An examination of the reproduction-flight syndrome in the Texas field cricket, *Gryllus texensis*

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And I'll be…

Takin' care of crickets, every day

Takin' care of crickets, every way

I've been takin' care of crickets, they're all mine

Takin' care of crickets and working overtime

Workout!

(with apologies to Bachman-Turner Overdrive)

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Summary

In flying insects, migration by flight and reproduction commonly trade-off as each are energetically costly activities. This trade-off is found among wing dimorphic species, where a long-winged (LW) morph can fly and invests in flight-capability at the cost of reproduction, while a short-winged (SW) morph cannot fly but has greater reproductive output. In a meta-analysis of the literature on wing dimorphic insects, I found that the trade-off was evident in females, where LW females typically have delayed ovarian development and reduced fecundity, relative to SW females. In contrast, less work has been done with males, and it was unclear if the trade-off occurs in males.

To determine whether or not a trade-off occurs in males, I compared the male flight-morphs in the wing dimorphic cricket, *Gryllus texensis*, in two behaviours that can greatly influence male reproductive success: courtship and aggression. I found that LW males had a lower probability of courting a female and of fighting a rival relative to SW males. Once LW males could no longer fly through the histolysis of their flight-muscles, I found that they had a similar probability of courting females as SW males, and that they were more aggressive than LW males who could still fly. I also compared the sizes of the mandibles of the male flight-morphs. Mandibles can be used in aggressive displays and as weapons, and previous work has shown that males with larger mandibles are more likely to win fights. I found that in addition to being more aggressive than LW males in encounters with rivals, SW males had significantly larger mandibles for their body size than LW males.

In previous studies, animals were not flown, hence the role of flight-capability on the trade-off, and not flight itself, was investigated. I found that

flight had a profound effect on the trade-off in both sexes in *G. texensis*. After flight, the ovary development of LW females was similar to that of SW females and greater than LW females who did not fly. Flown LW males had a greater probability of courting females, and were more aggressive than LW males who did not fly under certain contexts.

My results suggest that the trade-off may have been previously overestimated in wing dimorphic insects, as animals were not flown in previous studies. Moreover, wing dimorphism might reflect a reproduction-flight syndrome, where members of the different flight-morphs possess alternative strategies with respect to reproduction and aggression. Here, flight initiates reproductive investment in LW males and females. Less mobile SW males appear to have behavioural and morphological adaptations to better compete in variable habitats where resources can be limited.

Résumé

Chez les insectes volants, la migration et la reproduction sont souvent vues comme étant des activités énergétiquement coûteuses et dans lesquelles le choix d'apport énergétique varie dans un sens ou dans l'autre. Ce compromis énergétique est observé pour les insectes ayant une variation morphologique des ailes. D'un côté, une morphologie avec de longues ailes (LA) permet à l'insecte de voler et ainsi y investir plus d'énergie au détriment de celle investie pour la reproduction. D'un autre côté, une morphologie avec de courtes ailes (CA) éliminant la possibilité de vol permet une concentration de l'apport d'énergie dans la reproduction. Dans une méta-analyse de la littérature, j'ai trouvé que ce compromis énergétique était évident pour les femelles. Les femelles LA ont un développement ovarien retardé causant une réduction de la fécondité contrairement aux femelles CA. En contrepartie, moins d'études furent faites concernant les males laissant obscure l'application de concept pour ceux-ci.

Pour évaluer le possible compromis énergétique chez les males, j'ai comparé la morphologie de grillons males aux ailes dimorphiques, *Gryllus texensis,* pour deux comportements pouvant grandement influencer le succès de reproduction des males: la capacité à faire la cour et l'agressivité. J'ai trouvé que les males LA ont une probabilité moins élevée de faire la cour aux femelles ainsi que de combattre un adversaire, relativement aux males CA. Lorsque les males LA ne peuvent plus voler étant donné l'histolyse de leurs muscles de vols, ils ont une probabilité de faire la cour aux femelles semblable à celle des males CA. De plus, ils devenaient plus agressifs que les males pouvant toujours voler. J'ai aussi comparé la grosseur des mandibules de

males ayant la morphologie pour voler. Les mandibules pouvant être utilisées lors de manifestations agressives ou comme armes. Des études précédentes ont montré que les males avec de plus grosses mandibules étaient plus sujet à gagner un combat. En plus d'être plus agressif que les males LA, j'ai trouvé que les males CA avaient des mandibules significativement plus grosses comparativement à leur grosseur corporelle que les males LA.

Dans les études précédentes, les insectes n'ont pas eu la possibilité de voler, ainsi le rôle de la capacité à voler dans le compromis énergétique a été évalué et non l'effet du vol comme tel. Après un vol, j'ai observé que le développement des ovaires des femelles LA était semblable à celui des femelles CA, mais plus développé que pour les femelles LA n'ayant pas volées précédemment. Les males LA ayant volés avaient une plus grande probabilité de faire la cour aux femelles et étaient plus agressifs (dans des situations précises) que des males LA n'ayant pas volés précédemment.
Mes résultats suggèrent que le compromis énergétique existant chez les insectes ayant les ailes dimorphiques a pu être surestimé dans les études précédentes. Cependant, le dimorphisme des ailes pourrait refléter un syndrome de reproduction-habilité de vol, où les membres de différentes morphologies d'ailes possèderaient certaines stratégies alternatives. Dans le cas présent, le vol déclencherait l'investissement d'énergie pour la reproduction chez les males et femelles LA. Les males CA moins mobiles paraissent avoir un comportement et une morphologie mieux adaptée pour compétitionner dans des habitats variables où les ressources peuvent être limitées.

Contributions of Authors

Chapter 1 is in revision in Biological Reviews. I conducted this meta-analysis in its entirety.

Chapter 2 was published in the Journal of Insect Behavior (2007, 20: 377-387). The study and analysis was designed and performed by me. G. S. Pollack co-authored the published manuscript.

Chapter 3 was published in Biology Letters (2009, 5: 229-231). The initial idea for the experiment was G. S. Pollack’s. I designed and conducted the experiment, and analyzed the data. The published paper was co-authored by G. S. Pollack.

Chapter 4 has been accepted pending revision in Animal Behaviour. Experiments were designed and conducted by me. I also analyzed the data. G. S. Pollack co-authored the manuscript.

Chapter 5 is in preparation for submission. I designed the study, and collected and analyzed the data. The manuscript was co-authored by G. S. Pollack.

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General Introduction

General Introduction

Migration, insect flight, and variation in flight performance

Many species live in variable environments, where habitats can be both temporally and spatially heterogeneous. The ephemeral and dynamic nature of these habitats has selected for the evolution of strategies that allow individuals to be able to escape or diminish the impact of a changing environment. One important strategy that has evolved in many taxa is that of migration (Dingle & Drake 2007; Roff & Fairbairn 2007a).

Migration has a variety of functions for animals living in spatiotemporally varied conditions. For example, migration can be an escape strategy, as it can facilitate the movement of animals from a habitat patch that has already deteriorated, to another one that is more suitable (Rankin & Burchsted 1992). Migration can also serve as a preemptive strategy where individuals will be able to exploit new resources. Some individuals will leave a given area when conditions have started to become adverse, but before the quality of their current habitat has eroded significantly (Dingle & Drake 2007). Finally, migration can be a colonizing strategy, as it can allow individuals to take advantage of alternative, and possibly better, resources found in other habitats, even when their current habitat patch is still stable (Rankin & Burchsted 1992). As such, migration can be adaptive for animals, as it can greatly influence the habitat and resource options that are available to them (Rankin & Burchsted 1992).

Insects represent one of a few taxonomic groups (the others being pterosaurs, birds, and bats) that have evolved powered flight as a method for migration. Flight permits insects to migrate over a wide range of distances, from several meters to over thousands of kilometers in some species (Rankin & Burchsted 1992; Roff & Fairbairn 1991, 2007). Moreover, flight enables individuals to better avoid and escape terrestrial predation, and allows for more efficient movement in three-dimensional space or over large areas during foraging and the search for mates, relative to flightless individuals (Roff 1994).

Insects, however, can also incur significant costs and risks due to flight and migration. Flight can be an energetically expensive activity (Wegener 1996), as the rate of metabolism during flight can be 50 times that of an individual's metabolic rate at rest (Roff 1991). Individuals must invest heavily into both developing and maintaining the flight apparatus (long flight wings, functional flight muscles, and flight fuels) (Zera & Denno 1997). During flight, insects expose themselves to additional predation risks not faced by non-fliers (e.g., aerially hawking bats; Hoy 1992), and the risk of being taken by wayward winds that can carry them far away from suitable conditions (Gatehouse 1997). Individuals have no guarantee that the new habitat patch that they will arrive at is any better or even similar to the one they had left, after migration. Moreover, they run the risk of not finding a new habitat patch at all (Roff & Fairbairn 2007a).

Flight performance can vary between individuals in volant insect species. First, in some species, individuals will all possess the necessary flight apparatus, with some that are very likely to fly, while others have a low propensity for flight (Fairbairn & Roff 1990). Second, individuals in certain species will all have functional flight-wings, but will vary in flight-muscle condition (Harrison 1980; Fairbairn & Roff 1990; Zera et al. 1997). The flight muscles of some individuals can remain underdeveloped or be absent even after the adult molt. In contrast, some individuals will have fully developed flight muscles during adulthood, but these will then degenerate as a result of histolysis at some point, making them unable to fly (Fairbairn & Roff 1990). Third, certain species are wing-dimorphic, where individuals are either long-winged or short-winged (Roff & Fairbairn 1991). Among wing dimorphic insects, there is variation among species in the relative flight ability of the wing morphs. In some wing dimorphic species, the flight-incapable morph will not possess wings at all (i.e., apterous morph). For some wing dimorphic species, both the long- and short-winged morphs can fly (e.g., beetles – Chaudhuri 2005), whereas in other species, neither morph can fly (e.g., firebugs – Socha 2006). Typically, however, only the long-winged morph can fly in wing dimorphic species (e.g., field crickets – Walker & Sivinski 1986), and long-winged individuals can become functionally flightless when their flight muscles have histolyzed.

A trade-off between flight-capability and reproduction

In general, individuals have a limited amount of resources to allocate to different biological processes and traits. When each of these traits and processes are energetically costly, it is predicted by life history theory that they will trade-off, i.e., they will be negatively associated with one another (Zera & Denno 1997; Zera & Harshman 2001). As flight is an energetically costly activity, it has been found to trade-off with other costly processes in insects. A well-established and important trade-off is that between flight-capability and reproduction. In this trade-off, one morph is flight-capable, as it invests in the ability to fly at the expense of reproduction. In contrast, another morph is flight-incapable, but has greater reproductive output (Harrison 1980; Roff 1986; Zera & Denno 1997).

The trade-off between flight capability and reproduction has been well studied in wing dimorphic insects, where the vast majority of work has focused on females (Roff 1986; Zera & Denno 1997; Zera & Harshman 2001). It has been established that flight-capable females have significantly delayed ovarian growth, a longer onset of reproduction, and lower adult fecundity than flight-incapable females (e.g., wing dimorphic field crickets: *Gryllus firmus* – Roff 1984; *Gryllus rubens* – Zera & Rankin 1989).

If flight-incapable individuals can have greater reproductive success than their flight-capable counterparts, why then does flight dimorphism exist in insects? One hypothesis is that flight capability remains as a result of habitat heterogeneity, where flight-capable animals are better at dealing with changing environments than less mobile, flight-incapable individuals. Therefore, the advantages of being able to migrate (as above) are predicted to offset the reproductive penalty associated with flight capability.

In contrast to females, significantly less work has examined the trade-off in males of wing dimorphic species. Some studies have reported the presence of a negative correlation between flight-capability and reproduction in males, supporting the existence of a trade-off. For example, relative to short-winged males, long-winged males can invest less into mate attraction signaling (field crickets – Crnokrak & Roff 1995), nuptial gifts (decorated crickets – Sakaluk 1997), early adult gonadal development (field crickets – Crnokrak & Roff 2002), and do not possess weapons that are used in combat against rivals (thrips – Crespi 1988). In contrast, some studies suggest the absence of the trade-off, as no significant difference in paternity between the morphs has been found (field crickets – Roff & Fairbairn 1991, 1993; Holtmeier & Zera 1993), and other studies have found no difference in gonadal investment between the morphs (field crickets – Roff & Fairbairn 1991, 1993; Zera et al. 1997).

Furthermore, the advantage that one morph can have over the other for a given trait can be context-dependent. For example, in planthoppers, long-winged males were better at finding mates and acquiring matings in sparse vegetation and at low female densities. In contrast, short-winged males were superior in finding and mating with females in contiguous vegetation and when females were in high densities (Langellotto & Denno 2001).

Therefore, the lack of a clear trade-off in males suggests that differences in flight capability between the male flight-morphs may not have evolved as a result of the trade-off, i.e., short-winged males have not evolved due to a relative fitness advantage as compared with long-winged males. Instead, wing dimorphism in male insects may simply result from genetic correlations with females, where there is strong selection in females for increased reproductive output at the expense of flight capability (Roff & Fairbairn 1991).

The failure to find a consistent trade-off in males may also result from the different ways the sexes invest into reproduction: females usually invest significantly more into gonads and gametes than males (Zera & Denno 1997; Cunningham & Birkhead 1998). Consistent with this difference in reproductive investment between the sexes, is the fact that trade-offs in females are expressed in terms of smaller gonads and lower fecundity in flight-capable animals relative to flight-incapable individuals, whereas there is no significant difference in siring success, and gonad size, in males of the different flight-morphs. As the reproductive investment of males is focused primarily on traits related to acquiring a mate, e.g., mate attraction displays and overt competition with rivals for mates (Cunningham & Birkhead 1998), this might explain why some studies failed to find a difference in reproduction between the different male flight-morphs.

The capability to fly and actual flight

Previous work has shown that the production and maintenance of functional flight muscles are the underlying factors in the trade-off between flight-capability and reproduction. For example, in field crickets, long-winged females with functional flight muscles have decreased reproductive output relative to long- and short-winged females with non-functional flight muscles (Zera et al. 1997). Functional flight muscles are larger, and consist of muscle fibers that are both larger and greater in number, as compared to non-functional flight muscles. Moreover, functional flight muscles possess a higher content of mitochondria and cytochrome, as indicated by their red-to-pink colouration, than non-functional, white flight muscles (Shiga et al. 1991; Gomi et al. 1995; Zera et al. 1997). In addition to the cost associated with possessing functional flight muscles, flight-capable individuals also incur the cost of synthesizing high levels of high-energy triglyceride flight fuels, substances that their flight-incapable counterparts need not produce (Zera et al. 1994).

Although a large amount of work has examined the differences in reproductive investment between flight-capable and flight-incapable individuals in wing dimorphic species, in those experiments, flight-capable animals did not actually fly. Hence, the effect of flight on the trade-off in wing dimorphic insects was not examined (Zera 2005). Interestingly, the act of flight itself can have both a positive and negative effect on the reproduction of insects. For example, flight can either enhance (e.g., migratory grasshoppers – McAnelly & Rankin 1986; field crickets – Dyakonova & Krushinsky 2008) or reduce (e.g., fruit flies – Roff 1977), the reproductive output of some wing monomorphic species.

As the onset of reproduction can be delayed until after a migration event in some insect species (i.e., the oogenesis-flight syndrome – Johnson 1969; Roff & Fairbairn 2007a), this suggests that migration and reproduction can be successive stages in the life history of insects (Rankin & Burchsted 1992). Therefore, if flight-capable individuals have increased reproductive output after migration, it is possible that the differences in reproduction between the flight-morphs seen prior to flight in wing dimorphic insects, is due to a reproduction-flight syndrome where flight initiates reproduction. Moreover, if flight-capable animals remain flight-capable after flight (i.e., they still possess functional flight muscles), yet have increased reproductive output, this would indicate that animals have sufficient energy resources to support both flight-capability and reproduction. Therefore, wing dimorphism would not necessarily reflect a trade-off in energetic investment between flight-capability and reproduction. Instead, wing dimorphism might indicate alternative strategies within a species, where some individuals are adapted to be colonists of new habitats, and reproduction occurs once animals have undergone a migratory event (Rankin & Burchsted 1992).

Field crickets: a model system

Field crickets (Orthoptera; Gryllidae) have been used extensively as a model system in biology, as they are a diverse taxonomic group, can be reliably reared in the laboratory, and are easily collected in the field (Capinera et al. 2005). With respect to the trade-off between flight-capability and reproduction, field crickets have been used extensively in studies examining the evolution and quantitative genetics of migration and the life history trade-offs related to this activity (see Roff & Fairbairn 2007a, b), as well as the physiological and endocrine mechanisms that control the trade-off (see Zera 2004). Moreover, given their rich, yet easily described and quantifiable behavioural repertoire, they are frequently chosen as an ideal organism in studies examining mating (e.g., Crnokrak & Roff 1995; Zuk et al. 2008) and aggressive (e.g., Adamo & Hoy 1995; Jang et al. 2008) behaviours and strategies.

Goals and aims

In this dissertation, I will examine the life history trade-off between flight capability and reproduction in wing dimorphic insects, with the goal of investigating how various factors can influence the expression of the trade-off. I aim to: 1) review the literature to ask how the trade-off is expressed across taxa, within the sexes, and among different life history traits; 2) test the hypothesis that there is a trade-off between flight capability and behaviours correlated with reproductive investment in males; and 3) determine if there are factors that might mitigate the expression of the trade-off in wing dimorphic species.

In chapter 1, I use meta-analysis to review the literature examining the trade-off in wing dimorphic insects. I determine whether or not the trade-off occurs in both males and females across many species, and determine which traits trade-off with flight in both sexes. I also examine if long-winged individuals possess an advantage in some traits, relative to short-winged individuals, that might either eliminate or at least attenuate, the reproductive cost of being able to fly. Given the diversity and different evolutionary histories of wing dimorphic insect species, I also investigate whether or not the expression of the trade-off might also vary taxonomically. Finally, given that wing dimorphic insect species can vary in the relative flight ability of the different wing-morphs, I ask if a trade-off exists in species when there is no difference in the flight capability of the wing-morphs. If the reproductive output of the wing-morphs is similar in species where the wing-morphs do not differ in flight capability, this would support the idea that differences in the energetic investment into flight of different wing-morphs is what underlies the trade-off.

In chapters 2 and 4, I test the hypothesis that there is a trade-off between flight capability and reproduction in males of wing dimorphic insects, using males of the wing dimorphic field cricket, *Gryllus texensis* Cade & Otte (2000). *Gryllus texensis* males will court females and fight rivals for access to mates. In crickets, both of these behaviours can be energetically costly (courtship: Hack 1998; fighting: Hack 1997) and influence the ability of males to acquire mates (courtship: Balakrishnan & Pollack 1996; fighting: Simmons 1986). Here, I predict that long-winged males will have a lower probability of courting a female (chapter 2) and of fighting a rival (chapter 4), relative to short-winged males. I also examine how the loss of flight capability in long-winged *G. texensis* males can influence their courtship and fighting behaviour. I predict that with the occurrence of flight muscle histolysis, the probability of courtship and fighting in long-winged males will be greater than that of long-winged males who still possess functional flight muscles. Moreover, I predict that the behaviour of long-winged males without functional flight muscles will be similar to that of short-winged males. If courtship and fighting behaviours are negatively correlated with flight capability, this would support the existence of a phenotypic trade-off in males, such that the inability to fly in males can be adaptive.

In chapters 3 and 4, I determine how the performance of flight can affect the occurrence of a trade-off in wing dimorphic insects. Here, I determine the impact of flight on the gonadal investment of long-winged females (chapter 3), and the courtship (chapter 3) and fighting (chapter 4) behaviour of long-winged males, in *G. texensis*. Currently, it is unknown how flight might affect the expression of the trade-off in wing dimorphic insects, as animals in previous experiments were not flown.

As the decreased mobility of short-winged males effectively limits them to the resources that are immediately available in their habitat, I predict that short-winged males will be more aggressive and have a higher probability of fighting a rival than long-winged males, as increased aggression can assist in acquiring resources (chapter 4). Therefore, in chapter 5, I examine whether or not short-winged males possess adaptations that mitigate their decreased mobility relative to long-winged males. In field crickets, males use mandibles as weapons in aggressive interactions (e.g., aggressive displays and overt fighting – Adamo & Hoy 1995; Hofmann & Schildberger 2001). Thus, I predict that short-winged males will invest more into the production of mandibles: short-winged males might have larger mandibles, as larger weapons might enable them to be better competitors against rivals (Judge & Bonanno 2008).

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Chapter 1

Evaluating the life history trade-off between flight capability and reproduction in wing dimorphic insects: a meta-analysis

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Abstract

The life history trade-off between flight capability and reproduction is important in wing dimorphic insects. Here, a long-winged morph is flight-capable at the expense of reproduction, while a short-winged morph cannot fly, is less mobile, but has greater reproductive output. Using meta-analysis, I reviewed the literature to ask specific questions regarding the trade-off. The trade-off in females was expressed primarily as a later onset in reproduction and lower fecundity in long-winged females relative to short-winged females. Although considerably less work has been done with males, the trade-off exists for males among traits primarily related to mate acquisition. The trade-off is potentially mitigated in males only, as long-winged individuals possess an advantage in traits that can mitigate the costs of flight capability, e.g., long-winged males develop faster than short-winged males. The strength and direction of trends differed significantly between insect orders, and there was a relationship between the strength and direction of trends with relative flight capabilities between the morphs. I discuss how the trade-off might be both under- and overestimated in the literature, especially in light of work that has examined how actual flight might affect the expression of the trade-off.

Introduction

Occurring in many insect taxa where flight is the chief mode of dispersal is an important and well-established trade-off between flight capability and reproduction. Here, one morph is flight capable, and expends energy developing and maintaining the flight apparatus at the expense of reproduction. Alternatively, another morph is flight-incapable, but has greater reproductive output, relative to the flight-capable morph. This trade-off occurs as both flight-capability and reproduction are each energetically costly, and when different traits are each energetically costly, some traits can be emphasized at the expense of others (Roff, 1986; Zera & Denno, 1997; Zera & Harshman, 2001). In this paper, I examine the trade-off in species where flight dimorphism is characterized in its most extreme form, that of hind-wing dimorphism. One morph is long-winged, as it possesses long, functional flight wings (i.e., macropterous and alate individuals). In contrast, another morph is short-winged and is incapable of flight, due to having either reduced (i.e., micropterous) or underdeveloped, rudimentary wings (i.e., brachypterous). Flightless individuals can also be wingless, i.e., apterous (in this paper, I include apterous individuals within the short-winged category) (Harrison, 1980; Roff, 1986; Zera & Denno, 1997). Using meta-analysis, I quantitatively reviewed the literature in order to ask specific questions regarding the trade-off in wing dimorphic insects.

The trade-off in wing dimorphic insects has been previously reviewed qualitatively (see Harrison, 1980; Zera & Denno, 1997) and quantitatively (see Roff, 1986; Denno *et al.*, 1989; Roff & Fairbairn, 1991; Roff 1995). These reviews have examined the trade-off using data primarily (e.g., Roff, 1986; Roff & Fairbairn, 1991; Roff 1995) or exclusively from females (e.g., Denno *et al.*, 1989). Flight-capable females have delayed ovarian growth, longer reproductive latency, and lower fecundity relative to their flight-incapable counterparts (Roff, 1986; Zera & Denno, 1997; Zera & Harshman, 2001). It is possible, however, that flight-capable females can mediate the reproductive costs related to flight capability if they possess an advantage in other traits relative to flight-incapable females. For example, flight-capable females may accrue similar reproductive success as flight-incapable females if they live significantly longer. Therefore, I examined female traits that are possibly involved in the trade-off, as well as traits that might attenuate the trade-off, in order to ask if trade-offs might be transient in females.

In contrast to females, the trade-off in males has received much less attention. Some studies have observed the trade-off in certain male traits (e.g., calling effort – Crnokrak & Roff, 1995; courtship behavior – Guerra & Pollack, 2007), while the trade-off is absent in other traits (e.g., siring success – Holtmeier & Zera, 1993; Roff & Fairbairn, 1993). These conflicting results suggest as there is strong selection in females for individuals with enhanced reproductive output and reduced flight ability, males may have evolved morphs incapable of flight because of genetic correlations with females (Roff & Fairbairn, 1991). Hence, by evaluating many male traits, I asked 1) if the trade-off occurs in males as in females, and 2) what type of traits are involved in the trade-off in males.

