water source and ground rat chow for food (Harland's Teklad Rodent diet 8604; Harlan Teklad, Madison, Wisconsin, USA). Male long distance mate signalling displays were monitored in the greenhouse at the Brackenridge Field Laboratory of the University of Texas at Austin. The greenhouse environment provides lighting and temperature fluctuations that mimic conditions in the cricket's natural environment. Cricket signalling effort does not appear to be affected by the greenhouse environment, as signalling displays do not differ when crickets are monitored in their natural environment and the greenhouse environment (Bertram 2002).

To test whether flight capable males differed from flightless males in their long distance mate attraction signals, I electronically monitored the signalling displays of the 40 flight capable and 35 flightless male *G. texensis* over a 16-h period. Signalling behaviour was monitored from 6:00 PM to 10:00 AM on the evening of Oct. 4, 2005 using an electronic acoustic recorder (EAR). The EAR simultaneously quantified each male's signalling behaviour by continuously sampling his acoustic environment (for details refer to Bertram & Johnson 1998; Bertram et al. 2004). Seven centimetres of acoustic foam separated each cricket from his nearest neighbours, minimizing the effects of neighbouring signals. A microphone was hung within each container, approximately 5 cm above the cricket. The EAR accessed each container's microphone, assessed the container's noise level, and recorded signalling and non-signalling to the computer's hard drive. Each microphone was sampled eight times a second for the entire 16-h period (Bertram & Johnson 1998; Bertram et al. 2004). I extracted from these data whether or not each male signalled at all through the night. For the signallers I extracted each male's total nightly signalling time (the number of minutes each male signals throughout the night), average trilling bout duration (the average length of time each cricket trills continually, without taking a break longer than 1 min), and hourly trilling bout number (that average number of trilling bouts produced each hour). The EAR sampling rate does not enable determination of dominant frequency, pulse rate, trill length, or inter-trill interval.

Following acoustic monitoring, each male was frozen. Later, males were dissected to ensure classification as flightless or flight capable was correct. All

males that were collected after being observed flying at lights and classified as flight capable had large flight muscles. All males that were collected using a pit-fall trap and classified as flight incapable had both short hind wings and rudimentary flight muscles.

During dissection, males were also examined for the presence of the parasitoid fly larvae, *Ormia ochracea*. Adult female *O. ochracea* acoustically locate signalling male crickets, laying their larvae on and around the cricket (Cade 1975). The larvae burrow into the cricket, where they feed and grow (Adamo et al. 1995). Parasitism significantly reduces cricket signalling behaviour: total nightly signalling time (Adamo et al. 1995), trilling bout duration and trilling bout rates are all greatly reduced 3–4 d after parasitism (Orozco & Bertram 2004). Within 7–10 d of parasitism, the cricket dies (Adamo et al. 1995). We examined each cricket for the presence of parasitoids because the flightless and flight capable males were collected from different locations. If the two locations where flightless and flight capable males were collected differed in rates of parasitism, then parasitism and not flight status might explain our results. We found no evidence of males being parasitized, thus alleviating this alternative hypothesis.

Statistical analyses were conducted using JMP software (SAS Institute Inc., 100 SAS Campus Drive, Cary, USA). The Shapiro–Wilk Goodness of Fit test was used to ensure data and their errors did not differ significantly from a normal distribution. Total nightly signalling time, average hourly trilling bout number and average trilling bout duration data were log-transformed to meet assumptions of normality. I used ANOVAS to determine if flightless males differed from flight capable males in their signalling behaviour. To account for the three ANOVAS performed, I adjusted the significance probability to $p < 0.0283$ using the Dunn–Šidák method (Sokal & Rohlf 1995). I used a chi-square analysis to determine if flightless males differed from males capable of flight in the proportion of individuals that signalled.