Given that insects are a very diverse group, it is possible that the expression of the trade-off can vary taxonomically. Roff (1995) found that among orthopteran species, it is the long-winged morph that develops faster, but that in other orders, it is the short-winged morph with faster development. Therefore, I also ask whether taxonomic differences influence the expression of the trade-off in wing dimorphic insect species. For example, I predicted that it would be the long-winged morph with a longer development time relative to the short-winged morph among orthopteran species, while this trend would be reversed among non-orthopteran species (Roff, 1995).

Species exhibiting wing dimorphism vary in the flight capabilities of the two wing- morphs. In some species both morphs can fly (e.g., *Oncopeltus fasciatus*), in other species only the long-winged morph can fly (e.g., *Gryllus texensis*), while in others neither morph is capable of flight (e.g., *Pyrrhocoris apterus*). Individuals that fly have higher resting metabolic rates than individuals that use types of locomotion that are less energetically demanding, e.g., walking (Reinhold, 1999). Flying individuals also shift a considerable amount of their metabolic resources into flight fuels, whereas non-flyers do not (Zera, 2005; Zera & Zhao, 2006). As such, I asked whether the trade-off exists in species even when there is no difference in flight ability between the wing morphs.

Methods

Data collection

I conducted a search for papers that compared the different wing-morphs (long-winged (LW): macropterous and alate morphs; short-winged (SW): micropterous, brachypterous, and apterous morphs) of the same species in different traits (Tables 1.1 and 1.2), when under the same treatment conditions. Using The Web of Science, PubMed, and Google Scholar, I performed search queries based on the following terms: *dispersal polymorphism*; *wing polymorphism*; *alary polymorphism*; *wing dimorphism*; *dispersal*; *reproduction*; *life history trade-off*; *trade-off between flight capability and reproduction*; *siring capability of male wing forms*, *winged*; *wingless*; *active*; *normal*.

I performed two types of meta-analysis for each of the different traits, one using significance statistics (p values) and another using effect size measures (correlation coefficient, *r*). A study was evaluated and included in both types of meta-analysis only if it followed these selection criteria: 1) it must have examined the wing-morphs of a given species under the same conditions; and 2) it must have at least reported a p value and the sample size associated with that p value, or contain enough data where I could calculate a p value. If there was only a single study providing adequate data for a given trait, meta-analysis was not performed on these data, but the paper was classified into a 'Single study' category. Papers containing anecdotal accounts of a difference between the wing-morphs (either the presence or absence), or which lacked sufficient data to calculate a p value and *r* value, were excluded from subsequent analyses and grouped into a 'Descriptive' category.

Collection of data for p value meta-analyses

P values and sample sizes were collected from papers. In studies that contained enough data, I calculated exact p values. If p values were reported more than once in a study (e.g., from different years, different temperature treatments), I calculated the average, and for studies that indicated a range, I used the mid-point. I ignored "greater than" and "less than" signs when recording values, e.g., $p < 0.01$ was recorded as 0.01. When the results of a paper were reported as non-significant and only $p > 0.05$ was provided, I converted this to a p value of $p = 1.00$ (Rosenthal & DiMatteo 2001). When there were multiple p values for a given trait for a single species (i.e., there were multiple studies investigating the same trait for a species), I calculated the average p value. As species was the unit of analysis in my meta-analyses, I pooled the sample sizes of studies for a specific trait, for a given species.

Collection of data for effect size meta-analyses

I calculated correlation coefficient effect size statistics (*r* values) from data contained in papers using established methods (Lipsey & Wilson, 2000; Rosenthal & DiMatteo 2001). Briefly, I took the p value (one-tailed) for a given trait from a study, and converted it into its associated standard normal deviate. I then took this standard normal deviate value and divided it by the square root of its associated sample size to produce an *r* value. When multiple *r* values could be generated from data provided in a study (e.g., from different years and/or different treatments, with respect to a single trait), I first transformed each *r* value into its Fisher *Z* transformation of *r* (*Z* values: Silver & Dunlap, 1987), and I then found the mean of these *Z* values. I then backtransformed this mean *Z* value into *r* to produce a mean correlation coefficient for the trait from that particular study (Silver & Dunlap, 1987). I followed the same procedure when there were multiple *r* values for a given trait for a single species as a result of multiple studies investigating the same trait within a species.

Meta-analysis

I performed separate meta-analyses on the different traits that compared the wing-morphs (Tables 1.1 and 1.2). I divided these analyses according to the type of statistic used (p or *r* value), according to the relative flight capabilities of the wing-morphs (both can fly, only the LW can fly, or neither can fly), and sex (male or female).

Meta-analyses using p values

I used "Meta-Analysis Software" version 5.3 (Schwarzer, 1989) for p value meta-analyses. The one-tailed probabilities of collected *p* values were converted to *z* score test statistics. When p values were significant but in the opposite direction of what I predicted, values were entered as negative during the analysis. These *z* scores were then used to generate an overall p value for the tested hypothesis for each trait (Stouffer's method; Stouffer *et al*. 1949). I used species as my unit of analysis. Although the true level of replication is at the species level (Whitlock, 2005), I conducted weighted meta-analyses, where I weighed each p value by its corresponding sample size, to take into account that a p value based on a larger sample size (e.g., n = 1000) is worth more than one based on a smaller sample size (e.g., n = 10) (Lipsey & Wilson 2000).

I also conducted a test of homogeneity for each analysis. A significant departure from homogeneity shows that there were variations in trends among the studies included in the analysis. When this occurs, it is possible to look for modifier variables to account for the heterogeneity among studies, and conduct further analyses taking these variables into account (Lipsey & Wilson 2000; Rosenthal & DiMatteo 2001). As suggested by Roff (1995), when heterogeneity was identified, I performed further separate meta-analyses according to taxonomic distinctions for each trait. Here, I conducted analyses according to insect order when there were sufficient species within an order to conduct a subsequent analysis (i.e., n ≥ 2 species per order).

Meta-analyses using effect sizes

Previous quantitative reviews of the trade-off between flight-capability and reproduction have used statistical significance (i.e., p values) to evaluate the literature (Roff, 1986; Denno *et al.*, 1989; Roff & Fairbairn, 1991; Roff 1995). The approach of using statistical significance in hypothesis testing in biology, however, has been criticized. For example, in a recent review by Nakagawa & Cuthill (2007), the authors suggest that significance testing does not allow us to assess biological importance, since it does not allow us to measure the magnitude of an effect, nor does it allow us to adequately measure the relationships within data effectively. To address this concern, I also performed meta-analyses using effect size statistics (i.e., correlation coefficients, *r*), which measure the magnitude of an effect in the traits used to investigate the trade-off. For these analyses, species was also the unit of analysis (as above).

I conducted effect size meta-analyses using methods described in Lipsey & Wilson (2000), and software provided by the authors that operate in the statistical package SPSS (http://mason.gmu.edu/~dwilson/ma.html). I used SPSS Version 17 (SPSS Inc.) for analyses. Briefly, *r* values for a trait were converted to *Z* values using the Fisher Z transformation, and prior to analysis, each of these *Z* values was weighed by its inverse variance (n – 3; Lipsey & Wilson 2000). A mean *r* value, with its corresponding 95% confidence interval, was then calculated for the given trait. The magnitude of the effect for each mean *r* value was assessed using the established ranking scale of Cohen (1988). For example, *r* values ranging from 0.0 – 0.1 are considered trivial or having a negligible effect, those from 0.1 – 0.3 are judged as having a small or minor effect, those between 0.3 – 0.5 are considered as having a medium or moderate effect, and those ≥ 0.5 are judged as having a large or major effect.

As in my p value analyses, I assessed heterogeneity among *r* values using the Q test of heterogeneity. When significant heterogeneity was identified, I performed further analyses where I grouped data by insect order, as insect order might be an important moderator variable that helps explain the heterogeneity of the data set (Roff, 1995).

Assessment of publication bias

I addressed potential publication bias in the literature in several ways. First, given the "file-drawer" problem, where studies with negative results are less likely to be published, I included non-significant results (i.e., no difference was found between the morphs for a given trait) in both p and *r* value meta-analyses. Leaving out negative studies will substantially bias the result so that any relationship between the wing-morphs would appear to be more significant than it actually is.

Second, I generated fail-safe numbers for both p and *r* value analyses of the traits investigating the trade-off. The fail-safe number measures the robustness of the analysis, as it estimates the number of studies reporting an absence of the predicted relationship that would need to be included in the analysis to eliminate significance or an observed effect. To test the robustness of these fail-safe numbers, I compared each estimated fail-safe number to the actual number of unpublished studies that can negate the results of a given study (a tolerance level calculated as $5K + 10$, where K is the number of species included in each meta-analysis; Rosenthal, 1991). When the fail-safe number is larger than $5K + 10$, we can conclude that the results of our meta-analysis can be trusted. "Meta-Analysis Software" generated fail-safe numbers for p value analyses. I used methods described by Rosenberg (2005) and software provided by the author (http://www.rosenberglab.net/software.php) to generate two types of fail-safe numbers (Rosenberg N_1 and N_+ fail-safe numbers) for *r* value analyses.

Finally, I used funnel plots to assess publication bias, where I plotted *r* values against the standard error of these *r* values (Sterne & Egger, 2001). In funnel plots, asymmetry in the shape of the plot can indicate publication bias. The use of funnel plots to investigate for publication bias, however, has been criticized, as they do not accurately predict publication bias (Lau *et al*., 2006). For example, asymmetry in a funnel plot can result from other factors not necessarily related to publication bias, such as other dissemination biases, differences in the quality of studies (in particular, smaller studies), the existence of data set heterogeneity, and chance (Tang & Liu, 2000; Macaskill *et al*., 2001; Souza *et al*., 2007). In particular, when heterogeneity exists, it is possible to incorrectly infer publication bias (Terrin *et al*., 2003; Lau *et al*., 2006). Moreover, funnel plots cannot adequately be used if there are only a low number of data points to be plotted (Macaskill *et al*., 2001; Lau *et al*., 2006). Due to these caveats, I used funnel plots to visually inspect for asymmetry for traits where sample sizes were reasonably large only (i.e., $n \geq 20$).

Results

Differences in development between the morphs

Meta-analyses: females, only the LW morph can fly

No difference in development time between the morphs was observed ($n = 12$: mean $p = 0.40$, assessment: non-significant; Figure 1.1a and Table 1.3; mean *r*

= -0.04, 95% CI: -0.06 - -0.01, assessment: trivial/negligible effect; Figure 1.2a and Table 1.3). As strong heterogeneity existed in the data set (p value homogeneity test: 56.66, df = 11, p < 0.00001; *r* value Q: = 209.65, df = 11, p < 0.05), I used insect order as a modifier variable, as it accounted for significant variability in effect sizes (e.g., *r* value between insect order Q = 94.11, df = 1, p < 0.00001; single coleopteran and dermapteran species omitted).

Among hemipterans, the SW morph develops faster than the LW morph (n = 5: mean p = 0.0004, fail-safe number = 44, assessment: robust significant result; mean *r* = 0.25, 95% CI: 0.22 – 0.29, fail-safe numbers: 119/206, assessment: robust, small effect; Figure 1.2a). I found this group to be homogenous when p values were considered (homogeneity test: 6.77, df = 4, p = 0.15), but not when *r* values were used (Q = 11.96, df = 4, p = 0.02). In contrast, no difference in development among the morphs in orthopteran species was seen (n = 5: mean p = 0.08, assessment: non-significant; mean *r* = 0.07, 95% CI: 0.04 – 0.11, fail-safe numbers: 9/16, assessment: trivial/negligible effect; Figure 1.2a). There was some slight heterogeneity within this group (p value homogeneity test: 10.50, df = 4, p = 0.03; *r* value Q = 12.08, df = 4, p = 0.02).

Meta-analyses: females, neither morph can fly

The SW morph develops faster than the LW morph (n = 3: mean p = 0.01, assessment: significant but non-robust; mean *r* = -0.16, 95% CI: -0.19 – -0.12, fail-safe numbers: 19/52, assessment: robust, small effect; Table 1.3). Given heterogeneity in this group (p value homogeneity test: 8.67, df = 2, p = 0.01; *r* value Q = 24.54, df = 2, p < 0.001), I performed a subsequent analysis involving the homogenous hemipteran group only (p value homogeneity test: 0.9552, df = 1, p = 0.33; *r* value Q = 0.16, df = 1, p = 0.69). When hemipterans were considered separately, the trend for the SW morph to develop faster than the LW morph was still present (n = 2: mean p = 0.003, fail-safe number = 3 assessment: significant, but non-robust; Table 1.3; mean *r* = 0.18, 95% CI: 0.15 – 0.22, fail-safe numbers: 9/46; assessment: robust, small effect; Table 1.3).

Meta-analyses: males, only the LW morph can fly

I found no difference in development time between the morphs (n = 12: mean p = 0.22, assessment: non-significant; Figure 1b; mean *r* = 0.04, 95% CI: 0.01 – 0.06, fail-safe numbers: 13/16, assessment: trivial/negligible effect: Figure 1.2b). There was strong heterogeneity within this group (p value homogeneity test: 45.65, df = 11, p < 0.00001; *r* value Q = 425.99, df = 11, p < 0.00001), so I performed further analyses using insect order as a modifier variable. Insect order was found to account for significant variability in effect sizes (e.g., *r* value insect order Q = 341.81, df = 2, p < 0.00001; single dermapteran species omitted).

There was a trend for the SW morph to develop faster than the LW morph in thysanopterans (n = 2: mean p = 0.004, fail-safe number = 2, assessment: significant but non-robust; mean *r* = 0.17, 95% CI: 0.07 – 0.27, fail-safe numbers: 0.2/5, assessment: non-robust, small effect; Figure 1.2b) and hemipterans (n = 4: mean p = 0.003, fail-safe number = 15, assessment: significant but non-robust; mean *r* = 0.21, 95% CI: 0.18 – 0.24, fail-safe numbers: 70/141, assessment: robust, small effect). Both of these groups were homogenous (thysanopterans: p value homogeneity test: 1.78, df = 1, p = 0.18;

r value Q = 0.32, df = 1, p = 0.57; hemipterans; p value homogeneity test: 3.00, df = 3, p = 0.39; *r* value Q = 6.89, df = 3, p = 0.08). In contrast, the LW morph develops faster than the SW morph in orthopterans (n = 5: mean p = 0.03, fail-safe number = 3, assessment: significant but non-robust; mean *r* = 0.26, 95% CI: 0.23 – 0.29, fail-safe numbers: 175/302, assessment: robust, small effect). Orthopterans were found to be a heterogenous group (p value homogeneity test: 16.17, df = 4, p = 0.003; *r* value Q = 36.40, df = 4, p < 0.001).

Meta-analyses: males, neither morph can fly

Among hemipteran species, SW individuals develop faster than LW individuals (n = 2: mean p = 0.0003, fail-safe number = 5, assessment: significant but non-robust; mean *r* = 0.29, 95% CI: 0.25 – 0.32, fail-safe numbers: 23/117, assessment: robust, small effect; Table 1.3). This group was homogenous (p value homogeneity test: 2.54, df = 1, p = 0.11; *r* value Q = 1.69, df = 1, p = 0.19).

Single and descriptive studies

I found two studies (one for males, another for females) that showed when both morphs can fly, the LW morph takes longer to develop than the SW morph (Table 1.3). Among descriptive studies (Table 1.3), the LW morph was seen to have a longer development time in six cases, there was no difference between the morphs in five cases, one case was unclear, while only three cases showed that the SW morph has a longer development time.

Differences in the onset of reproduction between the morphs

Meta-analyses: females, only the LW morph can fly

LW females have a delayed onset of reproduction relative to SW females (n = 22: mean $p < 0.00001$, fail-safe number = 1363, assessment: highly significant and robust; Figure 3a; mean $r = 0.38$, 95% CI: 0.34 – 0.41, fail-safe numbers: 1470/1646, assessment: robust, medium effect; Figure 1.4a). This group was homogenous when p values were examined (homogeneity test: 14.14, df = 21, $p = 0.86$), but not when *r* values were examined ($Q = 102.03$, df = 19, $p < 0.00001$). As insect order significantly accounted for variability in effect sizes (between order $Q = 20.28$, df = 2, $p < 0.00001$; single coleopteran and dermapteran species pooled as one group), I performed separate *r* value analyses for hemipteran and orthopteran species. Among hemipterans, the LW morph had a longer onset of reproduction than the SW morph, and this effect was both large and robust (n = 16: mean *r* value = 0.44, 95% CI: 0.39 – 0.49, fail-safe numbers: 910/1065; Figure 1.4a). There was significant heterogeneity in effect sizes however ($Q = 42.95$, df = 15, $p = 0.0002$). For orthopterans, there was also a trend for the LW morph to have a later onset of reproduction relative to the SW morph, but in contrast to hemipterans, this effect was small and non-robust (n = 4: mean *r* value = 0.24, 95% CI: 0.16 – 0.32, fail-safe numbers: 14/29; Figure 1.4a). There was also significant heterogeneity in effect sizes for this group ($Q = 33.09$, df = 3, $p < 0.001$).

The funnel plot (Figure 1.5) for *r* values shows publication bias when insect order is not taken into account. The use of this funnel plot without considering insect order is inappropriate, however, given the significant heterogeneity among and within insect orders, as well as the low sample sizes for certain orders in the data set (coleopterans, n = 1; dermapterans, n = 1; orthopterans, n = 4). Consistent with the fail-safe numbers indicative of a robust result for hemipterans (above), there appears to be little asymmetry when hemipterans are considered on their own. This observation must be taken with caution, given the significant heterogeneity among *r* values, as well as the presence of an extreme outlier.

Meta-analyses: females, neither morph can fly

There was a weak trend for the LW morph to have a later onset of reproduction than the SW morph (n = 2: mean p < 0.0001, fail-safe number = 13, assessment: significant, but non-robust; mean *r* = 0.47, 95% CI: 0.34 – 0. 59, fail-safe numbers: 2/16, assessment: strong, but non-robust effect; Table 1.4).

Single and descriptive studies

When both morphs can fly, a single study in females showed no difference in the onset of reproduction between the morphs (Table 1.4). I found only one study that examined the onset of reproduction in males (a species where only the LW morph can fly), and it found that the LW morph has a later onset of reproduction (Table 1.4). For all 12 descriptive studies (Table 1.4), the LW morph had a later onset of reproduction than the SW morph.

Differences in longevity between the morphs

Meta-analyses: females, both morphs can fly

There was a weak trend for the LW morph to live longer than the SW morph (n = 2: mean p = 0.004, fail-safe number = 4, assessment: significant, but non-robust; mean *r* = 0.17, 95% CI: 0.05 – 0.29, fail-safe numbers = 0/0, assessment: non-robust small effect; Table 1.5). This group was homogenous (p value homogeneity test: 0.0037, df = 1, p = 0.9517; *r* value Q: 0.291, df = 1, p = 0.5896).

Meta-analyses: females, only the LW morph can fly

No difference in longevity between the morphs was seen (n = 24: mean p = 0.03, fail-safe number = 76, assessment: significant, but non-robust; Figure 1.6a; mean *r* = 0.08, 95% CI: 0.05 – 0.11, fail-safe numbers = 110/122, assessment: trivial and non-robust effect; Figure 1.7a). Significant heterogeneity was found in this group (p value heterogeneity test: 87.98, df = 23, p < 0.0001; *r* value Q: 116.93, df = 23, p < 0.0001). As insect order was found to be a significant moderator variable (between order Q: 30.02, df = 3, p < 0.000001; coleopteran and dermapteran species pooled into a single group), I performed separate analyses for hemipterans and orthopterans. For both orders, no difference was found between the morphs in longevity (hemipterans – n = 16: mean p = 0.03, fail-safe number = 3, assessment: significant, but non-robust; mean *r* = 0.09, 95% CI: 0.05 – 0.13, fail-safe numbers = 55/64, assessment: non-robust and trivial effect; Figure 7a; orthopterans – n = 6: mean p = 0.28, fail-safe number = 30, assessment: non-significant; mean *r* = 0.06, 95% CI: 0 – 0.12, fail-safe numbers = 0/0, assessment: non-robust and trivial effect; Figure 1.7a).

Meta-analyses: males, only the LW morph can fly

A weak trend for the LW morph to have greater longevity than the SW morph was observed (n = 14: mean p = 0.03, fail-safe number = 4, assessment: significant but non-robust; Figure 1.6b; mean *r* = 0.10, 95% CI: 0.04 – 0.16, fail-safe numbers = 21/25, assessment: non-robust, small effect; Figure 1.7b). As there was significant heterogeneity (p value homogeneity test: 44.57, df = 13, p < 0.001; *r* value Q: 56.95, df = 13, p < 0.0001), I performed further analyses distinguished by insect order (a significant moderator variable; between order Q: 29.37, df = 3, p < 0.00001).

No difference in longevity between the morphs was observed for hemipteran males (n = 5: mean p = 0.09, fail-safe number = 0.4, assessment: non-significant; mean *r* = 0.09, 95% CI: 0.02 – 0.16, fail-safe numbers = 0.16/0, assessment: trivial and non-robust effect; Figure 1.7b). Hemipterans composed a homogenous group (p value homogeneity test: 1.84, df = 4, p = 0.76; *r* value Q: 1.90, df = 4, p = 0.7538). In contrast, there was a modest trend for the LW morph to live longer than the SW morph in both hymenopteran (n = 5: mean p = 0.01, fail-safe number = 2, assessment: significant, but non-robust; mean *r* = 0.21, 95% CI: 0.07 – 0.35, fail-safe numbers = 1/1, assessment: non-robust, small effect; Figure 1.7b) and orthopteran males (n = 3: mean p = 0.01, fail-safe number = 3, assessment: significant but non-robust; mean *r* = 0.24, 95% CI: 0.06 – 0.39, fail-safe numbers = 0/0, assessment: non-robust, small effect; Figure 1.7b). Hymenopterans were heterogenous, with heterogeneity generated by a single species (p value homogeneity test: 15.60, df = 4, p < 0.01; *r* value Q: 21.58, df = 4, p = 0.0003; Figure 1.7b). Orthopterans, in contrast, were homogenous (p value homogeneity test: 5.28, df = 2, p = 0.07; *r* value Q: 4.25, df = 2, p = 0.12; Figure 1.7b).

Single and descriptive studies

I found 13 descriptive studies. 9 studies showed that the LW morph lived longer than the SW morph, and these studies consisted primarily of species where both morphs can fly (n = 3), and data from males (n = 4). Only four studies showed no difference between the morphs, and these were all from female data (n = 4) (Table 1.5).

Differences in traits comparing mating investment: females

Meta-analyses: only the LW morph can fly

SW females invested more into gonads than LW females (n = 5: mean p = 0.05, fail-safe number = 67, assessment: marginally significant and robust; mean *r* = 0.39, 95% CI: 0.35 – 0.42, fail-safe numbers = 318/548, assessment: robust medium effect; Table 1.6). P value data were homogenous (homogeneity test: 3.98, df = 4, p = 0.41), but *r* value data were not (Q: 12.37, df = 4, p = 0.01). Insect order was not a significant moderator variable that could explain the heterogeneity, however (between order Q: 3.56, df = 1, p = 0.06). There was no difference in mating propensity between the morphs (n = 3: mean p = 0.19, fail-safe number = 0.13, assessment: non-significant; mean *r* = 0.01, 95% CI: 0.02 – 0.17, fail-safe numbers = 0/0, assessment: trivial effect). There was no significant heterogeneity (p value homogeneity test: 1.92, df = 2, p = 0.38; *r* value Q: 6.14, df = 2, p = 0.05; Table 1.6). There was a weak trend for SW females to defend resources more than LW females (n =2: mean p = 0.01, fail-safe number = 3, assessment: significant, but non-robust; mean *r* = 0.19, 95% CI: 0.04 – 0.33, fail-safe numbers = 0/0, assessment: non-robust small effect; Table 1.6). No significant heterogeneity was found (p value homogeneity test: 0.01, df = 1, p = 0.92; *r* value Q: 0.31, df = 1, p = 0.58).

Single and descriptive studies

In a single coleopteran species, where only the LW morph can fly, the LW morph invests more into gonads than the SW morph. A single study showed that when neither morph can fly, the SW has a greater mating propensity than the LW morph (Table 1.6). Three descriptive studies showed that the SW morph invests more into gonads than the LW morph.

Differences in traits comparing mating investment: males

Meta-analyses: only the LW morph can fly

There was no difference in gonadal investment between the morphs (n = 3: mean p = 0.05, fail-safe number = 10, assessment: non-significant; mean *r* = 0.12, 95% CI: 0.09 – 0.16, fail-safe numbers: 9/25, assessment: non-robust small effect; Table 1.7). Heterogeneity was found for effect sizes only, but all three species were orthopterans (p value homogeneity test: 2.61, df = 2, p = 0.27; *r* value Q: 7.29, df = 2, p = 0.03). A weak trend showed that the LW morph invested more into accessory glands than the SW morph (n = 2: mean p < 0.01, fail-safe number = 4, assessment: significant but non-robust; mean *r* = 0.30, 95% CI: 0.12-0.47, fail-safe numbers: 0/0, assessment: non-robust medium effect; Table 1.7). There was no significant heterogeneity (p value homogeneity test: 2.89, df = 1, p = 0.09; *r* value Q: 1.44, df = 1, p = 0.23).

SW males invest more into mate attraction than LW males, but only when effect sizes were considered (n = 3: mean p = 0.05, assessment: non-significant; mean *r* = 0.31, 95% CI: 0.24 – 0.38, fail-safe numbers: 17/47, assessment: robust medium effect; Table 1.7). No significant heterogeneity was found (p value homogeneity test: 0.85, df = 2, p = 0.65; *r* value Q: 4.61, df = 2, p = 0.10). SW males also had a greater propensity for mating than LW males, but this trend was modest (n = 2: mean p = 0.0001, fail-safe number = 4, assessment: highly significant, but non-robust; mean *r* = 0.31, 95% CI: 0.15 – 0.45, fail-safe numbers = 0/0, assessment: medium effect, but non-robust;

Table 1.7). Heterogeneity was only found for p values (p value homogeneity test: 5.52, df = 1, p = 0.02; *r* value Q: 0.33, df = 1, p = 0.57).

There was no difference in competitive ability between the morphs (n = 3: mean p = 0.22, assessment: non-significant; mean *r* = 0.11, 95% CI: 0.0007 – 0.21, fail-safe numbers = 0/0, assessment: non-robust small effect; Table 1.7). Heterogeneity was seen only with effect sizes (p value homogeneity test: 2.86, df = 2, p = 0.24; *r* value Q: 8.42, df = 2, p = 0.01). Insect order was a significant moderator variable (between order Q: 7.6161, df = 1, p = 0.0058). No difference in competitive ability between the morphs was seen for hemipterans on their own (n = 2: mean *r* = 0.09, 95% CI: -0.02 – 0.19, fail-safe numbers = 0/0, assessment: trivial effect). No significant heterogeneity was found (*r* value Q: 0.80, df = 1, p = 0.37).

Meta-analyses: neither morph can fly

Data for a single species showed a weak trend for the SW morph to engage in greater mating activity than the LW morph (n = 2: mean p = 0.003, fail-safe number = 3, assessment: highly significant, but non-robust; mean *r* = 0.26, 95% CI: 0.15 – 0.35, fail-safe numbers = 1/1, assessment: small, non-robust effect; Table 1.7). Significant heterogeneity was found only for effect sizes (p value homogeneity test: 2.24, df = 1, p = 0.13; *r* value Q: 7.47, df = 1, p < 0.01).

Single and descriptive studies

SW males invest more into nuptial gifts than LW males (single study: both morphs can fly; single study: only the LW male can fly), and invest more into accessory glands (single study: neither morph can fly). SW males also invest more into weapons used for combat (single study: only the LW male can fly) (Table 1.7).

Among descriptive studies, SW males invest more into gonads (n = 1), accessory glands (n = 1), and mate attraction (n = 1). One study found that LW males have larger genitalia, while another study found no difference in mating activity between the morphs. In two of three studies, the SW morph out competes the LW morph; the third study showed no difference in competitive ability among the morphs (Table 1.7).

Differences in traits comparing mating success: females

Meta-analyses: only the LW morph can fly

There was a weak trend for SW females to have greater mating success than LW females (n = 4: mean p = 0.03, fail-safe number = 9, assessment: significant but non-robust; mean *r* = 0.11, 95% CI: 0.06 – 0.16, fail-safe numbers = 5/10, assessment: non-robust small effect; Table 1.8a). No significant heterogeneity was found (p value heterogeneity test: 5.76, df = 3, p = 0.12; *r* value Q: 6.48, df = 3, p = 0.10).

Differences in traits comparing mating success: males

Meta-analyses: only the LW morph can fly

There was a weak trend for SW males to acquire more matings than LW males (n = 8: mean p = 0.01, fail-safe number = 15, assessment: significant, non-robust; mean *r* = 0.15, 95% CI: 0.08 – 0.22, fail-safe numbers = 15/22, assessment: small, non-robust effect; Table 1.8b). No significant heterogeneity was found (p value homogeneity test: 4.28, df = 7, p = 0.75; *r* value Q: 6.39, df = 7, p = 0.50). Data from one species showed that females preferred SW males (n = 4: mean p < 0.00001, fail-safe number = 42, assessment: highly significant and robust; mean *r* = 0.40, 95% CI: 0.31 – 0.49, assessment: robust medium effect; Table 1.8b). Data for this species were homogenous for p values (homogeneity test: 3.85, df = 3, p = 0.28), but not effect sizes (*r* value Q: 19.17, df = 4, p = 0.0003).

Meta-analyses: neither morph can fly

Data for a single species showed that SW males acquire more matings than LW males, but this trend was weak (n = 2: mean p = 0.002, fail-safe number = 4, assessment: highly significant, but non-robust; mean *r* = 0.27, 95% CI: 0.16 – 0.38, fail-safe numbers: 0.26/0, assessment: non-robust small effect; Table 1.8b). No heterogeneity was found (p value homogeneity test: 0.75, df = 1, p = 0.39; *r* value Q: 1.88, df = 1, p = 0.17).

Single and descriptive studies

One descriptive study showed that SW males acquire more matings than LW males (Table 1.8b).

Differences in female fecundity between the morphs

Meta-analyses: both morphs can fly

There was no difference in fecundity between the morphs (n = 3: mean p = 0.20, assessment: non-significant; mean *r* = 0.12, 95% CI: 0.03 – 0.21, fail-safe numbers = 0/0, assessment: non-robust small effect; Table 1.9). There was significant heterogeneity, with all three species belonging to different orders (p value homogeneity test: 14.18, df = 2, p < 0.001; *r* value Q: 17.57, df = 2, p < 0.001).

Meta-analyses: only the LW morph can fly

SW females had greater fecundity than LW females (n = 36: mean p < 0.0001, fail-safe number = 459, assessment: highly significant and robust; Figure 1.8

and Table 9; mean *r* = 0.18, 95% CI: 0.16 – 0.21, fail-safe numbers = 2041/2186, assessment: robust small effect; Figure 1.9 and Table 1.9). There was highly significant heterogeneity in the data (p value homogeneity test: 157.80, df = 35, $p < 0.00001$; *r* value Q: 278.09, df = 35, $p < 0.00001$), with order significantly accounting for variability (e.g., between order Q: 152.50, df = 3, $p < 0.00001$).

For coleopteran females, the LW morph was more fecund than the SW morph (n = 6: mean $p < 0.00001$, fail-safe number = 118, assessment: highly significant and robust; Figure 1.8; mean *r* = 0.31, 95% CI: 0.23 – 0.38, fail-safe numbers = 47/74, assessment: robust medium effect; Figure 1.9). There was no significant heterogeneity for p values (homogeneity test: 2.23, df = 5, p = 0.82), and marginal heterogeneity among *r* values (Q: 11.51, df = 6, p = 0.04).

For hemipteran females, the SW morph was the more fecund morph (n = 21: mean $p < 0.001$, fail-safe number = 445, assessment: highly significant and robust; Figure 1.8; mean *r* = 0.22, 95% CI: 0.19 – 0.25, fail-safe numbers = 871/981, assessment: robust, but small effect; Figure 1.9). P values were homogenous (homogeneity test: 24.71, df = 20, p = 0.21), but *r* values were significantly heterogenous (Q: 96.17, df = 20, $p < 0.00001$). Similarly, the SW was the more fecund morph for orthopteran females (n = 7: mean $p < 0.001$, fail-safe number = 55, assessment: highly significant and robust; Figure 1.8; mean *r* = 0.21, 95% CI: 0.18 – 0.25, fail-safe numbers = 140/204, assessment: robust, but small effect; Figure 1.9). As with hemipterans, p values were homogenous (homogeneity test: 7.21, df = 6, p = 0.30), but *r* values were heterogenous (Q: 17.75, df = 6, $p < 0.01$), for orthopterans.

The funnel plot for effect sizes (Figure 1.10) is asymmetrical, but this is likely due to heterogeneity in *r* values due to taxonomic differences in trends (e.g., coleopteran effect sizes favour the LW morph to have greater fecundity, while the other orders favour the SW morph). There appears to be asymmetry for hemipteran *r* values suggesting publication bias, but asymmetry may be due to other factors due to strong heterogeneity among these data. Similarly, orthopteran effect sizes appear to be distributed asymmetrically, although there are too few data points, and strong heterogeneity among these data as well.

SW females contribute more to egg quality than LW females, but this trend was only seen for *r* values (n = 5: mean p = 0.15, assessment: non-significant; mean *r* = 0.21, 95% CI: 0.15 – 0.31, fail-safe numbers = 24/43, assessment: robust, small effect; Table 1.9). There was highly significant heterogeneity among both types of data (p value homogeneity test: 28.28, df = 4, $p < 0.00001$; *r* value Q: 61.72, df = 5, $p < 0.0001$). Order was a significant moderator variable (between order Q: 44.77, df = 1, $p < 0.000001$; single hemipteran and orthoperan species pooled). The SW morph contributed more to eggs in the hemipteran and orthopteran species only; in contrast, the LW morph contributed more to eggs among thysanopteran females (n = 3: mean p = 0.0005, fail-safe number = 5, assessment: highly significant, but non-robust; mean *r* = -0.29, 95% CI: -0.45 – -0.12, fail-safe numbers = 0/0, assessment: small, but non-robust effect; Table 1.9). There was significant heterogeneity for the thysanopteran data that was driven by one out of the three species (p value homoegeniety: 17. 83, df = 2, $p < 0.001$; *r* value Q: 16.77, df = 2, $p < 0.001$).

Single and descriptive studies

For a species where only the LW morph can fly, a single study showed that SW females had better quality offspring than LW females (Table 1.9). Among descriptive studies, nine species found SW females to have greater fecundity than LW females (both morphs can fly: n = 3; only the LW morph can fly: n = 6), four species found no difference between the morphs (only the LW morph can fly: n = 3; neither morph can fly: n = 1), and two species found LW females to be more fecund (only the LW morph can fly). One descriptive study found no difference among the morphs in the development of offspring, while another descriptive study found the SW morph to contribute more to eggs than the LW morph (Table 1.9).

Differences in reproductive success between the morphs: males

Meta-analyses: only the LW morph can fly

There was no difference in siring success between the morphs (n = 5: mean p = 0.32, fail-safe number = 11, assessment: non-significant; mean *r* = 0.07, 95% CI: -0.03 – 0.17, fail-safe numbers = 0/0, assessment: trivial effect; Table 1.10). Heterogeneity was found only among *r* values (p value homogeneity test: 6.18, df = 4, p = 0.19; *r* value Q: 15.73, df = 4, p < 0.01). Heterogeneity among insect orders in *r* values was caused by the single hymenopteran species, as order was no longer a significant moderator variable with it removed from the analysis (between order Q: 0.5564, df = 1, p = 0.46). The trend for no difference in siring success was still present for both hemipterans and orthopterans (hemipterans – n = 2, mean *r* = 0.11, 95% CI: -0.08 – 0.29, fail-safe numbers = 0/0, assessment: non-robust small effect; orthopterans – n = 2, mean *r* = 0.02, 95% CI: -0.10 – 0.15, fail-safe numbers = 0/0, assessment:

trivial effect; Table 1.10). The *r* values for both groups showed no significant heterogeneity (hemipteran *r* value Q: 3.79, df = 1, p =0.05; orthopteran *r* value Q: 2.33, df = 1, p = 0.13).

Meta-analyses: neither morph can fly

Data from a single species showed no difference in siring success between the morphs (n = 2: mean p = 0.13, assessment: non-significant; mean *r* = 0.37, 95% CI: 0.17 – 0.55, fail-safe numbers = 0/0, assessment: medium, but non-robust effect; Table 1.10). No significant heterogeneity among data was found (p value homogeneity test: 0.06, df = 1, p = 0.80; *r* value Q: 1.39, df = 1, p = 0.24).

Discussion

Using meta-analysis, I found evidence for both sexes that supports the presence of a trade-off between flight capability and reproduction in wing-dimorphic insects. Overall, the trends in traits used to examine the trade-off were consistent between both p value and *r* value meta-analyses. It appears, however, that the trade-off is potentially mitigated in males, as long-winged individuals possess an advantage in certain traits that can attenuate the penalty of being able to fly. The taxonomic order to which a species belongs to can significantly affect the direction and strength of the trend of a given trait, for that particular species. Moreover, the trade-off is also affected by whether or not a difference in relative flight-capability exists between the morphs.

The trade-off in females: compensation in LW females?

The presence of a trade-off in females was found across most species, where evidence was largely from species where only the LW morph can fly. Overall, the strongest evidence supporting the trade-off was that LW females have a later onset of reproduction, lower fecundity, and invest less into gonads than SW females. Similarly, weaker evidence supporting the trade-off was also found in other traits, e.g., LW females would contribute less to egg quality and defend resources to a lesser degree, than SW females. The impact of the trade-off does not appear to be mitigated in LW females, since there was no advantage for LW females in traits that can compensate for the costs of flight capability. For example, if LW females were to develop faster of live considerably longer than SW females, LW females might potentially have similar life-time reproductive output as SW females (Zera & Denno, 1997). I did not find LW females to develop faster or live longer than SW females, however.

The trade-off in males: does it exist and among what traits?

In contrast to females, there have been far fewer studies examining the trade-off in males. Studies that have examined the trade-off have yielded conflicting results as to the cost of being able to fly in males, as some traits support a trade-off whereas others do not (Zera & Denno, 1997). This has led to the suggestion that flight-incapable males may occur simply because of genetic correlations with females, where selection for enhanced reproductive output, at the expense of flight capability, may be strong (Roff & Fairbairn, 1991). I found that the trade-off also exists in males, and appears to be expressed primarily as differences in traits related to mating activity. For example, the strongest evidence for a trade-off in males was the robust medium effect that LW males invest less into attracting mates than SW males. Similarly, I also found that LW males had a lower propensity for mating, invested less into nuptial gifts, acquired fewer matings, and are less preferred by females as potential mates, than SW males. The trends for these traits, however, are either rather modest in strength (e.g., mating propensity), based on a single study (e.g., nuptial gifts), or based solely on information for a single species (e.g., female preferences). More work is necessary to bolster the data asserting the existence of a trade-off in males. Nevertheless, my analysis suggests a potential fitness cost to being able to fly in males given that LW males mate less, and that the absence of the ability to fly may be adaptive for males, as it is for females.

In contrast to females, it is possible that the trade-off is mitigated in males, at least within some insect orders. My meta-analyses found that LW males develop faster than SW males among orthopteran species where only the LW morph can fly, and that LW males tend to live longer than SW males in species of the Hymenoptera and Orthoptera. For example, in field cricket males, the difference in courtship propensity between the flight-morphs occurs primarily at younger adult ages (first week of adult life, *Gryllus texensis* – Guerra & Pollack, 2007). Here, if flight-capable males live significantly longer, they can achieve similar or even greater lifetime reproductive success as that of flight-incapable males (Zera & Denno, 1997). Increased longevity might be one possible mechanism by which the flight-capable morph is maintained in populations.

Although intriguing, it remains to be seen whether or not the decreased development time and increased longevity of LW males relative to SW males of certain species can actually mitigate the trade-off. Even though LW males are at an advantage among these traits, it may not be sufficient enough to counterbalance the difference in mating activity between the morphs. For example, the survival of individuals is usually considerably reduced in the field as opposed to the laboratory (where the majority of studies have been conducted), as stress on animals can be intensified under natural conditions. To illustrate, male *G. texensis* can live past 60 days of adulthood in the lab (Gray & Cade, 2000), while the oldest male *G. texensis* collected in the field were only 24 days old as adults (Murray & Cade, 1995). Such differences can be due to animals being severely food restricted or having poorer quality diets in the field relative to animals in the laboratory; these limiting conditions have been shown to strengthen the trade-off (Zera & Denno, 1997). Moreover, insects that fly in the field expose themselves to risks, such as predation by aerially hawking predators (Hoy, 1992), which they do not face in the laboratory and that are not faced by flight-incapable individuals. Additional data are required to determine the existence and persistence of the trade-off in males, especially under field conditions.

Taxonomic differences affect the expression of the trade-off

Roff (1995) suggested that the trade-off be studied over a wide range of species, as the trends of traits used to study the trade-off may not be generalizable across taxa. Ignoring the diversity of groups can obscure any consistent patterns that are taxa-specific. Indeed, I found that the direction and strength of these trends differ considerably according to taxonomic lines, namely that of insect order. This suggests that the widely accepted trade-off between flight capability and reproduction in wing dimorphic insect species cannot be generalized (either in direction or strength) to all species.

Although LW females are considered to have decreased reproductive output than SW females overall (e.g., LW females have substantially lower fecundity than SW females), previous reviews have noted a few exceptions where it is the LW morph with increased reproductive output (Roff, 1986; Zera & Denno, 1997). My meta-analyses show, however, that rather than being an anomaly, LW females of certain insect orders can consistently be greatly more fecund than SW females. This is seen in species of the Coleoptera where only the LW morph can fly (all six species in my analyses). Similarly, there was a trend for LW thysanopteran females to contribute more to egg quality than SW congenerics; this is the opposite of what was seen with hemipteran and orthopteran species.

Trends in traits measured in males also reflect differences related to insect order. For example, LW males have a longer development time than SW males for species of the Thysanoptera and Hemiptera; in contrast, LW males develop faster than SW males in the Orthoptera. Similarly, there is no difference in the longevity of the flight-morphs of hemipteran males, but there is a trend for LW males to live longer than SW males among hymenopteran and orthopteran species. Thus, it also appears that the potential for the trade-off to be lessened in males (see above) can also differ according to insect order, e.g., the trade-off is more likely to be attenuated in orthopteran species as opposed to hemipteran species, as LW males of orthopteran species develop faster and live longer than SW males, but not in hemipteran species.

The strength of the relationship between flight capability and a trait used to examine the trade-off, i.e., the magnitude of the trade-off effect, can also differ among taxa. For example, the trend for a trade-off between flight capability and the onset of reproduction is much stronger and more robust for hemipteran females (mean $r = 0.44$, 95% CI: 0.39 – 0.49), than it is for orthopteran females (mean $r = 0.24$, 95% CI: 0.16 – 0.32).

Differences in flight ability between the morphs affect the trade-off

In some wing dimorphic species, there is no difference in flight capability between the morphs. Both morphs can fly or neither morph can fly (see Appendix for list of species). In contrast to species where only the LW morph can fly, fewer studies have examined the trade-off in species when there is no difference in flight capability.

Overall, there appears to be little support for a clear trade-off in species where both morphs can fly. Single studies (one for each sex) showed that LW individuals develop slower than SW individuals, while another single study showed that SW males have larger nuptial gifts than LW males. In contrast, no difference in female reproductive onset was found between the morphs (single study), LW individuals can live longer than their SW counterparts in both males and females, and meta-analysis found no difference in fecundity between the morphs (although three descriptive studies found the SW to be more fecund). These results suggest that when both morphs can fly, and therefore presumably incur similar energetic costs of flight-capability, a trade-off is not apparent. For species where both morphs can fly, LW individuals might exist in populations and be favored in certain traits (e.g., longevity), as they may be selected for dispersing and colonizing new habitats, possibly due to them being better fliers (Zera & Denno, 1997).

In contrast, a trend for a trade-off appears in species when neither morph can fly. LW females take longer to develop, and have a longer reproductive onset, than SW females. For males, although there is no difference in siring success between the morphs, the LW morph takes longer to develop, invests less into accessory glands, engages less in mating activity, and acquires fewer matings than the SW morph. These results support the notion that the existence of the trade-off is not specifically related to differences in flight capability per se, since the trade-off occurs even in the absence of flight capability.

It has been shown that the LW morph for species where neither morph can fly has higher dispersal activity via walking, and that the LW morph may play an important role in dispersal (e.g., *Pyrrhocoris apterus* – Socha & Zemek, 2003). Thus, it appears that selection for increased dispersal propensity, rather than the cost of specific methods of locomotion (e.g., flight and the ability to do so), is what underlie the trade-off in wing dimorphic species. These results advocate further study of the trade-off for species where the costs of dispersal are similar, since it has long been thought that the trade-off between dispersal and reproduction arose primarily from the high costs of flight incurred by only one morph.

Can the trade-off be under- or overestimated?

Ways that the trade-off can be underestimated

Generally, the sexes differ in the way that they invest into reproduction. Females typically invest more into offspring and gamete production than males, creating a difference in parental investment between the sexes. As a result, males usually are the sex that competes for mating opportunities, and therefore invests more into the competition for mates (Cunningham & Birkhead 1998). It is therefore possible that the expression of the trade-off might differ between the sexes according to how each sex primarily invests into reproduction (Zera & Denno, 1997, and references therein). In females, my analysis shows that the major penalties of flight capability that are consistent across most taxa are that of a decreased investment into gonads and lowered fecundity. In contrast, my analysis indicates that the male flight-morphs do not differ in their gonadal investment, and have similar siring success. These results would suggest that there is no trade-off in males. Given that the cost of reproduction in males can be heavily biased towards competing with rivals for mates, the trade-off might be far more evident in traits related to obtaining mates (e.g., courtship and fighting behaviour), rather than traits that directly measure reproductive success (e.g., siring success) once mating has already occurred. This appears to be the case, as I found that LW males invest less into attracting mates than SW males (see above). Therefore, the different ways in which the sexes invest in reproduction does affect the expression of the trade-off, and can lead it to be underestimated in males.

Historically, work that has examined the trade-off has characterized differences in flight capability between individuals using differences in hind-wing length only. More recent work, however, has shown that once flight muscles of LW individuals undergo histolysis, they have a similar reproductive output as that of SW individuals. Therefore, earlier work may have underestimated or missed entirely the trade-off (Zera *et al.*, 1997). For example, in the field cricket, *Gryllus texensis*, LW males are significantly less likely to engage in courtship behaviour when they are capable of flight, relative to SW conspecific males. Once LW males can no longer fly due to muscle histolysis, males readily engage in courtship behaviour with a similar probability as SW males (Guerra & Pollack, 2007).

In conjunction with differences in flight-muscle condition, flight-capable individuals can also significantly differ in their propensity for flight (Harrison, 1980; McAnelly & Rankin 1986; Fairbairn & Roff, 1990). Differences in flight propensity among LW individuals may mask the presence of a trade-off (Roff & Fairbairn, 1991). For example, LW individuals with low flight propensity would be predicted to histolyze their flight muscles earlier than LW individuals with greater flight propensity. Therefore, LW individuals with a low propensity for flight, although able to fly, may potentially invest into reproduction as much as SW individuals, or at least more than LW individuals with high flight propensity. Future work should address how differences in flight propensity affect the trade-off, especially in cases where an absence of a difference between morphs was previously observed.

Finally, environmental conditions can mask the detection of a trade-off. For example, in the field cricket, *Gryllus firmus*, LW females have reduced fecundity relative to SW females (Roff, 1984). Mole & Zera (1994), however, found that LW females compensate for the metabolic costs of being able to fly by eating more food relative to SW females in *G. firmus*. As a result, in contrast to Roff (1984), they found no difference in reproductive output between the morphs. In their experiment, all females were fed a high-quality *ad libitum* diet. It is possible, however, that in the absence of resource-rich conditions (as might be found in the field), the trade-off may occur (Mole & Zera, 1994). Therefore, in some species, the trade-off can be underestimated, as its occurrence might be precluded by various environmental factors, such as the availability of food.