Results

Almost twice as many of the flight capable males signalled during the monitoring period in comparison to the flightless males [50% of the flight capable males (20/40) vs. 26% of the flightless males (9/35)]; these proportions of signallers vs. non-signallers differ significantly across these two wing morphs (Pearson $\chi^2 = 4.642$, $p = 0.031$, $df = 74,1$, $R^2 = 0.047$). Further, average signalling time for flight capable males was twice that of flightless males

Table 1: Description of *Gryllus texensis* flight capable and flightless male long distance mate attraction signals. Only males that signalled acoustically are included in the analyses. Significance levels are Sidak's adjusted to $p < 0.0283$ to account for the three ANOVAS

Signaling parameter	Species	x	SD	Variance	Skewness	CV	n	p-Value	F	R ² _{adj}	df
Signaling time (min)	Flight capable	127.22	109.69	12031	1.10	86.22	20	0.0275	5.43	0.14	1,27
	Flight incapable	56.27	69.59	4842	0.85	123.65	9				
Bout duration (min)	Flight capable	37.86	65.47	4286	3.21	172.93	20	0.0854	3.19	0.07	1,27
	Flight incapable	35.83	67.05	4495	1.63	187.11	9				
Hourly bout number	Flight capable	0.28	0.57	0	4.16	207.59	20	0.7477	0.11	0.03	1,27
	Flight incapable	0.12	0.29	0	3.54	253.62	9				

(Table 1), this difference was significant (ANOVA $F = 5.430$, $df = 27,1$, $R^2_{adj} = 0.137$, $p = 0.028$). The two wing morphs did not, however, differ in their hourly trilling bout number or their average trilling bout duration (Table 1).

Discussion

Flight capability in Texas field cricket males appears to have a real benefit. Not only can flight capable males move to a new location when access to food and/or females warrant it, they appear to be twice as likely to signal acoustically, and to do so for twice the duration of their flightless counterparts. These results tentatively suggest that the trade-off model proposed to account for the maintenance of wing dimorphism does not fit this species.

Crnokrak and Roff (1998) suggest that discussions of how trade-offs between traits might constrain evolution should also address the quantitative genetic basis of the trade-off. The sand cricket, *G. firmus*, has been shown to exhibit both a phenotypic and genetic trade-off between dispersal and signalling time (Crnokrak & Roff 1995; Crnokrak & Roff 1998). All traits involved in the trade-off have significant heritabilities and the genetic correlations between these traits are also significant, suggesting that the trade-off between wing dimorphism and signalling time may be of evolutionary significance (Crnokrak & Roff 1998). It is entirely likely, however, that the cricket examined here, *G. texensis*, has a very different genetic architecture from *G. firmus*, as heritability of signalling time differs dramatically between these two species. Heritability of signalling time in *G. texensis* is minimal and does not differ significantly from zero ($h^2 = 0.006 \pm 0.045$; Bertram et al. in press), while the heritability of signalling time in *G. firmus* is quite high ($h^2 = 0.75$; Crnokrak & Roff 1998). Even though signalling time in *G. texensis* exhibits minimal heritability, it is possible that it could display a significant genetic correlation with wing morph. The genetic correlations between

signalling time and wing morph in the Texas field cricket need to be examined.

Future research should also examine whether differences in signalling time correlate (phenotypically and genetically) with differences in triglyceride levels. Triglyceride is the most abundant energy storage molecule in crickets and is the main fuel they use for flight (Zera 2005). Research suggests flight capable crickets biosynthesize substantially more triglycerides and have a decreased rate of fatty acid oxidation than crickets incapable of flight (Zhao & Zera 2002; Zera 2005). While this accumulation of triglycerides in flight capable crickets constrains ovarian growth in females (Zera & Harshman 2001; Zera 2005), it will provide the necessary fuel for the energetically demanding task of acoustic signalling in males. Under this hypothesis, instead of a trade-off between signalling time and dispersal ability, one would predict a positive relationship between the two. A positive relationship between triglyceride stores and signalling time in long and short winged morphs would explain why flight capable males are twice as likely to sing and sing for twice as long as flightless males in this population of *G. texensis*.

It is, of course, entirely possible that there may be a trade-off between male dispersal and reproduction, but this study did not capture it. If this study were repeated over more nights, or at a different time of the year, a trade-off might be revealed. For example, *Gryllus texensis* is a bivoltine species, so a resampling of the spring population (which develops in a very different environment) could reveal a trade-off between flight capability and signalling. Another possibility is that the cost of flight capability is not rendered at the level of signal production and is instead rendered at any one of a number of areas associated with reproduction, such as sperm volume, the number of offspring sired, or the total number of matings obtained. Future research should therefore also address the idea that the cost of dispersal materializes in a factor that was not investigated in this study.

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