Ways that the trade-off can be overestimated

Environmental conditions can also overestimate the existence of a trade-off, such that a trade-off can be found in one condition, but its expression can be eliminated in another. For example, Roff (1990) found that the difference in fecundity between LW and SW females in *G. firmus* was significantly influenced by temperature conditions: LW females had a fecundity disadvantage at 30°C, but not at 28°C, as compared with SW females. Therefore, the disadvantage in fecundity of LW females in *G. firmus* is context-dependent, as it can disappear at lower temperatures.

The trade-off is also context-dependent and can be overestimated in males, as seen in the planthoper, *Prokelisia dolus* (Langellotto *et al*., 2000; Langellotto & Denno, 2001). For example, the type of mates available to males influences the relative mating success of the wing-morphs. Langellotto *et al*. (2000) found that when SW females were contested, SW males had a mating advantage, but when LW females were used, LW males obtained the majority of matings. Langellotto & Denno (2001) show that under contiguous vegetation and when females are abundant, SW males are more successful at finding mates. In contrast, LW males are much better at locating and mating with females, in sparse vegetation and when females are found at low densities in the environment. These results underscore the idea that trade-offs can only be fully understood when conditions that impact the expression of the trade-off are known (Mole & Zera, 1994).

Although a large body of work has examined the differences in reproductive investment between the flight-morphs, in these experiments, of which the vast majority were laboratory based, flight-capable individuals were not flown. Therefore, the effect of flight on the trade-off was not examined (Zera, 2005). Recently, however, Guerra & Pollack (2009) found that a short bout of flight eliminated the trade-off in males and females in *G. texensis*. In female *G. texensis*, the LW morph invests less into ovaries relative to the SW morph (Guerra & Pollack, 2009). LW individuals had ovaries comparable to those of SW individuals two days later after a flight bout. In contrast, the ovaries of LW females not allowed to fly were still significantly lighter than both of these groups. In male *G. texensis*, the LW morph capable of flight has a significantly lower courtship propensity than SW males (Guerra & Pollack, 2007). Flight markedly increased the courtship propensity of LW males relative to unflown LW males (Guerra & Pollack, 2009). In fact, when the courtship propensity of flown LW males (all flown LW males court, n = 16; Guerra & Pollack, 2009) is compared to that of SW males (75% of SW males court, n = 72; Guerra & Pollack, 2007), flown LW males have an even greater courtship propensity than SW males (Fisher's Exact test: $p = 0.03$).

Consistent with the effect of flight observed in the laboratory, Bertram (2007) found that LW male *G. texensis* captured in the field after having been observed flying, invested more into mate attraction (i.e., they had enhanced calling behaviour) relative to SW males also captured in the field. In summary, it appears that the trade-off attributed solely to differences in flight capability, may have been overestimated in previous studies that compared the different wing-morphs. Future work should therefore take into account the potential impact of flight on the expression of the trade-off.

Possible differences in the function of flight in wing dimorphic species

An important result from my meta-analyses is that the LW morph does not always suffer a reproductive penalty for being capable of flight in wing dimorphic species. The difference in reproductive output between LW individuals according to different taxonomic groups (insect order) suggests different functions for flight among wing dimorphic species, according to whether or not LW individuals incur a reproductive penalty for being able to fly. The possible difference in the function of flight across taxa implies that there is no necessary constraint for the evolution of wing dimorphism, where the function of flight and flightlessness is not fixed. The selective pressure behind the evolution of wing dimorphism need not be similar from species to species, since the costs and benefits of flight are so easily shifted in different species, and can presumably evolve under a variety of conditions.

The ability to fly allows individuals to escape deteriorating conditions, but usually at the cost of other energetically expensive activities, namely reproduction, due to the limited resources an individual has (Harrison, 1980). As SW individuals are less able to escape unfavourable conditions, it has been suggested that flight capability and enhanced mobility, is selected for and maintained by heterogeneity in the environment (Harrison, 1980; Roff, 1994; Zera & Denno, 1997). When it is the flight-capable morph that invests less into reproduction, this suggests that the function of flight is primarily a bet-hedging strategy related to a stochastic environment.

In contrast, when it is the flight-capable morph that has greater reproductive output, this suggests that the possible function of flight is to assist individuals in colonizing new habitats and resources (Harrison, 1980; Zera & Denno, 1997). Flight-capable individuals are thus potential colonizers who are favoured by selection due to their enhanced dispersal capabilities and their increased reproductive output (Rankin & Burchsted, 1992). Here, flight capability (and presumably dispersal and migratory capability) is not just an adaptive strategy to deal with uncertain and adverse conditions, but is an adaptation for colonization. Wing dimorphism is presumably maintained among these species, since the SW condition is dominant (e.g., members of the Coleoptera: *Calathus cinctus*, *C. melanocephalus*; Aukema, 1991), or since the development of flight-capable individuals is indicative of good conditions that permit both flight-capability and enhanced reproduction to occur in tandem (Ritchie *et al*., 1987).

Reproduction in many flight-capable insects is suggested to occur principally after flight (the "oogenesis-flight syndrome; Johnson 1969; Wheeler 1996). Here, flight-capable individuals must first fly in order to fully engage and invest into reproduction (Kennedy & Booth, 1964). Consistent with this idea, the reproductive penalty suffered by the LW morph documented in many wing dimorphic species, but observed in the absence of flight, might reflect an overall "reproduction-flight syndrome". For at least some species, differences between the flight-morphs found prior to the occurrence of flight (e.g., Guerra & Pollack, 2007), cannot be seen as just a trade-off between the ability to deal with ephemeral or unsuitable habitats versus reproduction, since the reproductive investment of LW individuals can be enhanced to the same level as that of their SW counterparts after flight (Guerra & Pollack, 2009). Instead, flight may play a role in a larger adaptive strategy (e.g., the colonization of new resources, see above), and flight must happen in order to initiate reproduction. Field data, such as what conditions induce flight and when individuals fly in their life cycle, are necessary to better understand the selective forces underlying the relationship between the function of flight and wing dimorphism across insect taxa.

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Table 1.1 Traits used to exam the trade-off between flight-capability and reproduction in females of wing dimorphic species.

Trait group	Specific trait	Predicted relationship between the flight-morphs
Life history	Development time	SW > LW
	Onset of reproduction	LW > SW
	Longevity	LW > SW
Investment into mating	Investment into gonads	SW > LW
	Mating propensity	SW > LW
	Mating frequency	SW > LW
	Defense of resources	SW > LW
Success in mating activity	Matings acquired	SW > LW
Reproductive success	Characteristics of eggs	SW > LW
	Fecundity	SW > LW
	Development of offspring	SW > LW
	Offspring quality	SW > LW

Table 1.2 Traits used to examine the trade-off between flight-capability and reproduction in males of wing dimorphic species.

Trait group	Specific trait	Predicted relationship between the flight-morphs
Life history	Development time	SW > LW
	Onset of reproduction	LW > SW
	Longevity	LW > SW
Investment into mating	Investment into gonads	SW > LW
	Investment into accessory glands	SW > LW
	Investment into genitalia	SW > LW
	Investment into mate attraction	SW > LW
	Mating propensity	SW > LW
	Level of mating activity	SW > LW
	Investment into nuptial gifts	SW > LW
	Competition with rivals	SW > LW
	Investment into weapons for combat	SW > LW
Success in mating activity	Preferred by mates	SW > LW

Table 1.2 Continued

Trait group	**Specific trait**	**Predicted relationship between the flight-morphs**
Success in mating activity	Matings acquired	SW > LW
Reproductive success	Siring success	SW > LW

Table 1.3 Differences in developmental time between the flight-morphs of wing dimorphic insect species.

Flight ability	Type of analysis	Sex	Results	Trend
Both can fly	Descriptive papers	F	n=2 (1 species: LW>SW; 1 species: SW>LW)	None
LW only		F	n=9 (1 species: SW>LW; 4 species: SW=SW; 4 species LW>SW)	None
		M	n=2 (1 species: SW=LW; 1 species: SW>LW)	None
		?	n=2 (1 species: LW>SW; 1 species: unclear)	None
Both can fly	Single study with appropriate data	F	Coleoptera; *C. maculatus*: n=180; p=-0.003 (1-tailed); r=-0.18	LW>SW
		M	Coleoptera; *C. maculatus*: n=76; p=-0.03 (1-tailed); r=-0.22	LW>SW
LW only	p value[d]	F	n=12; *z*=-0.25; p=0.4; n/a; no; p<0.00001; no	SW=LW
		M	n=12; *z*=-0.79; p=0.22; n/a; no; p<0.00001; no	SW=LW
	Effect size[e]	F	n=12; *Z*=-3.08; p=0.002; r=-0.04 (-0.06 – -0.01); 12/15; no; p<0.05; no	SW=LW
		M	n=12; *Z*=3.11; p=0.002; r=0.04 (0.01 – 0.06); 13/16; no; p<0.05; no	SW=LW
LW only (H[a])	p value	F	n=5; *z*=3.37; p=0.0004; 44; yes; p=0.15; yes	LW>SW
		M	n=4; *z*=2.78; p=0.003; 15; no; p=0.39; yes	LW>SW
	Effect size	F	n=5; *Z*=12.82; p<0.001; r=0.25 (0.22 – 0.29); 119/206; yes; p=0.02; no	LW>SW
		M	n=4; *Z*=11.91; p<0.001; r=0.21 (0.18 – 0.24); 70/141; yes; p=0.08; yes	LW>SW
LW only (O[b])	p value	F	n=5; *z*=1.42; p=0.08; n/a; no; p=0.03; no	SW=LW
		M	n=5; *z*=1.95; p=0.03; 3; no; p=0.003; no	SW>LW
	Effect size	F	n=5; *Z*=4.25; p<0.001; r=0.07 (0.04 – 0.11); 9/16; no; p=0.02; no	SW=LW
		M	n=5; *Z*=15.43; p<0.001; r=0.26 (0.23 – 0.29); 175/302; yes; p<0.001; no	SW>LW

[a]=Hemiptera; [b]=Orthoptera; [c]=Thysanoptera; [d]=p value meta-analysis: (sample size, species=unit; mean *z* value; 1-tailed mean p value; Rosenthal fail-safe number; >5*K*+10: yes or no; homogeneity test p value; homogenous group: yes or no); [e]=Effect size meta-analysis: (sample size, species=unit; *Z*-test statistic and p value; back transformed mean effect size, r, and 95% confidence interval; Rosenberg fail-safe numbers, N_1/N_+; >5*K*+10: yes or no; Q Homogeneity test p value; homogenous group: yes or no)

Table 1.3 Continued

Flight ability	Type of analysis	Sex	Results	Trend
LW only (Tc)	p value	M	n=2; z=2.67; p=0.004; 2; no; p=0.18; yes	LW>SW
	Effect size	M	n=2; Z=3.21; p=0.001; r=0.17 (0.07 – 0.27); 0.2/5; no; p=0.57; yes	LW>SW
Neither	p value	F	n=3; z=-2.52; p=0.01; 3; no; p=0.01; no	LW>SW
	Effect size	F	n=3; Z=-8.61; p<0.001; r=-0.16 (-0.19 – -0.12); 19/52; yes; p<0.001; no	LW>SW
Neither (H)	p value	F	n=2; *z*=2.66; p=0.003; 3; no; p=0.33; yes	LW>SW
		M	n=2; *z*=3.44; p=0.0003; 5.44; no; p=0.11; yes	LW>SW
	Effect size	F	n=2; *Z*=9.93; p<0.0001; r=0.18 (0.15 – 0.22); 9/46; yes; p=0.69; yes	LW>SW
		M	n=2; *Z*=15.28; p<0.001; r=0.29 (0.25 – 0.32); 23/117; yes; 0.19; yes	LW>SW

Table 1.4 Differences in the onset of reproduction between the flight-morphs of wing dimorphic insect species.

Flight ability	Type of analysis	Sex	Results	Trend
Both can fly	Descriptive papers	F	n=3 (3 species: LW>SW)	LW>SW
LW only		F	n=9 (9 species: LW>SW)	LW>SW
Both can fly	Single study with	F	Hemiptera; *O. fasciatus*: n=73; p=0.5 (1-tailed); r=0	SW=LW
LW only	appropriate data	M	Hemiptera: *C. saccharivorus*: n=35; p=0.004 (1-tailed); r=0.67	LW>SW
LW only	p value	F	n=22, *z*=9.54, p<0.00001; 1363; yes; p=0.86; yes	LW>SW
	Effect size	F	n=22, *Z*=17.08, p<0.00001; r=0.38 (0.34 – 0.41); 1470/1646; yes; p<0.00001; no	LW>SW
LW only (H)	Effect size	F	n=16, *Z*=16.13, p<0.00001; r=0.44 (0.39 – 0.49); 910/1065; yes; p=0.0002; no	LW>SW
LW only (O)	Effect size	F	n=4; *Z*=5.82; p<0.001; r=0.24 (0.16 – 0.32); 14/29; no; p<0.001; no	LW>SW
Neither	p value	F	n=2; *z*=4.03; p<0.0001; 13; no; p=0.28; yes	LW>SW
	Effect size	F	n=2; *Z*=6.30; p<0.001; r=0.47 (0.34 – 0.59); 2/16/ no; p=0.16; yes	LW>SW

Abbreviations and order of lists of values as in Table 1.3.

Table 1.5 Differences in longevity between the flight-morphs of wing dimorphic insect species.

Flight ability	Type of analysis	Sex	Results	Trend
Both	Descriptive papers	F	n=2 (2 species: LW>SW)	LW>SW
		M	n=1 (1 species: LW>SW)	LW>SW
LW only		F	n=6 (3 species: SW=LW; 3 species: LW>SW)	LW≥SW
		M	n=3 (3 species: LW>SW)	LW>SW
Neither		F	n=1 (1 species: SW=LW)	SW=LW
Both	p value	F	n=2; z=2.65; p=0.004; 4; no; p=0.95; yes	LW>SW
	Effect size	F	n=2; Z=2.78; p=0.01; r=0.17 (0.05 – 0.29); 0/0; no; p=0.59; yes	LW>SW
LW only	p value	F	n=24; z=1.82; p=0.03; 76; no; p<0.0001; no	SW=LW
		M	n=14; z=1.96; p=0.03; 4; no; p<0.001; no	LW>SW
	Effect size	F	n=24; Z=4.88; p<0.0001; r=0.08 (0.05 – 0.11); 110/122; no; p<0.0001; no	SW=LW
		M	n=14; Z=3.38; p<0.001; r=0.10 (0.04 – 0.16); 21/25; no; p<0.0001; no	LW>SW
LW only (H)	p value	F	n=16; z=1.85; p=0.03; 3; no; p<0.001; no	SW=LW
		M	n=5; z=1.37; p=0.09; 0.4; no; p=0.76; yes	SW=LW
	Effect size	F	n=16; Z=4.67; p<0.0001; r=0.09 (0.05 – 0.13); 55/64; no; p<0.0001; no	SW=LW
		M	n=5; Z=2.61; p=0.009; r=0.09 (0.02 – 0.16); 0.16/0; no; p=0.7538; yes	SW=LW
LW only (O)	p value	F	n=6; z=0.58; p=0.28; 30; no; p=0.20; yes	SW=LW
		M	n=3; z=2.36; p=0.01; 3; no; p=0.07; yes	LW>SW
	Effect size	F	n=6; Z=1.99; p=0.04; r=0.06 (0 – 0.12); 0/0; no; p<0.001; no	SW=LW
		M	n=3; Z=2.66; p<0.01; r=0.24 (0.06 – 0.39); 0/0; no; p=0.12; yes	LW>SW
LW only (Hy[a])	p value	M	n=5; z=2.40; p=0.01; 2; no; p<0.01; no	LW>SW
	Effect size	M	n=5; Z=2.89; p<0.01; r=0.21 (0.07 – 0.35); 1/1; no; p=0.0003; no	LW>SW

[a]=Hymenoptera; other abbreviations and order of lists of values as in Table 1.3.

Table 1.6 Differences between the flight-morphs in traits that measure female mating investment.

Flight ability	Type of analysis	Trait	Results	Trend
Both	Descriptive papers	Gonadal investment	n=1 (1 species: SW>LW)	SW>LW
LW only			n=2 (2 species: SW>LW)	SW>LW
LW only	Single study with appropriate data		Coleoptera; *P. aptera*; n=48; p=0.00005 (1-tailed); r=0.56	LW>SW
Neither		Mating frequency	Hemiptera; *P. apterus*; n=80; p<0.00001 (1-tailed); r=0.39	SW>LW
LW only	p value	Gonadal investment	n=5; *z*=1.68; p=0.05; 67; yes; p=0.41; yes	SW=LW
	Effect size		n=5; *Z*=20.66; p<0.0001; r=0.39 (0.35 – 0.42); 318/548; yes; p=0.01; no	SW>LW
	p value	Mating propensity	n=3; *z*=0.86; p=0.19; 0.13; no; p=0.38; yes	SW=LW
	Effect size		n=3; *Z*=2.58; p=0.01; r=0.01 (0.02 – 0.17); 0/0; no; p=0.05; yes	SW=LW
	p value	Resource defense	n=2; *z*=2.35; p=0.01; 3; no; p=0.92; yes	SW>LW
	Effect size		n=2; *Z*=2.45; p=0.01; r=0.19 (0.04 – 0.33); 0/0; no; p=0.58; yes	SW>LW

Abbreviations and order of lists of values as in Table 1.3.

Table 1.7 Differences between the flight-morphs in traits that measure male mating investment.

Flight ability	Type of analysis	Trait	Results	Trend
Both	Descriptive papers	Gonads	n=1 (1 species: SW>LW)	SW>LW
		Accessory glands	n=1 (1 species: SW>LW)	SW>LW
LW only		Genitalia	n=1 (1 species: LW>SW)	LW>SW
		Attraction	n=1 (1 species: SW=LW)	SW=LW
		Competition	n=2 (1 species: SW>LW; 1 species: SW=LW)	none
Neither		Activity	n=1 (1 species: SW=LW)	SW=LW
Both	Single study	Nuptial gift	Orthoptera; *C. discolor*; n=12; p=0.05 (1-tailed); r=0.47	SW>LW
LW only			Orthoptera; *G. sigillatus*; n=68; p=0.001 (1-tailed); r=0.39	SW>LW
		Weapons	Thysanoptera; *H. karnyi*; n=267; p=0.00005 (1-tailed); r=0.24	SW>LW
Neither		Accessory glands	Hemiptera; *P. apterus*; n=20; p=0.002 (1-tailed); r=0.64	SW>LW
LW only	p value	Gonads	n=3; z=1.64; p=0.05; 10; no; p=0.27; yes	SW=LW
	Effect size		n=3; Z=6.31; p<0.0001; r=0.12 (0.09 – 0.16); 9/25; no; p=0.03; no	SW=LW
	p value	Accessory glands	n=2; z=3.07; p<0.01; 4; no; p=0.09; yes	SW>LW
	Effect size		n=2; Z=3.26; p<0.01; r=0.30 (0.12 – 0.47); 0/0; no; p=0.23; yes	SW>LW
	p value	Attraction	n=3; z=1.62; p=0.05; n/a; no; p=0.65; yes	SW=LW
	Effect size		n=3; Z=8.23; p<0.001; r=0.31 (0.24 – 0.38); 17/47; yes; p=0.10; yes	SW>LW
	p value	Propensity	n=2; z=3.74; p=0.0001; 4; no; p=0.02; no	SW>LW
	Effect size		n=2; Z=3.78; p<0.001; r=0.31 (0.15 – 0.45); 0/0/ no; p=0.57; yes	SW>LW
	p value	Competition	n=3; z=0.80; p=0.22; 2; no; p=0.24; yes	SW=LW
	Effect size		n=3; Z=1.97; p=0.05; r=0.11 (0.0007 – 0.21); 0/0; no; p=0.01; no	SW=LW
LW only (H)	Effect size		n=2; Z=1.55; p=0.12; r=0.09 (-0.02 – 0.19); 0/0; no; p=0.37; yes	SW=LW

Abbreviations and order of lists of values as in Table 1.3.

Table 1.7 Continued

Flight ability	Type of analysis	Trait	Results	Trend
Neither (single species)	p value	Activity	n=2; *z*=2.8; p=0.003; 3; no; p=0.13; yes	SW>LW
	Effect size		n=2; *Z*=4.81; p<0.001; r=0.26 (0.15 – 0.35); 1/1; no; p<0.01; no	SW>LW

Table 1.8a Differences between the flight-morphs in traits that measure female mating success.

Flight ability	Type of analysis	Trait	Results	Trend
LW only	p value	Matings acquired	n=4; *z*=1.84; p=0.03; 9; no; p=0.12; yes	SW>LW
	Effect size		n=4; *Z*=4.05; p<0.001; r=0.11 (0.06 – 0.16); 5/10; no; p=0.10; yes	SW>LW

Table 1.8b Differences between the flight-morphs in traits that measure male mating success.

Flight ability	Type of analysis	Trait	Results	Trend
Neither	Descriptive papers	Matings acquired	n=1 (1 species: SW>LW)	SW>LW
LW only	p value		n=8; *z*=2.53; p=0.01; 15; no; p=0.75; yes	SW>LW
	Effect size		n=8; *Z*=3.94; p<0.001; r=0.15 (0.08 – 0.22); 15/22; no; p=0.50; yes	SW>LW
Neither (single species)	p value		n=2; *z*=2.90; p=0.002; 4; no; p=0.39; yes	SW>LW
	Effect size		n=2; *Z*=4.58; p<0.001; r=0.27 (0.16 – 0.38); 0.26/0; no; p=0.17; yes	SW>LW
LW only (single species)	p value	Preferred by mates	n=4; *z*=4.73; p<0.00001; 42; yes; p=0.28; yes	SW>LW
	Effect size		n=4; *Z*=8.20; p<0.001; r=0.40 (0.31 – 0.49); 31/63; yes; p=0.0003; no	SW>LW

Abbreviations and order of lists of values as in Table 1.3.

Table 1.9 Differences between the flight-morphs in traits that measure female reproductive success.

Flight ability	Type of analysis	Trait	Results	Trend
Both	Descriptive papers	Fecundity	n=3 (3 species: SW>LW)	SW>LW
LW only		Development of offspring	n=1 (1 species: SW=LW)	SW=LW
		Egg characteristics	n=1 (1 species: SW>LW)	SW>LW
		Fecundity	n=11 (6 species: SW>LW; 3 species: SW=LW; 2 species: LW>SW)	none
Neither			n=1 (1 species: SW=LW)	SW=LW
LW only	Single study	Offspring quality	Hemiptera; *R. padi*; n=192; p=0.0005 (1-tailed); r=0.24	SW>LW
LW only	p value	Egg characteristics	n=5; *z*=1.02; p=0.15; n/a; no; p<0.00001; no	SW=LW
	Effect size		n=5; *Z*=5.35; p<0.001; r=0.23 (0.15 – 0.31); 24/43; yes; p<0.0001; no	SW>LW
LW only (T)	p value		n=3; *z*=-3.31; p=0.0005; 5; no; p<0.001; no	LW>SW
	Effect size		n=3; *Z*=-3.29; p=0.001; r=-0.29 (-0.45 – - 0.12); 0/0; no; p<0.001; no	LW>SW
Both	p value	Fecundity	n=3; *z*=0.83; p=0.20; n/a; no; p<0.001; no	SW=LW
	Effect size		n=3; *Z*=2.66; p=0.01; r=0.12 (0.03 – 0.21); 0/0; no; p<0.001; no	SW=LW
LW only	p value		n=36; *z*=3.86; p<0.0001; 459; yes; p<0.00001; no	SW>LW
	Effect size		n=36; *Z*=15.37; p<0.001; r=0.18 (0.16 – 0.21); 2041/2186; yes; p<0.00001; no	SW>LW
LW only (C[a])	p value		n=6; *z*=6.02; p<0.00001; 118; yes; p=0.82; yes	LW>SW
	Effect size		n=6; *Z*=7.27; p<0.001; r=0.31 (0.23 – 0.38); 47/74; yes; p=0.04; no	LW>SW

[a]=Coleoptera; abbreviations and order of lists of values as in Table 1.3.

Table 1.9 Continued

Flight ability	Type of analysis	Trait	Results	Trend
LW only (H)	p value		n=21; *z*=3.13; p<0.001; 445; yes; p=0.21; yes	SW>LW
	Effect size		n=21; *Z*=13.56; p<0.001; r=0.22 (0.19 – 0.25); 871/981; yes; p<0.00001; no	SW>LW
LW only (O)	p value		n=7; *z*=3.14; p<0.001; 55; yes; p=0.30; yes	SW>LW
	Effect size		n=7; *Z*=10.83; p<0.001; r=0.21 (0.18 – 0.25); 140/204; yes; p<0.01; no	SW>LW

Table 1.10 Differences between the flight-morphs in traits that measure male reproductive success.

Flight ability	Type of analysis	Trait	Results	Trend
LW only	p value	Siring success	n=5; *z*=0.48; p=0.32; 11; no; p=0.19; yes	SW=LW
	Effect size		n=5; *Z*=1.32; p=0.19; r=0.07 (-0.03 – 0.17); 0/0; no; p<0.01; no	SW=LW
LW only (H)	Effect size		n=2; *Z*=1.13; p=0.26; r=0.11 (-0.08 – 0.29); 0/0; no; p=0.05; yes	SW=LW
LW only (O)			n=2; *Z*=0.34; p=0.73; r=0.02 (-0.10 – 0.15); 0/0; no; p=0.13; yes	SW=LW
Neither (single species)	p value		n=2; *z*=1.11; p=0.13; n/a; no; p=0.80; yes	SW=LW
	Effect size		n=2; *Z*=3.46; p<0.001; r=0.37 (0.17- 0.55); 0/0; no; p=0.24; yes	SW=LW

Abbreviations and order of lists of values as in Table 1.3.

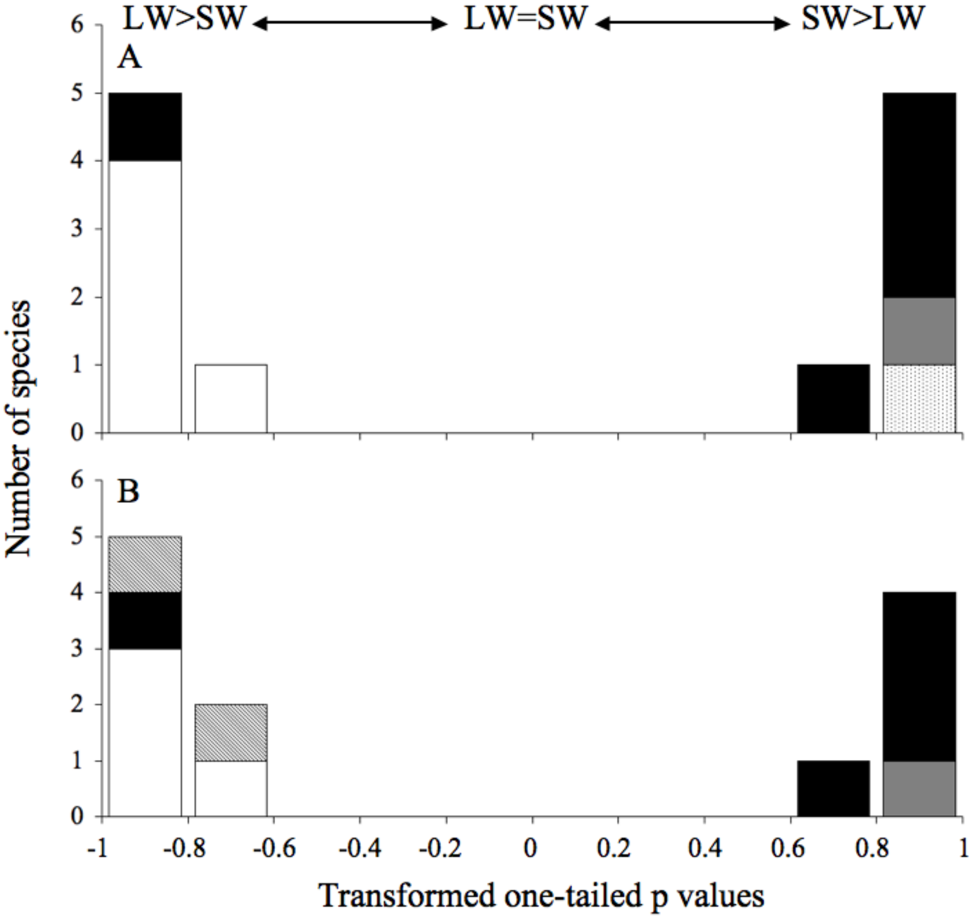

Fig. 1.1 The relationship between wing-morph and development in females (A) and males (B) of species where only the LW morph is flight-capable examined using one-tailed p values. P value data were transformed to reflect the direction of the trend (p values < 0: LW>SW; p values > 0: SW>LW). Black bars = orthopterans; White bars = hemipterans; Gray bars = dermapterans; Stippled bars = coleopterans; Bars with diagonal lines = thysanopterans.

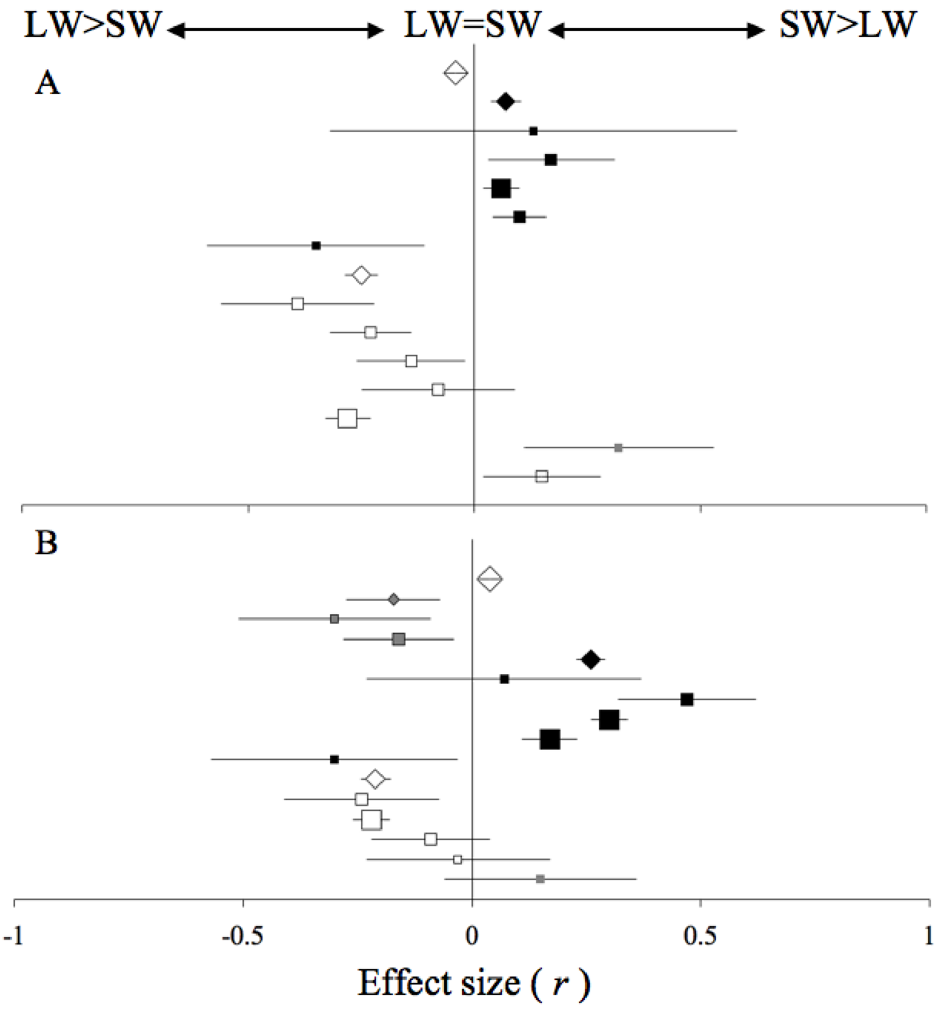

Fig. 1.2 The relationship between wing-morph and development in females (A) and males (B) of species where only the LW morph is flight-capable examined using effect sizes (coefficients of correlation, *r*). Shown are the 95% confidence intervals around *r* values, where the sign of the *r* value indicates the direction of the trend for the effect size (*r* value < 0: LW>SW; *r* value > 0: SW>LW). Vertical line at 0 (x-axis) indicates no effect. Diamond with horizontal bar (top most marker of each graph) is the mean *r* value from meta-analysis. Diamonds

represent *r* values from meta-analyses done according to insect order. Squares represent *r* values for each species. Relative size of markers reflects sample size differences (i.e., a larger marker represents an r value with a larger sample size than that of a smaller marker). Black markers = orthopterans; White markers = hemipterans; Gray markers = dermapterans; White markers with horizontal line = coleopterans; Gray markers with black border = thysanopterans.

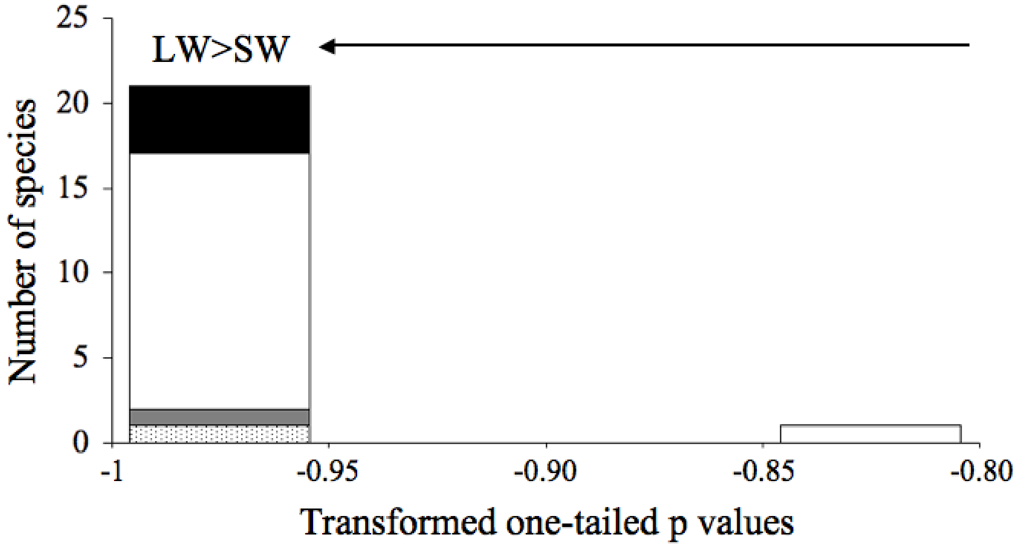

Fig. 1.3 The relationship between wing-morph and the onset of reproduction in females where only the LW morph can fly examined using one-tailed p values. One-tailed p value groupings, plotting, and legend are as in Figure 1.1.

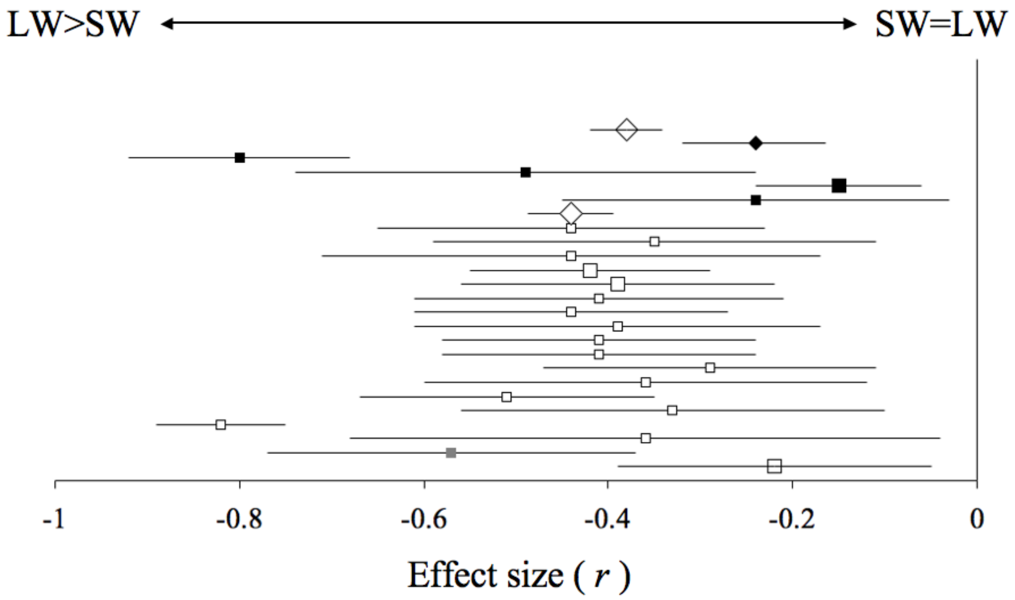

Fig. 1.4 The relationship between wing-morph and the onset of reproduction in females where only the LW morph can fly examined using *r* values. Effect size groupings, plotting, and legend are as in Figure 1.2.

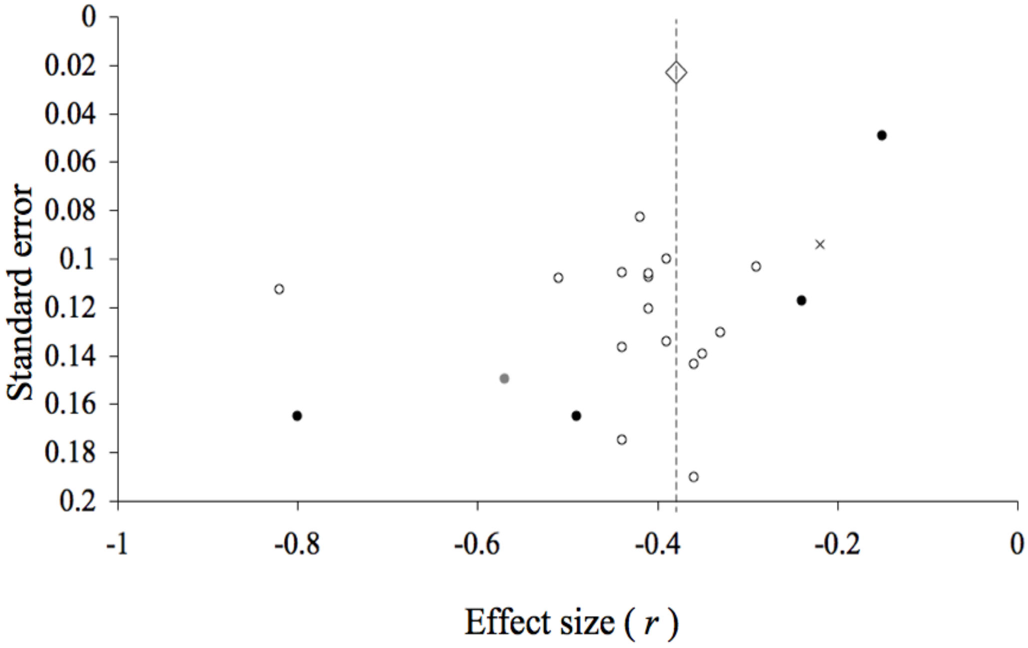

Fig. 1.5 Funnel plot showing the relationship between *r* values and standard error, for *r* values examining the relationship between wing-morph and development in females where only the LW morph can fly. Black dots = orthopterans; White dots = hemipterans; Gray dots = dermapterans; X = coleopterans.

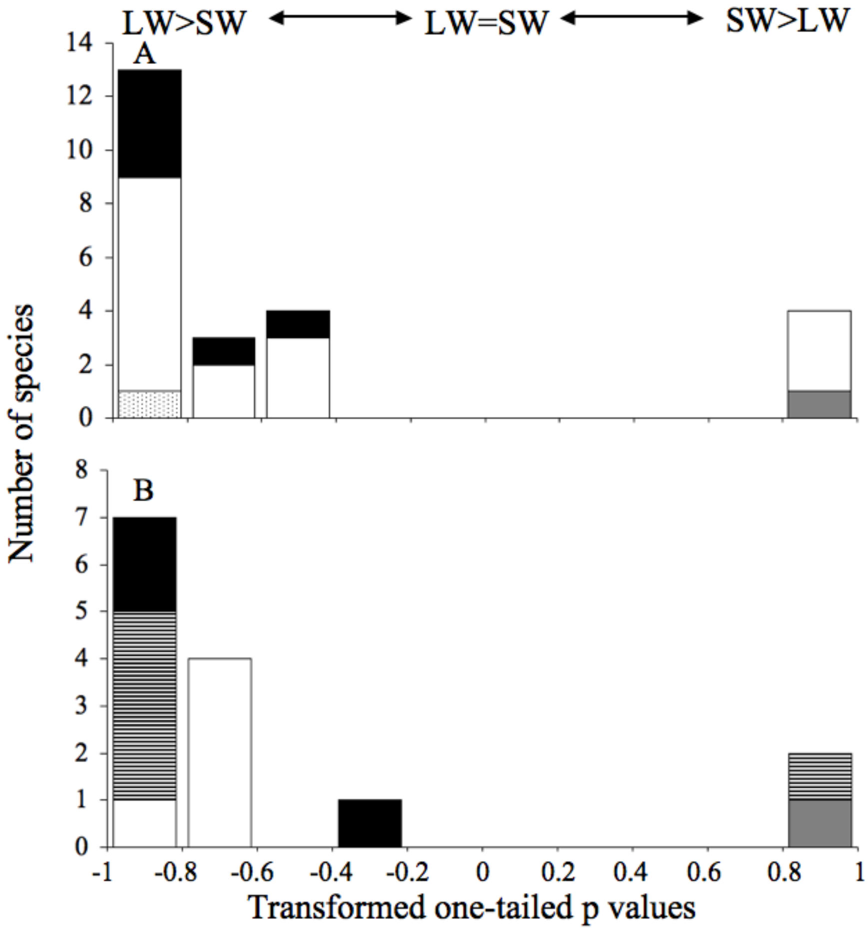

Fig. 1.6 The relationship between wing-morph and longevity in (A) females and (B) males in species where only the LW morph can fly examined using one-tailed p values. One-tailed p value groupings, plotting, and legend are as in Figure 1.1, with the following added: Bars with horizontal lines = hymenopterans.

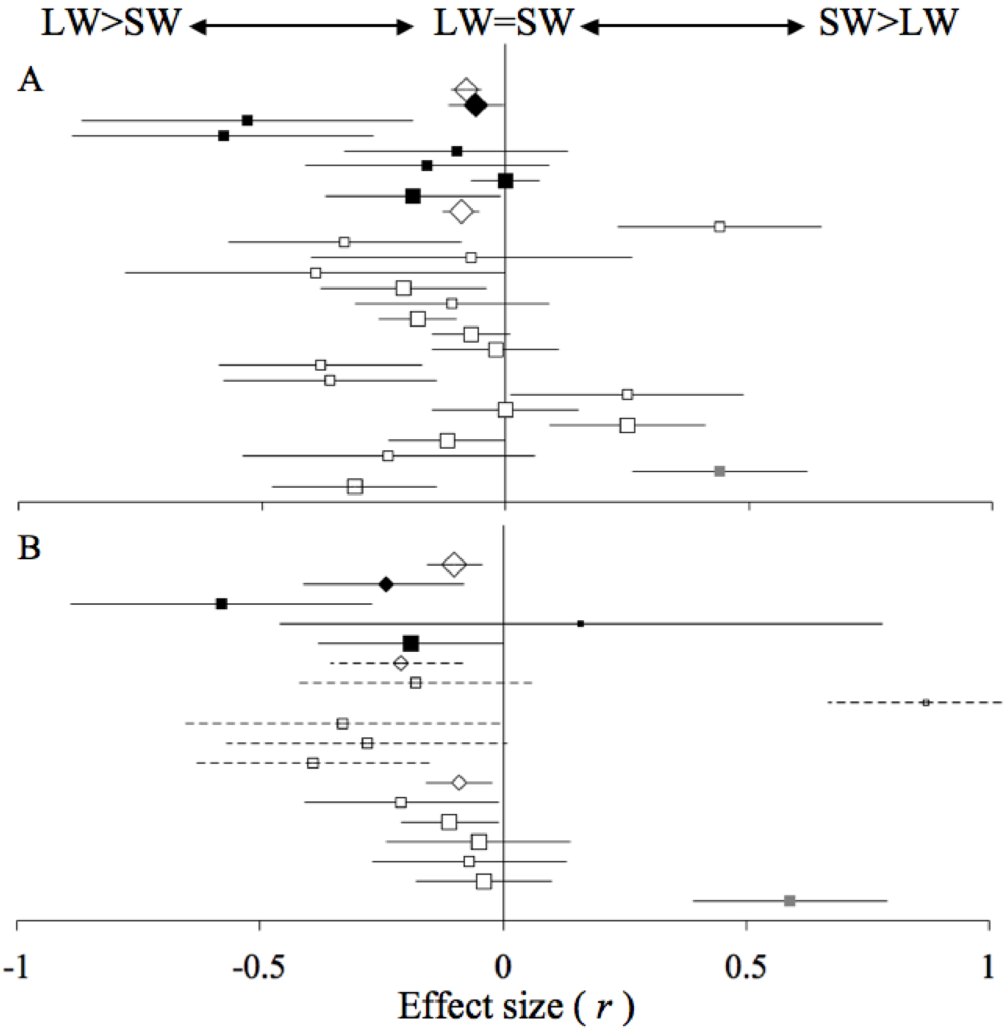

Fig. 1.7 The relationship between wing-morph and longevity in (A) females and (B) males in species where only the LW morph can fly examined using *r* values. Effect size groupings, plotting, and legend are as in Figure 1.2, with the following added: markers with dashed lines as 95% confidence intervals = hymenopterans.

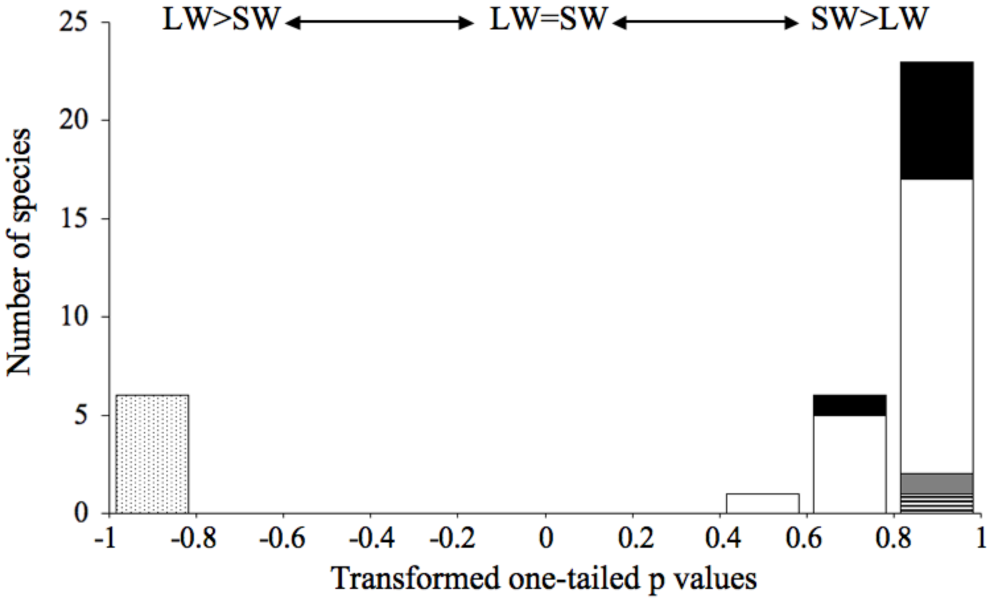

Fig. 1.8 The relationship between wing-morph and fecundity in females where only the LW morph is flight-capable examined using one-tailed p values. One-tailed p value groupings, plotting, and legend are as in Figure 1.6.

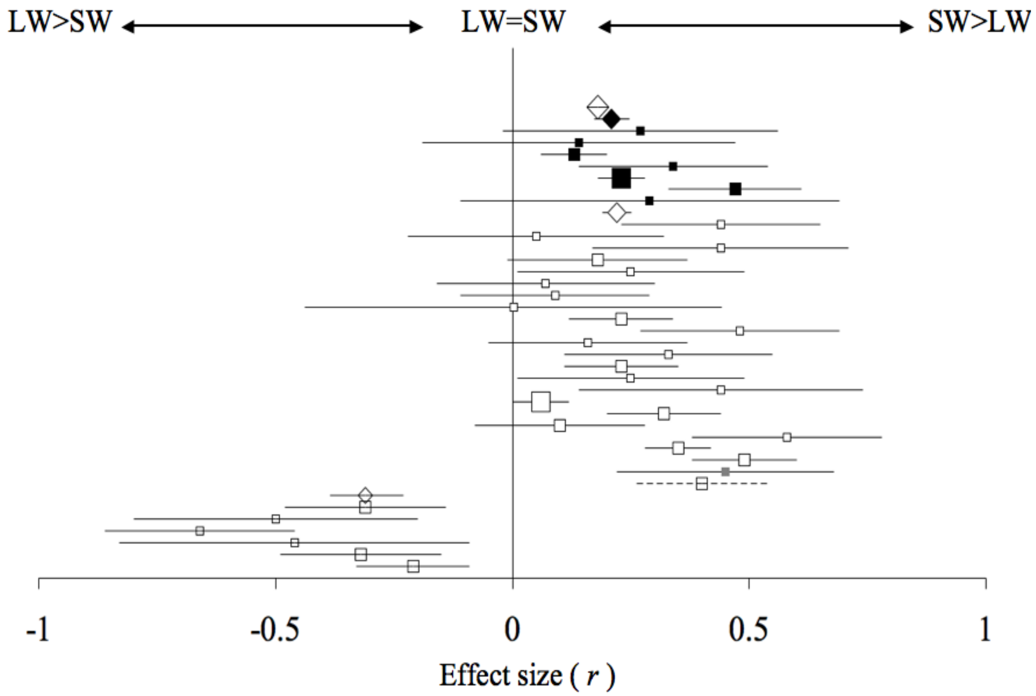

Fig. 1.9 The relationship between wing-morph and fecundity in females where only the LW morph is flight-capable examine using *r* values. Effect size groupings, plotting, and legend are as in Figure 1.7.

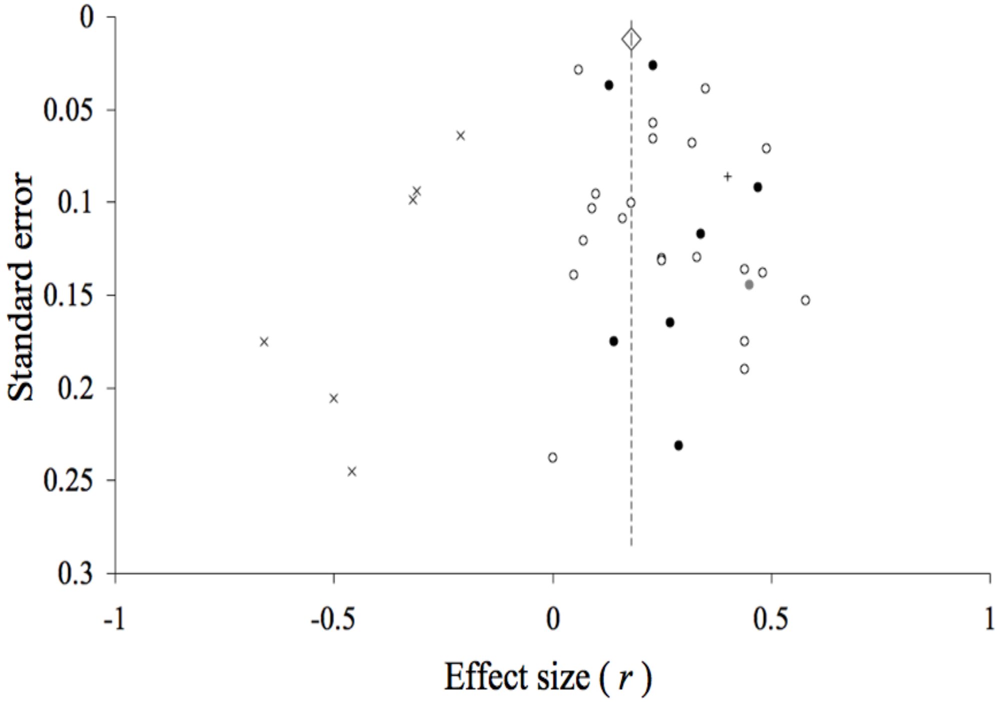

Fig. 1.10 Funnel plot showing the relationship between *r* values and standard error, for *r* values examining the relationship between wing-morph and fecundity in females where only the LW morph can fly. Black dots = orthopterans; White dots = hemipterans; Gray dots = dermapterans; X = coleopterans, with the following added: + = hymenopterans.

Appendix 1 Data investigating the trade-off between flight-capability and reproduction in wing dimorphic insect species. Information includes the trait examined, type of resource found in the literature, taxonomy (species order and name), sex, total sample size for each species studied, one-tailed p value and back transformed effect size (r, correlation coefficient) used in meta-analyses, and references.

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Development	Descriptive	Coleoptera; *Callosobruchus maculatus**	F	n/a	LW>SW	Caswell (1960)
		Hemiptera; *Oncopeltus fasciatus**	F	n/a	SW>LW	Palmer & Dingle (1986)
		Hemiptera; *Acyrthosiphon pisum***	F	n/a	LW>SW	Tsumuki et al (1990)
		Hemiptera; *Laodelphax striatellus***	F	n/a	SW=LW	Mitsuhashi & Koyama (1974)
		Hemiptera; *Leptopterna dolobrata***	F	n/a	SW=LW	Braune (1983)
		Hemiptera; *Macrosiphum granarium***	F	n/a	LW>SW	Noda (1960b)
		Hemiptera; *Rhopalosiphum prunifoliae***	F	n/a	LW>SW	Noda (1960b)
		Hemiptera; *Aphis maidis***	F	n/a	LW>SW	Noda (1960b)
		Orthoptera; *Scapsipedus aspedus***	F	n/a	SW=LW	Saeki (1966)

Species wing dimorphism: *both morphs flight-capable, **only long-winged morph flight-capable, ***both morphs flight-incapable

Negative p values and *r* effect sizes indicate a significant trend in the direction opposite of what was predicted

Sex: F = female; M = Male; ? = Not indicated in paper(s)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Development	Descriptive	Orthoptera; *Pteronemobius nitidus***	F	n/a	SW=LW	Tanaka (1978)
		Orthoptera; *Modicogryllus* sp.**	F	n/a	SW>LW	Masaki & Sugahara (1992)
		Orthoptera; *Scapsipedus aspedus***	M	n/a	SW=LW	Saeki (1966)
		Orthoptera; *Modicogryllus* sp.**	M	n/a	SW>LW	Masaki & Sugahara (1992)
		Hemiptera; *Gerris asper***	?	n/a	LW>SW	Guthrie (1959)
		Orthoptera; *Gryllodes sigillatus***	?	n/a	Unclear	Arai (1978), Ghouri & McFarlane (1958)
	Single study	Coleoptera; *Callosobruchus maculatus**	F	180, -0.0031, -0.1843	LW>SW	Chaudhuri (2005)
		Coleoptera; *Callosobruchus subinnotatus**	M	76, -0.025, -0.2248	LW>SW	Appleby & Credland (2001)
	p and Effect size meta-analysis	Coleoptera; *Adalia bipunctata***	F	231, 0.0125, 0.1474	SW>LW	Ueno et al (2004)
		Dermaptera; *Paralabella dorsalis***	F	72, 0.0032, 0.3214	SW>LW	Briceño & Eberhard (1987)
		Hemiptera; *Myzus persicae***	F	1569, -0.0146, -0.2819	LW>SW	Liu & Meng (1999)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Development	p and Effect size meta-analysis	Hemiptera; *Gerris remigis***	F	139, 0.0875, 0.0850	SW=LW	Fairbairn (1988)
		Hemiptera; *Javesella pellucida***	F	262, 0.2222, 0.1356	SW=LW	Mochida (1973), Ammar (1973)
		Hemiptera; *Jadera haematoloma***	F	417, -0.0005, -0.2340	LW>SW	Carroll et al (2003)
		Hemiptera; *Limnnoporus canaliculatus***	F	100, -0.00005, -0.3891	LW>SW	Zera (1984)
		Orthoptera; *Modicogryllus confirmatus***	F	51, -0.0063, -0.3494	LW>SW	Tanaka & Suzuki (1998)
		Orthoptera; *Gryllus rubens***	F	969, 0.1139, 0.0990	SW=LW	Walker (1987)
		Orthoptera; *Gryllus firmus***	F	2139, 0.1725, 0.0623	SW=LW	Roff (1984, 1995)
		Orthoptera; *Allonemobius fasciatus***	F	186, 0.0693, 0.1738	SW=LW	Roff (1984)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Development	p and Effect size meta-analysis	Orthoptera; *Zonocerus variegatus***	F	19, 0.2893, 0.1273	SW=LW	McCaffery & Page (1978)
		Hemiptera; *Pyrrhocoris sibiricus****	F	148, 0.1110, 0.2134	SW=LW	Sakashita et al (1998)
		Hemiptera; *Pyrrhocoris apterus****	F	2756, -0.0046, -0.1802	LW>SW	Honek (1987)
		Orthoptera; *Chorthippus parallelus****	F	35, 0.2302, 0.1247	SW=LW	Ritchie et al (1987)
		Dermaptera; *Paralabella dorsalis***	M	87, 0.0835, 0.1482	SW=LW	Briceño & Eberhard (1987)
		Hemiptera; *Gerris remigis***	M	96, 0.125, 0.0296	SW=LW	Fairbairn (1988)
		Hemiptera; *Javesella pellucida***	M	216, 0.2282, 0.0909	SW=LW	Mochida (1973), Ammar (1973)
		Hemiptera; *Nilaparvata lugens***	M	2734, -0.0051, -0.2221	LW>SW	Novotný (1995)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Development	p and Effect size meta-analysis	Hemiptera; *Limnoporus canaliculatus***	M	125, -0.0031, -0.2448	LW>SW	Zera (1984)
		Thysanoptera; *Hoplothrips karnyi***	M	267, -0.005, -0.1576	LW>SW	Crespi (1988)
		Thysanoptera; *Microcephalothrips abdominalis***	M	76, 0.2458, 0.2294	SW=LW	Nakao (1999)
		Orthoptera; *Modicogryllus confirmatus***	M	46, -0.0213, -0.2992	LW>SW	Tanaka & Suzuki (1998)
		Orthoptera; *Gryllus rubens***	M	1017, 0.0164, 0.1663	SW>LW	Walker (1987)
		Orthoptera; *Gryllus firmus***	M	2190, 0.1469, 0.3046	SW=LW	Roff (1984, 1995), Roff & Fairbairn (1993)
		Orthoptera; *Pteronemobius nitidus***	M	100, 0.0005, 0.4695	SW>LW	Tanaka (1978)
		Orthoptera; *Zonocerus variegatus***	M	43, 0.3745, 0.0706	SW=LW	McCaffery & Page (1978)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Development	p and Effect size meta-analysis	Hemiptera; *Pyrrhocoris sibiricus****	M	163, 0.1323, 0.1950	SW=LW	Sakashita et al (1998)
		Hemiptera; *Pyrrhocoris apterus****	M	2487, -0.00038, -0.2947	LW>SW	Honek (1987)
Onset of reproduction	Descriptive	Coleoptera; *Callosbruchus maculatus**	F	n/a	LW>SW	Utida (1972)
		Hemiptera; *Jadera aeola**	F	n/a	LW>SW	Tanaka & Wolda (1987)
		Orthoptera; *Conocephalus discolor**	F	n/a	LW>SW	Ando & Hartley (1982)
		Hemiptera; *Stenocranus minutus***	F	n/a	LW>SW	May (1975)
		Hemiptera; *Leptopterna dolobrata***	F	n/a	LW>SW	Braune (1983)
		Hemiptera; *Sogata furcifera***	F	n/a	LW>SW	Kisimoto (1957)
		Hemiptera; *Nilaparvata lugens***	F	n/a	LW>SW	Kisimoto (1957)
		Hemiptera; *Delphacodes striatella***	F	n/a	LW>SW	Kisimoto (1957)
		Hemiptera; *Javesella pellucida***	F	n/a	LW>SW	Waloff (1973)
		Hemiptera; *Doratura stylata***	F	n/a	LW>SW	Waloff (1973)
		Hemiptera; *Cavelerius saccharivorus***	F	n/a	LW>SW	Murai (1979)
		Orthoptera; *Pteronemobius taprobanensis***	F	n/a	LW>SW	Tanaka (1976)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Onset of reproduction	Single study	Hemiptera; *Oncopeltus fasciatus**	F	73, 0.5, 0	SW=LW	Palmer & Dingle (1989)
	p and Effect size meta-analysis	Hemiptera; *Cavelerius saccharivorus***	M	35, 0.0037, 0.6748	LW>SW	Fujisaki (1992)
		Coleoptera; *Adalia bipunctata***	F	116, 0.01, 0.2160	LW>SW	Ueno et al (2004)
		Dermaptera; *Paralabela dorsalis***	F	47, 0.00005, 0.5676	LW>SW	Briceño & Eberhard (1987)
		Hemiptera; *Laodelphax striatellus***	F	30, 0.025, 0.3578	LW>SW	Mishiro et al (1994)
		Hemiptera; *Acyrthosiphon pisum***	F	81, 0.00005, 0.8191	LW>SW	Campbell & Mackauer (1977)
		Hemiptera; *Drepanosiphum dixoni***	F	61, 0.005, 0.3298	LW>SW	Dixon (1972)
		Hemiptera; *Sitobion avenae***	F	88, 0.0004, 0.5082	LW>SW	Araya et al (1996)
		Hemiptera; *Prokelisia dolus***	F	51, 0.005, 0.3607	LW>SW	Denno et al (1989)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Onset of reproduction	p and Effect size meta-analysis	Hemiptera; *Gerris remigis***	F	96, 0.0262, 0.2910	LW>SW	Fairbairn (1988)
		Hemiptera; *Gerris buenoi***	F	89, 0.00005, 0.4124	LW>SW	Harada & Spence (2000)
		Hemiptera; *Javesella pellucida***	F	91, 0.00005, 0.4079	LW>SW	Mochida (1973)
		Hemiptera; *Nilaparvata lugens***	F	58, 0.1806, 0.3898	SW=LW	Oh (1979), Manjunath (1977)
		Hemiptera; *Horvathiolus gibbicollis***	F	92, 0.0028, 0.4446	LW>SW	Solbreck (1986)
		Hemiptera; *Jadera haematoloma***	F	71, 0.0241, 0.4136	LW>SW	Carroll et al (2003)
		Hemiptera; *Sipha flava***	F	102, 0.00005, 0.3853	LW>SW	Hentz & Nuessly (2004)
		Hemiptera; *Cavelerius saccharivorus***	F	148, 0.0169, 0.4194	LW>SW	Fujisaki (1986, 1992, 1993)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Onset of reproduction	p and Effect size meta-analysis	Hemiptera; *Microvelia horvathi***	F	35, 0.005, 0.4354	LW>SW	Muraji & Nakasuji (1988)
		Hemiptera; *Microvelia douglasi***	F	54, 0.005, 0.3505	LW>SW	Muraji & Nakasuji (1988)
		Hemiptera; *Microvelia kyushuensis***	F	56, 0.0005, 0.4398	LW>SW	Muraji & Nakasuji (1988)
		Orthoptera; *Gryllus rubens***	F	75, 0.0188, 0.0.2426	LW>SW	Zera & Rankin (1989)
		Orthoptera; *Gryllus firmus***	F	419, 0.01, 0.1455	LW>SW	Roff (1990)
		Orthoptera; *Modicogryllus confirmatus***	F	39, 0.001, 0.4948	LW>SW	Tanaka (1993)
		Orthoptera; *Eobiana engelhardti subtropica***	F	39, 0.0005, 0.7979	LW>SW	Higaki & Ando (2003)
		Orthoptera; *Chorthippus parallelus****	F	9, 0.0088, 0.792	LW>SW	Ritchie et al (1987)
		Hemiptera; *Pyrrhocoris apterus****	F	146, 0.00005, 0.4560	LW>SW	Socha & Šula (1996)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Longevity	Descriptive	Coleoptera; *Callosbruchus maculatus**	F	n/a	LW>SW	Caswell (1960), Utida (1972)
		Hemiptera; *Jadera aeola**	F	n/a	LW>SW	Tanaka & Wolda (1987)
		Hemiptera; *Laodelphax striatellus***	F	n/a	SW=LW	Mitsuhashi & Koyama (1974)
		Hemiptera; *Acyrthosiphon pisum***	F	n/a	SW=LW	Campbell & Mackauer (1977)
		Hemiptera; *Sogata furcifera***	F	n/a	LW>SW	Kisimoto (1957)
		Hemiptera; *Nilaparvata lugens***	F	n/a	LW>SW	Kisimoto (1957)
		Hemiptera; *Delphacodes striatella***	F	n/a	LW>SW	Kisimoto (1957)
		Hemiptera; *Sipha flava***	F	n/a	SW=LW	Hentz & Nuessly (2004)
		Orthoptera; *Chorthippus parallelus****	F	n/a	SW=LW	Ritchie et al (1987)
		Coleoptera; *Callosobruchus maculatus**	M	n/a	LW>SW	Utida (1972)
		Hemiptera; *Sogata furcifera***	M	n/a	LW>SW	Kisimoto (1957)
		Hemiptera; *Nilaparvata lugens***	M	n/a	LW>SW	Kisimoto (1957)
		Hemiptera; *Delphacodes striatella***	M	n/a	LW>SW	Kisimoto (1957)
	p and Effect size meta-analysis	Coleoptera; *Callosobruchus maculatus**	F	180, 0.0204, 0.1525	LW>SW	Chaudhuri (2005)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Longevity	p and Effect size meta-analysis	Coleoptera; *Callosobruchus subinnotatus**	F	76, 0.025, 0.2248	LW>SW	Appleby & Credland (2001)
		Coleoptera; *Adalia bipunctata***	F	116, 0.0005, 0.3056	LW>SW	Ueno et al (2004)
		Dermaptera; *Paralabella dorsalis***	F	79, -0.00005, -0.4378	SW>LW	Briceño & Eberhard (1987)
		Hemiptera; *Acyrthosipon pisum***	F	39, 0.0708, 0.2354	SW=LW	MacKay & Wellington (1975)
		Hemiptera; *Sitobion avenae***	F	274, 0.5275, 0.1239	SW=LW	Wratten (1977), Araya et al (1996)
		Hemiptera; *Metopolophium dirhodum***	F	135, -0.0022, -0.2457	SW>LW	Wratten (1977)
		Hemiptera; *Aphis fabae***	F	179, 0.5, 0	SW=LW	Dixon & Wratten (1971)
		Hemiptera; *Prokelisa dolus***	F	62, -0.025, -0.2489	SW>LW	Denno et al (1989)
		Hemiptera; *Cavelerius saccharivorus***	F	62, 0.025, 0.3597	LW>SW	Fujisaki (1986, 1993)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Longevity	p and Effect size meta-analysis	Hemiptera; *Stenocranus minutus***	F	66, 0.0494, 0.3763	SW=LW	May (1975)
		Hemiptera; *Javesella pellucida***	F	240, 0.4403, 0.0216	SW=LW	Mochida (1973), Ammar (1973)
		Hemiptera; *Macrosiphum granarium***	F	636, 0.1002, 0.0719	SW=LW	Noda (1960a)
		Hemiptera; *Rhopalosiphum prunifoliae***	F	633, 0.0671, 0.1773	SW=LW	Noda (1960a)
		Hemiptera; *Horvathious gibbicollis***	F	96, 0.2823, 0.1071	SW=LW	Solbreck (1986)
		Hemiptera; *Limnoporus canaliculatus***	F	121, 0.0121, 0.205	LW>SW	Zera (1984)
		Hemiptera; *Nilaparvata lugens***	F	20, 0.0417, 0.3871	SW=LW	Manjunath (1977)
		Hemiptera; *Microvelia horvathi***	F	35, 0.3489, 0.0656	SW=LW	Muraji & Nakasuji (1988)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Longevity	p and Effect size meta-analysis	Hemiptera; *Microvelia douglasi***	F	54, 0.0083, 0.3263	LW>SW	Muraji & Nakasuji (1988)
		Hemiptera; *Microvelia kyushuensis***	F	56, -0.0005, -0.4398	SW>LW	Muraji & Nakasuji (1988)
		Orthoptera; *Modicogrylus confirmatus***	F	106, 0.025, 0.1904	LW>SW	Tanaka & Suzuki (1998)
		Orthoptera; *Allonemobius socius***	F	883, 0.5, 0	SW=LW	Roff & Bradford (1996)
		Orthoptera; *Allonemobius fasciatus***	F	61, 0.1051, 0.1604	SW=LW	Roff (1984)
		Orthoptera; *Gryllus firmus***	F	70, 0.2132, 0.0951	SW=LW	Roff (1984)
		Orthoptera; *Pteronemobius taprobanensis***	F	20, 0.005, 0.5760	LW>SW	Tanaka (1976)
		Orthoptera; *Eobiana engelhardti subtropica***	F	39, 0.0005, 0.5270	LW>SW	Higaki & Ando (2003)
		Dermaptera; *Paralabella dorsalis***	M	44, -0.00005, -0.5866	SW>LW	Briceño & Eberhard (1987)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Longevity	p and Effect size meta-analysis	Hemiptera; *Javesella pellucida***	M	239, 0.3793, 0.0439	SW=LW	Mochida (1973), Ammar (1973)
		Hemiptera; *Horvathiolus gibbicollis***	M	96, 0.3317, 0.0726	SW=LW	Solbreck (1986)
		Hemiptera; *Prokelisia dolus***	M	102, 0.3675, 0.0479	SW=LW	Langelotto et al (2000)
		Hemiptera; *Acyrthosiphon pisum***	M	343, 0.2075, 0.1073	SW=LW	Sack & Stern (2007)
		Hemiptera; *Limnoporus canaliculatus***	M	88, 0.0271, 0.2052	SW=LW	Zera (1984)
		Hymenoptera; *Cardiocondyla wroughtoni***	M	48, 0.1670, 0.3936	SW=LW	Kinomura & Yamauchi (1987)
		Hymenoptera; *Cardiocondyla emeryi***	M	40, 0.0375, 0.2814	SW=LW	Heinze et al (1998)
		Hymenoptera; *Cardiocondyla minutior***	M	29, 0.04, 0.3252	SW=LW	Heinze et al (1998)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Longevity	p and Effect size meta-analysis	Hymenoptera; *Cardiocondyla* sp. 5**	M	11, -0.002, -0.8678	SW>LW	Heinze et al (1998)
		Hymenoptera; *Cardiocondyla obscurior***	M	63, 0.08, 0.1770	SW=LW	Schrempf et al (2007)
		Orthoptera; *Modicogryllus confirmatus***	M	102, 0.025, 0.1941	LW>SW	Tanaka & Suzuki (1998)
		Orthoptera; *Gryllus firmus***	M	10, 0.69, -0.1568	SW=LW	Crnokrak & Roff (1998a)
		Orthoptera; *Pteronemobius taprobanensis***	M	20, 0.005, 0.5760	LW>SW	Tanaka (1976)
Mating investment: Gonadal investment	Descriptive	Coleoptera; *Callosbruchus subinnotatus**	F	n/a	SW>LW	Appleby & Credland (2001)
		Hemiptera; *Nilaparvata lugens***	F	n/a	SW>LW	Ayoade et al (1999)
		Orthoptera; *Gryllus firmus***	F	n/a	SW>LW	Zhao & Zera (2004)
		Coleoptera; *Callobruchus subinnotatus***	M	n/a	SW>LW	Appleby & Credland (2001)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Mating investment: Gonadal investment	Single study	Coleoptera; *Ptinella aptera***	F	48, -0.00005, -0.5616	LW>SW	Taylor (1978)
	p and Effect size meta-analysis	Hemiptera; *Myzocallis myricae***	F	31, 0.0005, 0.5911	SW>LW	Dixon & Kindlmann (1999)
		Hemiptera; *Megoura viciae***	F	36, 0.0005, 0.5485	SW>LW	Dixon et al (1993)
		Orthoptera; *Gryllus texensis***	F	29, 0.00005, 0.7225	SW>LW	Guerra & Pollack (2009)
		Orthoptera; *Gryllus firmus***	F	2481, 0.0627, 0.3740	SW=LW	Mole & Zera (1994), Roff & DeRose (2001), Roff & Fairbairn (2007), Roff & Gélinas (2003), Stirling et al (2001), Zera & Brink (2000), Zera et al (2007), Zera & Zhao (2006), Zhao & Zera (2006)
		Orthoptera; *Modicogryllus confirmatus***	F	20, 0.025, 0.6198	SW>LW	Tanaka (1993)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Mating investment: Gonadal investment	p and Effect size meta-analysis	Orthoptera; *Gryllodes sigillatus***	M	68, 0.0005, 0.4146	SW>LW	Sakaluk (1997)
		Orthoptera; *Gryllus firmus***	M	2501, 0.0631, 0.1130	SW=LW	Crnokrak & Roff (2002), Roff & Fairbairn (1993), Saglam et al (2008)
		Orthoptera; *Modicogryllus confirmatus***	M	45, 0.125, 0.2266	SW=LW	Tanaka (1999)
Mating investment: Mating frequency	Single study	Hemiptera; *Pyrrhocoris apterus****	F	80, 0.00029, 0.3852	SW>LW	Socha & Zemek (2004a)
Mating investment: Mating propensity	p and Effect size meta-analysis	Hemiptera; *Aquarius remigis***	F	380, 0.1708, 0.1537	SW=LW	Fairbairn & Preziosi (1996)
		Hemiptera; *Cavelerius saccharivorus***	F	24, 0.025, 0.4001	SW>LW	Fujisaki (1986)
		Hymenoptera; *Melittobia digitata***	F	283, 0.5, 0	SW=LW	González & Matthews (2005)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Mating investment: Mating propensity	p and Effect size meta-analysis	Orthoptera; *Gryllus texensis***	M	137, 0.0001, 0.3177	SW>LW	Guerra & Pollack (2007)
		Hymenoptera; *Cardiocondyla obscurior***	M	11, 0.3453, 0.1200	SW=LW	Schrempf et al (2007)
Mating investment: Resource defense	p and Effect size meta-analysis	Thysanoptera; *Oncothrips tepperi***	F	119, 0.043, 0.1574	SW=LW	Perry et al (2003)
		Hemiptera; *Aquarius remigis***	F	57, 0.0318, 0.2457	SW=LW	Kaitala & Dingle (1993)
Mating investment: Accessory glands	Descriptive	Coleoptera; *Callosobruchus subinnotatus**	M	n/a	SW>LW	Appleby & Credland (2001)
	Single study	Hemiptera; *Pyrrhocoris apterus****	M	20, 0.0021, 0.6402	SW>LW	Socha (2004)
	p and Effect size meta-analysis	Orthoptera; *Gryllodes sigillatus***	M	68, 0.00075, 0.3870	SW>LW	Sakaluk (1997)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Mating investment: Accessory glands	p and Effect size meta-analysis	Orthoptera; *Modicogryllus confirmatus***	M	45, 0.22, 0.1688	SW=LW	Tanaka (1999)
Mating investment: Genitalia	Descriptive	Thysanoptera; *Iotatubothrips kranzae***	M	n/a	LW>SW	Mound et al (1998)
Mating investment: Mate attraction	Descriptive	Hemiptera; *Nilaparvata lugens***	M	n/a	SW=LW	Ichikawa (1982)
	p and Effect size meta-analysis	Orthoptera; *Gryllus firmus***	M	575, 0.0608, 0.3392	SW=LW	Crnokrak & Roff (1995, 1998a,b), Roff et al (2003), Webb & Roff (1992)
		Orthoptera; *Gryllus rubens***	M	52, 0.2205, 0.1297	SW=LW	Bertram & Bowen (2006)
		Orthoptera; *Gryllus texensis***	M	33, 0.4, 0.0479	SW=LW	Souroukis et al (1992)
Mating investment: Mating activity	Descriptive	Hemiptera; *Pyrrhocoris apterus****	M	n/a	SW=LW	Socha & Zemek (2004b)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Mating investment: Mating activity	p and Effect size meta-analysis	Hemiptera; *Pyrrhocoris apterus******	M	192, 0.0018, 0.3744	SW>LW	Socha (2004)
		Hemiptera; *Pyrrhocoris apterus****	M	154, 0.2128, 0.0950	SW=LW	Socha et al (2004a)
Mating investment: Nuptial gift	Single study	Orthoptera; *Conocephalus discolor**	M	12, 0.05, 0.4749	SW>LW	Simmons & Thomas (2004)
		Orthoptera; *Gryllodes sigillatus****	M	68, 0.00075, 0.3870	SW>LW	Sakaluk (1997)
Mating investment: Competition	Descriptive	Hemiptera; *Nilaparvata lugens****	M	n/a	SW=LW	Ichikawa (1982)
		Hymenoptera; *Cardiocondyla wroughtoni****	M	n/a	SW>LW	Kinomura & Yamauchi (1987)
	p and Effect size meta-analysis	Hemiptera; *Nilaparvata lugens****	M	153, 0.343, 0.0327	SW=LW	Novotný (1995)
		Hemiptera; *Prokelisia dolus****	M	176, 0.265, 0.1319	SW=LW	Langellotto (2000)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Mating investment: Competition	p and Effect size meta-analysis	Thysanoptera; *Hoplothrips karnyi***	M	10, 0.005, 0.8146	SW>LW	Crespi (1988)
Mating investment: Weapons	Single study	Thysanoptera; *Hoplothrips karnyi***	M	267, 0.00005, 0.2381	SW>LW	Crespi (1988)
Mating success: Matings acquired	Descriptive	Hemiptera; *Pyrrhocoris apterus****	M	n/a	SW>LW	Socha & Zemek (2004b)
	p and Effect size meta-analysis	Hemiptera; *Gerris lacustris***	F	55, 0.05, 0.2218	SW=LW	Batorczak et al (1994)
		Hemiptera; *Leptopterna dolobrata***	F	795, 0.1674, 0.1075	SW=LW	Braune (1983)
		Hymenoptera; *Melittobia digitata***	F	223, 0.0005, 0.2204	SW>LW	González & Matthews (2005)
		Thysanoptera; *Oncothrips morrisi***	F	245, 0.5, 0	SW=LW	Kranz et al (2001b)
		Hemiptera; *Laodelphax striatellus***	M	83, 0.5, 0	SW=LW	Mishiro et al (1994)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Mating success: Matings acquired	p and Effect size meta-analysis	Hemiptera; *Prokelisia dolus***	M	121, 0.1807, 0.0857	SW=LW	Langellotto & Denno (2001), Langellotto et al (2000)
		Hemiptera; *Acyrthosiphon pisum***	M	226, 0.0983, 0.2234	SW=LW	Sack & Stern (2007)
		Hymenoptera; *Cardiocondyla emeryi***	M	12, 0.305, 0.1472	SW=LW	Heinze et al (1998)
		Hymenoptera; *Cardiocondyla obscurior***	M	15, 0.245, 0.1782	SW=LW	Schrempf et al (2007)
		Orthoptera; *Gryllodes sigillatus***	M	49, 0.01, 0.3323	SW>LW	Sakaluk (1997)
Mating success: Matings acquired	p and Effect size meta-analysis	Orthoptera; *Gryllus texensis***	M	84, 0.3565, 0.0402	SW=LW	Guerra & Pollack (2007)
		Hemiptera; *Aquarius remigis***	M	124, 0.03361, 0.1643	SW=LW	Kaitala & Dingle (1993)
		Hemiptera; *Pyrrhocoris apterus****	M	82, 0.0886, 0.1490	SW=LW	Socha & Zemek (2004a)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Mating success: Matings acquired	p and Effect size meta-analysis	Hemiptera; *Pyrrhocoris apterus****	M	192, 0.005, 0.322	SW>LW	Socha (2004)
Mating success: Preferred by females	p and Effect size meta-analysis	Orthoptera; *Gryllus firmus***	M	20, 0.01, 0.5201	SW>LW	Crnokrak & Roff (1995)
		Orthoptera; *Gryllus firmus***	M	42, 0.0001, 0.7400	SW>LW	Crnokrak & Roff (1998a)
		Orthoptera; *Gryllus firmus***	M	218, 0.0001, 0.2519	SW>LW	Crnokrak & Roff (1998b)
		Orthoptera; *Gryllus firmus***	M	100, 0.0794, 0.5138	SW=LW	Roff et al (2003)
Reproductive success: Egg characteristics	Descriptive	Lepidoptera; *Orgyia thyellina***	F	n/a	SW>LW	Kimura & Masaki (1977), Sato (1977)
	p and Effect size meta-analysis	Hemiptera; *Nilaparvata lugens***	F	200, 0.1254, 0.3611	SW=LW	Bertuso & Tojo (2002)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Reproductive success: Egg characteristics	p and Effect size meta-analysis	Orthoptera; *Gryllus firmus***	F	198, 0.0558, 0.3980	SW=LW	Cisper et al (2000), Zera et al (1994)
		Thysanoptera; *Oncothrips waterhousei***	F	53, -0.0005, -0.4521	LW>SW	Kranz et al (2001a)
		Thysanoptera; *Oncothrips habrus***	F	41, -0.0005, -0.5140	LW>SW	Kranz et al (2001a)
		Thysanoptera; *Oncothrips morrisi***	F	33, 0.03, 0.3274	SW=LW	Kranz et al (2001b)
Reproductive success: Fecundity	Descriptive	Coleoptera; *Callosobruchus maculatus**	F	n/a	SW>LW	Caswell (1960), Utida (1972)
		Hemiptera; *Jadera aeola**	F	n/a	SW>LW	Tanaka & Wolda (1987)
		Orthoptera; *Conocephalus discolor**	F	n/a	SW>LW	Ando & Hartley (1982)
		Lepidoptera; *Orgyia thyellina***	F	n/a	LW>SW	Sato (1977)
		Hemiptera; *Acyrthosipon pisum***	F	n/a	SW>LW	Tsumuki et al (1990)
		Hemiptera; *Laodelphax striatellus***	F	n/a	LW>SW	Mitsuhashi & Koyama (1974)
		Hemiptera; *Stenocranus minutus***	F	n/a	SW>LW	May (1975)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Reproductive success: Fecundity	Descriptive	Hemiptera; *Sogata furcifera***	F	n/a	SW>LW	Kisimoto (1957)
		Hemiptera; *Nilaparvata lugens***	F	n/a	SW=LW	Kisimoto (1957)
		Hemiptera; *Delphacodes striatella***	F	n/a	SW=LW	Kisimoto (1957)
		Hemiptera; *Cavelerius saccharivorus***	F	n/a	SW=LW	Murai (1979)
		Hemiptera; *Rhopalosiphum padi***	F	n/a	SW>LW	Khan & Port (2008)
Reproductive success: Fecundity	Descriptive	Orthoptera; *Gryllodes sigillatus***	F	n/a	SW>LW	Ghouri & McFarlane (1958)
		Orthoptera; *Pteronemobius taprobanensis***	F	n/a	SW>LW	Tanaka (1976)
		Orthoptera; *Chorthippus parallelus****	F	n/a	SW=LW	Ritchie et al (1987)
	p and Effect size meta-analysis	Hemiptera; *Oncopeltus fasciatus**	F	72, -0.00765, -0.2858	LW>SW	Palmer & Dingle (1989)
		Coleoptera; *Callosobruchus maculatus**	F	360, 0.1478, 0.1677	SW=LW	Chaudhuri (2005)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Reproductive success: Fecundity	p and Effect size meta-analysis	Orthoptera; *Conocephalus discolor**	F	37, 0.0025, 0.4615	SW>LW	Simmons & Thomas (2004)
		Coleoptera; *Calathus cinctus***	F	245, -0.0005, -0.2103	LW>SW	Aukema (1991)
		Coleoptera; *Calathus melanocephalus***	F	105, -0.0005, -0.3212	LW>SW	Aukema (1991)
		Coleoptera; *Pogunus chalceus***	F	19, -0.0227, -0.4588	LW>SW	Desender (1989)
		Coleoptera; *Ptinella aptera***	F	35, -0.00005, -0.6577	LW>SW	Taylor (1978)
		Coleoptera; *Ptinella errabunda***	F	26, -0.0053, -0.5013	LW>SW	Taylor (1978)
		Coleoptera; *Adalia bipunctata***	F	116, -0.0005, -0.3056	LW>SW	Ueno et al (2004)
		Hymenoptera; *Melittobia digitata***	F	137, 0.0005, 0.3981	SW>LW	Cônsoli & Vinson (2002)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Reproductive success: Fecundity	p and Effect size meta-analysis	Dermaptera; *Paralabella dorsalis***	F	50, 0.0007, 0.4518	SW>LW	Briceño & Eberhard (1987)
		Hemiptera; *Acyrthosiphon pisum***	F	201, 0.04, 0.4872	SW=LW	Campbell & Mackauer (1977), Mackay et al (1983)
		Hemiptera; *Sitobion avenae***	F	656, 0.0493, 0.3513	SW=LW	Araya et al (1996), Khan & Port (2008), Watt (1984), Wratten (1977)
		Hemiptera; *Gerris lacustris***	F	45, 0.00005, 0.5800	SW>LW	Batorczak et al (1994)
		Hemiptera; *Aquarius remigis***	F	112, 0.2074, 0.1041	SW=LW	Fairbairn & Preziosi (1996)
		Hemiptera; *Metopolophium dirhodum***	F	219, 0.009, 0.3229	SW>LW	Wratten (1977)
		Hemiptera; *Cavelerius saccharivorus***	F	1193, 0.3349, 0.0568	SW=LW	Fujisaki (1985, 1986, 1993)
		Hemiptera; *Laodelphax striatellus***	F	30, 0.0085, 0.4358	SW>LW	Mishiro et al (1994)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Reproductive success: Fecundity	p and Effect size meta-analysis	Hemiptera; *Drepanosiphum dixoni***	F	61, 0.025, 0.2510	SW>LW	Dixon (1972)
		Hemiptera; *Aphis fabae***	F	233, 0.1062, 0.2255	SW=LW	Dixon & Wratten (1971)
		Hemiptera; *Prokelisia dolus***	F	62, 0.005, 0.3272	SW>LW	Denno et al (1989)
		Hemiptera; *Gerris remigis***	F	87, 0.1640, 0.1552	SW=LW	Fairbairn (1988)
		Hemiptera; *Gerris buenoi***	F	55, 0.0002, 0.4773	SW>LW	Harada & Spence (2000)
		Hemiptera; *Nilaparvata lugens***	F	309, 0.1959, 0.2270	SW=LW	Manjunath (1977), Mochida (1964), Oh (1979)
		Hemiptera; *Javesella pellucida***	F	20, 0.4973, 0.0016	SW=LW	Mochida (1973)
		Hemiptera; *Horvathiolus gibbicollis***	F	96, 0.2632, 0.0918	SW=LW	Solbreck (1986)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Reproductive success: Fecundity	p and Effect size meta-analysis	Hemiptera; *Jadera haematoloma***	F	71, 0.3465, 0.0663	SW=LW	Carroll et al (2003)
		Hemiptera; *Limnoporus canaliculatus***	F	60, 0.025, 0.2530	SW>LW	Zera (1984)
		Hemiptera; *Sipha flava***	F	102, 0.0318, 0.1837	SW=LW	Hentz & Nuessly (2004)
		Hemiptera; *Microvelia horvathi***	F	35, 0.005, 0.4354	SW>LW	Muraji & Nakasuji (1988)
		Hemiptera; *Microvelia douglasi***	F	54, 0.3630, 0.0478	SW=LW	Muraji & Nakasuji (1988)
		Hemiptera; *Microvelia kyushuensis***	F	56, 0.0005, 0.4398	SW>LW	Muraji & Nakasuji (1988)
		Orthoptera; *Gryllotalpa orientalis***	F	21, 0.2584, 0.2874	SW=LW	Endo (2006)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Reproductive success: Fecundity	p and Effect size meta-analysis	Orthoptera; *Modicogryllus confirmatus***	F	120, 0.002, 0.4747	SW>LW	Tanaka (1993), Tanaka & Suzuki (1998)
		Orthoptera; *Gryllus firmus***	F	1474, 0.0829, 0.2262	SW=LW	Cisper et al (2000), Mole & Zera (1994), Roff (1984, 1989, 1990), Roff et al (1997), Stirling et al (1999)
		Orthoptera; *Gryllus rubens***	F	75, 0.0067, 0.3351	SW>LW	Zera & Rankin (1989)
		Orthoptera; *Allonemobius socius***	F	720, 0.00025, 0.1297	SW>LW	Roff & Bradford (1996)
		Orthoptera; *Allonemobius fasciatus***	F	35, 0.198, 0.1435	SW=LW	Roff (1984)
		Orthoptera; *Eobiana engelhardti subtropica***	F	39, 0.1163, 0.2719	SW=LW	Higaki & Ando (2003)
Reproductive success: Development of offspring	Descriptive	Hemiptera; *Rhopalosiphum padi***	F	n/a	SW=LW	Dixon (1976)

Appendix 1 Continued

Trait	Resource	Order; Species	Sex	*n*, p value, *r* value	Trend	Reference(s)
Reproductive success: Offspring quality	Single study	Hemiptera; *Rhopalosiphum padi***	F	192, 0.0005, 0.2375	SW>LW	Dixon (1976)
Reproductive success: Siring success	p and Effect size meta-analysis	Hemiptera; *Laodelphax striatellus***	M	83, 0.5, 0	SW=LW	Mishiro et al (1994)
Reproductive success: Siring success	p and Effect size meta-analysis	Hemiptera; *Prokelisia dolus***	M	30, 0.01, 0.4082	SW>LW	Langellotto et al (2000)
		Hymenoptera; *Cardiocondyla emeryi***	M	9, 0.005, 0.8587	SW>LW	Heinze et al (1998)
		Orthoptera; *Gryllus rubens***	M	14, 0.05, 0.4396	SW=LW	Holtmeier & Zera (1993)
		Orthoptera; *Gryllus firmus***	M	225, 0.5, 0	SW=LW	Roff & Fairbairn (1993)
		Hemiptera; *Pyrrhocoris apterus****	M	20, 0.2685, 0.1380	SW=LW	Socha et al (2004a)
		Hemiptera; *Pyrrhocoris apterus****	M	64, 0.1667, 0.4317	SW=LW	Socha (2008)

Bridge from Chapter 1 to Chapter 2

In Chapter 1, a meta-analysis was conducted on the literature examining the life history trade-off between flight capability and reproduction in wing dimorphic insects. A key result was that with respect to the different sexes, the trade-off was evident in females, but not in males. Long-winged females had significantly reduced reproduction relative to short-winged females. In males, however, the existence of a trade-off was unclear. Overall, data in males were lacking, as fewer studies have been performed with males.

In Chapter 2, we addressed whether or not a trade-off exists in males, by comparing the different male flight-morphs of *G. texensis* in their propensity to court a female in paired interactions. Here, we predicted that flight-capable males would have a lower probability of courting a female, as compared to flight-incapable males. Moreover, we asked whether or not other factors might affect the expression of the trade-off, if it exists in males.

Chapter 2

A life history trade-off between flight ability and reproductive behavior in male field crickets (*Gryllus texensis*)

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ABSTRACT

Flight dimorphic male field crickets (*Gryllus texensis*) incur a life history trade-off between flight ability and reproduction, where flight ability comes with a male fitness cost. In courtship trials, flight-capable males produce courtship song, a necessary signal for mating success, with a significantly lower probability than flight-incapable males. The trade-off was most pronounced in younger males. Males that lose the ability to fly through histolysis of flight muscles produce courtship song with a similar probability as males incapable of flight for their entire lives. Many males may not live long enough in nature for this to occur, however. Time of day did not affect the expression of the trade-off. Neither male morph nor time of day influenced female mating behavior.

INTRODUCTION

Life history theory predicts that certain traits may trade off with one another, especially when each trait is energetically costly (Zera and Denno, 1997; Zera and Harshman, 2001). One well-established trade-off is between flight ability and reproduction. Here, a flight-capable (and, presumably, dispersal-capable) morph expends energy developing and maintaining the flight apparatus at the expense of reproduction. Another morph, in contrast, is flight-incapable but has greater reproductive output. This is an important trade-off in insects, in particular field crickets (Orthoptera; Gryllinae) (Harrison, 1980; Roff, 1986; Zera and Denno, 1997). The majority of previous work has focused on females, and has established that flight-capable females have delayed ovarian growth, longer reproductive latency, and lower fecundity early in adulthood, relative to flight-incapable females (Roff, 1986; Zera and Denno, 1997; Zera and Harshman, 2001). In contrast, some studies on male field crickets have suggested the absence of a trade-off (e.g., no paternity difference: Roff and Fairbairn, 1991, 1993; Holtmeier and Zera, 1993; similar gonad size: Roff and Fairbairn, 1991, 1993; Zera *et al.*, 1997; no difference in calling song structure: Souroukis *et al.*, 1992), whereas others have shown differences between flight morphs suggestive of a trade-off (e.g., difference in calling song duration: Crnokrak and Roff, 1995, 1998a, 1998b, 2000; early age difference in gonad size: Crnokrak and Roff, 2002; difference in male nuptial gift size: Sakaluk, 1997).

We studied the possibility of a trade-off in males in the flight-dimorphic field cricket, *Gryllus texensis*, using the probability of producing courtship song as a measure of reproductive behavior. Previously used measures to investigate flight-morph specific differences in reproductive behavior were based on calling song (Crnokrak and Roff, 1995, 1998a, 1998b, 2000; Souroukis *et al.*, 1992). Although males that call more may have greater success at attracting mates (e.g., Crnokrak and Roff, 1995), differences in calling song production between males (e.g., reduced calling), are not necessarily related to the trade-off between flight ability and reproduction. For example, males form dominance hierarchies, and subordinates call infrequently (Cade, 1979a). Furthermore, males need not call at all in order to encounter females for mating. Cade and Wyatt (1984) demonstrated that male calling decreases in high-density populations, where males and females may meet one another by chance. Males can also employ alternative mating tactics, such as intercepting females attracted to nearby calling males (satellite behavior; Cade, 1979a). Finally, greater calling by males does not assure that mating will occur. Even if a female is attracted to a calling male, he must produce courtship song to elicit female mounting, a prerequisite for mating (Balakrishnan and Pollack, 1996). Thus courtship song is more closely coupled to reproduction than calling song.

We tested three hypotheses concerning a trade-off in male *G. texensis*. First, we hypothesized that flight-capable males would be less likely to produce courtship song than flight-incapable males, that is, that there is a trade-off between flight ability and reproduction. In females, the trade-off between flight ability and fecundity occurs only during the first week of adulthood (Roff, 1986; Zera and Denno, 1997). Our second hypothesis is that a similar effect of age on the expression of the trade-off occurs in males. Flight in *G. texensis* is restricted to the first few hours after sunset (Cade, 1979b). Moreover, juvenile hormone, which has been associated both with flight (Rankin, 1980) and reproduction (Engelmann, 1970), peaks in concentration in *Gryllus firmus* shortly before sunset, but only in flight-capable individuals (Zera and Cisper, 2001; Zhao and Zera, 2004a, 2004b). These observations prompted our third hypothesis, that a trade-off between flight ability and courtship song production would vary in expression according to the time of day. Finally, we asked whether females discriminate between flight-morphs in their mounting responses.

MATERIAL AND METHODS

Study System

Gryllus texensis were obtained from an established laboratory colony (G. S. P., McGill University, Montréal, Québec). Crickets were reared and maintained in an environmentally controlled chamber (12:12 L:D; 27 °C; 50% humidity) with *ad libitum* Purina cat chow and water. Crickets were reared communally until their sex could be determined, when they were segregated by sex. Every second day, newly emerged adults were collected and housed individually in inverted mesh-covered plastic cups.

We tested virgin short-winged and long-winged males that were between 5 and 11 days of adult age. We tested males starting on day 5 of adulthood, as this is the age at which males start producing spermatophores, an indicator of sexual maturity (Cade and Wyatt, 1984). The age range we used also encompasses the mean age (6.9 ± 3.3 days) at which males start producing calling song (Cade and Wyatt, 1984). The upper age limit (11 days adulthood) is similar to the mean age of males found in the field (weighted mean ± pooled standard deviation: 12.68 ± 3.01 days; Murray and Cade, 1995). We used 7-9 day-old, long-winged virgin adult females in courtship trials. Each animal was only used once. The order of trials was randomized via a coin flip (for the time of day) in combination with the roll of a six-sided die (for male age/wing morph class).

Apparatus and Trial Protocol

Courtship interactions were staged between a single male and a single female in an anechoic chamber illuminated by red light (635 nm wavelength, Model E27-R24 light-emitting diode, http://www.superbrightleds.com) and at a temperature of 26-28 °C, during the animals' scotophase. Courtship interactions took place in an open-topped circular mesh arena (height: 10.5 cm; diameter: 15 cm), with a ring of acetate covering the top 4 cm of the arena walls to prevent animals from escaping. The arena was placed on a paper towel that itself was affixed with pushpins to a piece of polyurethane foam. After each trial, we rinsed the mesh arena with 100% ethanol and we changed the paper towel upon which the arena rested to remove olfactory cues that might have been left from a previous trial (Crnokrak and Roff, 1998).

To begin a trial, both the male and female were introduced into the arena, separated by an opaque divider. Once the animals had recovered from handling (i.e., explored their section of the arena in an apparently calm manner; ~ 30-60 s), the divider was removed and a trial commenced. There was no obvious difference in recovery time between the morphs. Trials were conducted according to the following latency criteria that were determined from previous pilot trials (n = 150). First, males were allowed 6 minutes to come into contact with the female. If the two animals failed to come into contact with one another, the trial was not counted. Next, if the crickets did come into contact, the male was allowed an added 5 minutes to produce courtship song. If no courtship singing occurred, the trial was terminated and the male was scored as non-courting. Finally, if courtship singing did occur, the female was allowed 5 minutes to mount the male. A male was scored as mounted only if his abdomen was covered fully by the female, and only if the female remained stationary for at least 10 s.

After each trial, the condition of the male's flight muscles was determined by dorsal dissection. Flight-muscle condition was recorded as either pink (=functional) or white (=non-functional) (Zera *et al.*, 1997). One individual (P. A. G.) was responsible for all dissections to insure the consistent assessment of flight muscle condition. The accuracy of the assessments of this individual was determined by comparing them, for a subset of animals, with those of three other observers. There was 100% agreement between all observers (*n* = 15 crickets: 7 pink-muscled and 8 white-muscled).

Data Analysis

Fisher's exact tests were conducted with the statistical package R (2005, R Development Core Team, http://www.R-project.org). All statistical tests were two-tailed.

RESULTS

Flight-Ability-Associated Differences in Courtship Song Production

We compared the production of courtship song between flight-capable (long-winged, pink-muscled: LW-P) and flight-incapable (long-winged, white-muscled: LW-W; short-winged, white-muscled: SW) males. Flight-capable males were significantly less likely to produce courtship song than flight-incapable males (Bonferroni-corrected Fisher's exact tests, $\alpha = 0.017$: LW-P versus LW-W, $P < 0.0001$; LW-P versus SW, $P = 0.0002$; Fig. 2.1). Among the two flight-incapable morphs, there was a trend towards higher probability of courtship singing for LW-W males, although this was non-significant (LW-W versus SW, $P = 0.066$; Fig. 2.1).

Does the Expression of the Trade-off Vary With Male Age?

We compared the production of courtship song of males grouped according to the following age classes: 5-7, 7-9, and 9-11 days of adulthood. For the 5-7 day age class, flight-capable males were less likely to produce courtship song than flight-incapable males, but, after Bonferroni correction, this was only significant when LW-P males were compared with SW males (Bonferroni-corrected Fisher's exact tests, α = 0.006; LW-P versus SW, *P* = 0.001; LW-P versus LW-W, *P* = 0.009; Fig. 2.2). For the 7-9 day age class, LW-P males did not differ in courtship singing propensity from SW males (*P* = 0.305), but did show a trend for a difference with LW-W males (*P* = 0.054) (Fig. 2.2). For the 9-11 day class, flight-capable males showed a trend for a lower probability of producing courtship song relative to flight-incapable males, but this was non-significant (LW-P versus SW, *P* = 0.097; LW-P versus LW-W, *P* = 0.052; Fig. 2.2). The two flight-incapable morphs (SW, LW-W) did not differ in courtship singing propensity for any age group (5-7 days: *P* = 0.653; 7-9 days: *P* = 0.296; 9-11 days, *P* = 0.553; Fig. 2.2). We conclude that the trade-off is most pronounced in young males.

Does the Trade-off Vary in Expression With the Time of Day?

Males were tested either at dusk (the first two hours of scotophase) or shortly before dawn (the last two hours of scotophase). Flight-capable males were less likely to produce courtship song than flight incapable males at both dusk and dawn (Fig. 2.3; Bonferroni-corrected Fisher's exact test, α = 0.008: compared with SW males at dusk, *P* = 0.005; SW males at dawn, *P* = 0.007; LW-W males at dusk, *P* = 0.00004), although when compared with LW-W males at dawn, this was not significant (*P* = 0.115). Among the two flight incapable morphs, LW-W males showed a trend for greater courtship singing propensity than SW males at dusk (*P* = 0.023), but did not differ at dawn (*P* > 0.9).

Female Mounting Preferences

We used female mounting behavior as our measure of male mating success. Females mounted only males that produced courtship song. Among courtship singers, they showed no preference between the three flight-morph classes (Fisher's exact test: $P = 0.713$; males pooled by flight-morph class; Fig. 2.4a). Females mounted males with similar probability at dusk and shortly before dawn (Fisher's exact test: $P = 0.562$, males pooled by the time of day tested; Fig. 2.4b).

DISCUSSION

Our results demonstrate a life history trade-off in male *G. texensis*. Flight-capable males had a lower probability of producing courtship song than flight-incapable males, particularly during the first week of adulthood. This was apparent at both dusk and dawn. Among flight-incapable males, there was a trend for LW-W males to produce courtship song with greater probability than SW males at dusk. Females mounted only courting males, but their mounting behavior was biased neither by male flight-morph nor by the time of day.

The Economics of a Trade-off in Males

For female crickets, the energetic basis for a trade-off between flight and reproduction is well established. Energy resources can be directed either towards the development of flight-capable muscles and the high metabolic rate that they require, or towards development of large numbers of yolk-rich oocytes (Zera, 2005). In males the costs of flight are presumably similar to those in females, but the costs of reproduction are of course different. Although production of gametes is less expensive for males than for females, reproductive behavior is nevertheless costly for males in other respects. First, production of the courtship song is itself expensive. In *Acheta domesticus*, the rate of oxygen consumption during courtship singing is 2.2 times greater than at rest (Hack, 1998). Energy expenditure during singing scales with sound-pulse rate (Prestwich, 1994), and pulse rate in courtship song of *G. texensis*, 62.2/sec (Fitzpatrick and Gray, 2001), is higher than that of *A. domesticus*, ca. 20/s (Nelson and Nolen, 1997). Thus, as in *A. domesticus*, the energetic cost of courtship singing can be expected to be high in *G. texensis*. Second, males on a restricted diet take longer than well-fed males to produce a spermatophore, suggesting that spermatophore production is also energetically costly (Wagner, 2005).

The Costs and Benefits of Flight

Males with long hind-wings, but histolyzed flight muscles, courted as readily as males that were flight-incapable throughout life, suggesting that a trade-off in males might be only transient. However, flight-muscle histolysis occurred in only 27% of the males in our experiments. The probability of histolysis increases with age, but becomes high only after age 11 days (Zera *et al.*, 1997), corresponding to the oldest males that we tested. This age also corresponds approximately to the mean age of field-captured males (12.68 ± 3.01 days; Murray and Cade, 1995). It thus seems likely that, in the field, many males may not live long enough for muscle histolysis to occur. Even if histolysis does occur in the field, males who begin to court only after histolysis will have forgone mating opportunities for several days during which their flight-incapable counterparts will have been reproductively more active. Considering that male reproductive behavior begins at 4-6 days of age (Cade and Wyatt, 1984; Crnokrak and Roff, 1995), and that the majority of LW males undergo wing-muscle histolysis later than age 11 (Zera *et al.*, 1997), non-courting LW-P males will have missed approximately one week's worth of mating opportunities. If they did court, our finding that females do not distinguish between the morphs suggests that they would have been as successful as flight-incapable males in mating. Thus, the decision of many flight-capable males (60% in our data) not to court is genuinely costly. A second flight-associated cost, which is not directly related to reproduction, is the increased risk of predation by aerially hawking bats.

One direct benefit of flight is that it allows dispersal. Flight-capable individuals can escape deteriorating and unfavourable conditions (Harrison, 1980), whereas flight-incapable individuals are less able to do so. Indeed, it has been suggested that flight dimorphism is maintained, despite the reproductive penalty incurred by flight-capable individuals, by heterogeneity in the environment (Roff, 1994; Zera and Denno, 1997).

Factors Affecting the Expression of the Trade-off

Consistent with the findings for females (see Roff, 1986; Zera and Denno, 1997), we found an effect of age on the difference in courtship song production between the flight-morphs. Flight-capable males had a lower probability of producing courtship song than flight-incapable males at early adult ages (i.e., 5-7 days).

The trade-off between flight ability and courtship singing was evident at both dusk and dawn. If courtship propensity were controlled in a proximate manner by juvenile hormone level then, because this cycles only in flight-capable individuals (Zhao & Zera, 2004a), one might have expected expression of the trade-off to also vary with time of day. That it did not argues against a major role for juvenile hormone in controlling courtship singing.

Problems with Uncovering the Trade-off in Males in Previous Work

Some previous studies with males have found a trade-off between flight and reproduction, whereas others have failed to do so. In most of the earlier studies, flight capability was judged solely by hind-wing length (e.g., Crnokrak and Roff, 1995, 1998a, 1998b; Roff and Fairbairn, 1991, 1993; Holtmeier and Zera 1993; Souroukis *et al.*, 1992). However, our results show that long-winged individuals in which the flight muscles have undergone histolysis are, for the most part, behaviorally equivalent to short-winged individuals. It thus seems possible that in some of this earlier work, a trade-off may have been underestimated, or missed entirely (cf. Zera *et al.*, 1997).

Two studies compared the number of offspring sired by males of different wing morphs, and found no difference (Roff and Fairbairn, 1993; Holtmeier and Zera, 1993), arguing against a trade-off between flight and reproduction. However, as pointed out by Holtmeier and Zera (1993), in these experiments two males, one from each flight-morph, were placed together with a female, and this design may have influenced the results. Placing males together can produce dominance hierarchies, in which the dominant male secures most matings (Burk, 1983). If the two flight morphs are equally likely to become dominant, then the effects of dominance on mating would obscure the detection of a trade-off.

As the majority of previous work failed to detect differences suggestive of a trade-off between flight-dimorphic males, it has been suggested that flight-incapable males may occur simply because of genetic correlations with females, where selection for enhanced reproductive output, at the expense of flight ability, may be strong (Roff and Fairbairn, 1991). Our results, however, demonstrate that the absence of flight ability may be adaptive for males, as well as for females.

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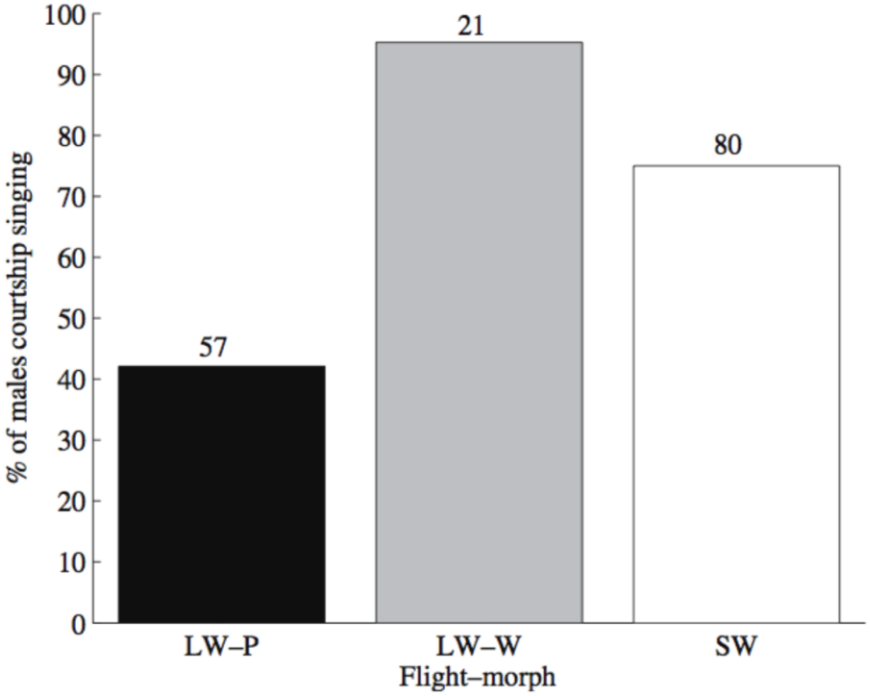

Fig. 2.1 Courtship singing propensity according to differences in flight ability. Numbers above bars indicate sample sizes. LW-P = long-winged, pink-muscled males; LW-W = long-winged, white-muscled males; SW = short-winged, white-muscled males.

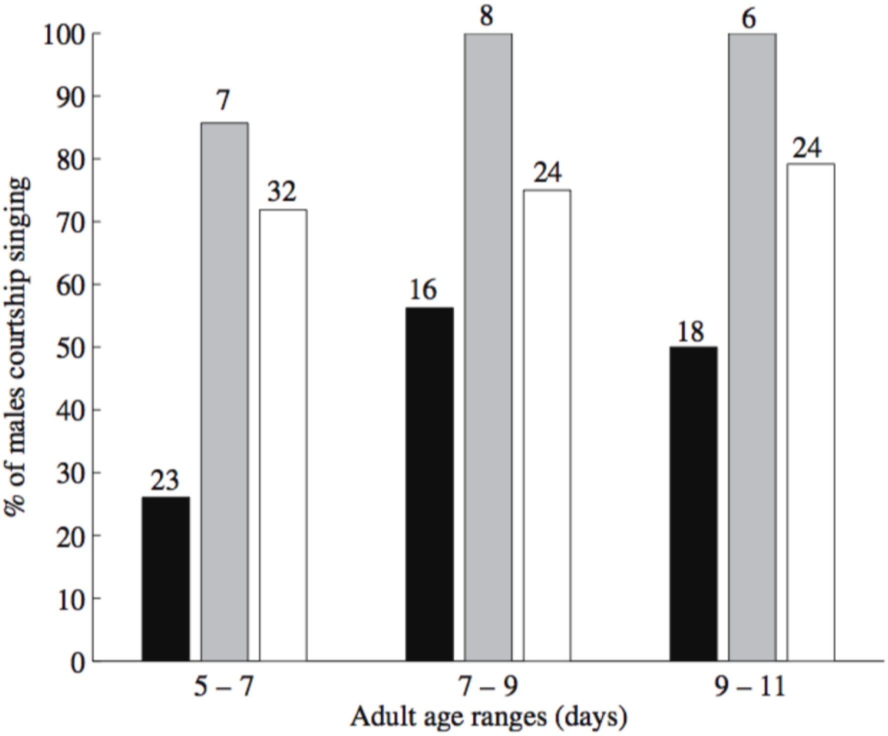

Fig. 2.2 Effect of age on courtship singing propensity. Numbers above bars indicate sample sizes. Black bars = LW-P males; Gray bars = LW-W males; White bars = SW males.

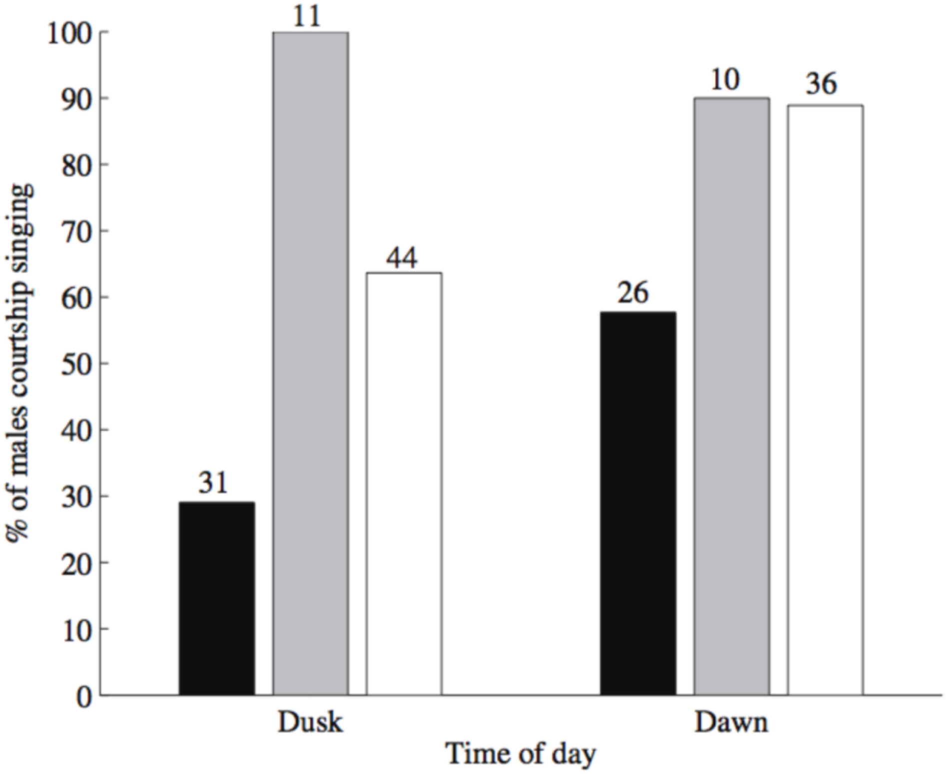

Fig. 2.3 The effect of the time of day on the probability of producing courtship song. Numbers above bars indicate sample sizes. Black bars = LW-P males; Gray bars = LW-W males; White bars = SW males.

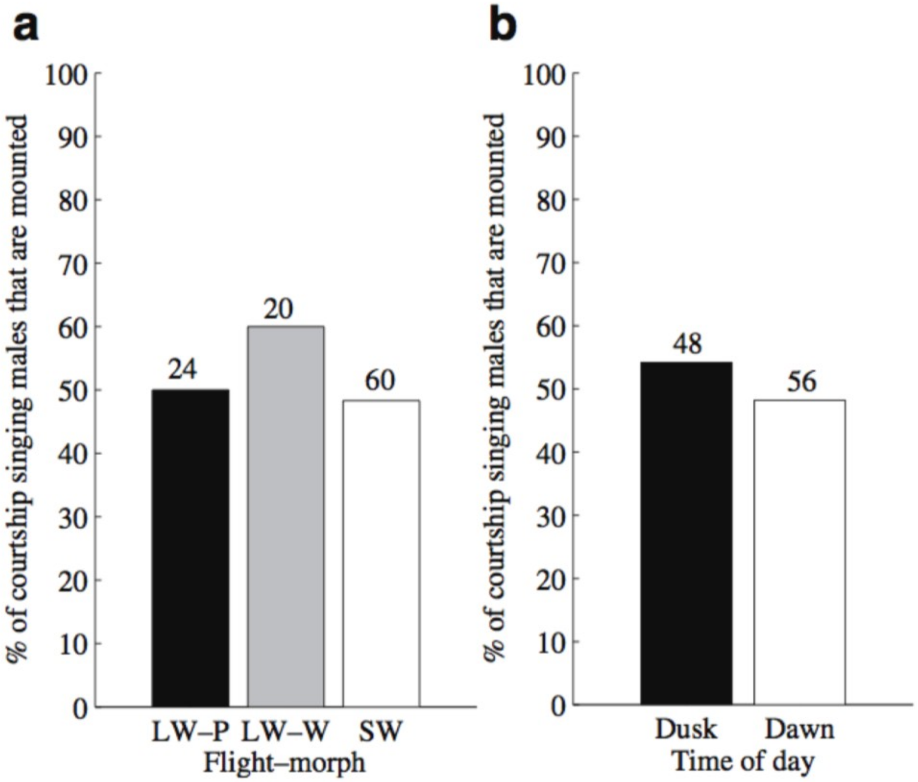

Fig. 2.4 Female mounting behavior is biased neither by A) male flight morph, nor B) the time of day for mating trials. Numbers above bars indicate sample sizes.

Bridge from Chapter 2 to Chapter 3

In Chapter 2, we investigated for a trade-off between flight capability and reproduction in male wing dimorphic insects. We found support for the trade-off as we observed that flight-capable males in the field cricket, *G. texensis*, had a significantly lower propensity to court a female than flight-incapable males. This trade-off was most evident among younger males, and its expression did not vary with the time of day males were tested.

Interestingly, previous work has not addressed how flight itself might affect the trade-off between flight capability and reproduction. In Chapter 3, we examined how flight would affect the expression of the trade-off in both males and females of *G. texensis*. Here, we tested for the effect of flight on male courtship behaviour and female ovary development.

Chapter 3

Flight behaviour attenuates the trade-off between flight capability and reproduction in a wing polymorphic cricket

Patrick A. Guerra & Gerald S. Pollack

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ABSTRACT

Flight-dimorphic insects have been used extensively to study trade-offs between energetically costly traits. Individuals may develop and maintain structures required for flight, or alternatively they may invest in reproduction. Previous experiments have not examined whether flight itself might affect investment into reproduction. As in other *Gryllus* species, flight-capable individuals of the wing polymorphic cricket, *Gryllus texensis*, incur an apparent reproductive penalty for being able to fly, expressed as smaller ovaries in females, and lower courtship propensity in males, than their flight-incapable counterparts. We find that a short bout of flight eliminates the trade-off. Two days after flight, the ovaries of flight-capable females were comparable to those of short-winged females. Similarly, flight markedly increased the probability of courtship behaviour. Our results suggest that the impact of the flight-reproduction trade-off described in earlier studies may have been overestimated.

INTRODUCTION

Life history theory predicts that when different traits are energetically costly, some traits may be emphasized at the expense of others (Roff 1986; Zera & Denno 1997; Zera & Harshman 2001). A well-established trade-off exists between flight ability and reproduction. This occurs in many insect taxa, and has been studied particularly intensively in wing-dimorphic field crickets (Harrison 1980; Roff 1986; Zera & Denno 1997). One morph is flight-capable, possessing long hind wings, well-developed flight musculature, and metabolic pathways to produce flight fuel. In females of this morph, ovarian growth is delayed, resulting in longer reproductive latency and lower early-adulthood fecundity relative to an alternative, flight-incapable morph that has short hind wings, poorly developed flight muscles, and metabolic pathways that favour yolk production. Similarly, flight-capable males invest less than flight-incapable males into production of a mate-attraction song (Crnokrak & Roff 1995; but c.f. Bertram 2007) and courtship behaviour (Guerra & Pollack 2007). Flight-capable individuals may, later in life, lose this ability and divert resources to reproduction (Roff 1986; Zera & Denno 1997; Guerra & Pollack 2007). Although a large body of work has investigated the differences in reproductive investment between flight morphs, in these experiments individuals were not flown; thus the effect of flight on this life-history trade-off was not examined (c.f. Zera 2005).

Flight has been shown to have both positive and negative effects on the reproductive output of insects. Flight enhances oviposition in the wing monomorphic migratory grasshopper, *Melanoplus sanguinipes* (McAnelly & Rankin 1986). By contrast, flight reduces egg production in the wing monomorphic fruit fly, *Drosophila melanogaster* (Roff 1977). In males, flight enhances mating behaviour in the wing-monomorphic cricket, *Gryllus bimaculatus* (Dyakonova & Krushinsky 2008). In a wing-polymorphic cricket, *Gryllus texensis*, males captured after having been observed flying in the field had enhanced calling behaviour relative to field-captured, short-winged males (Bertram 2007). To test whether flight modulates the trade-off between flight ability and reproduction, we measured the consequences of short bouts of tethered flight for both ovarian development and male courtship behaviour in *G. texensis*.

MATERIAL AND METHODS

Virgin *G. texensis* were obtained from an established laboratory colony. Animals were reared with *ad libitum* access to food and water, as described in Guerra & Pollack (2007). Long-winged crickets, aged 3-5 days after the last molt, were attached to a wooden applicator stick at the pronotum using wax and placed in front of a small fan to promote flight. Flight was terminated after 5 min. As a handling control, crickets were treated as above except that instead of flying they were placed on an air-supported styrofoam ball (which permitted tethered walking) for 5 min. Treatments were performed under dim red light, within the first 4 hours of scotophase, as this is when flight is most common in the field (Cade 1979b).

Effect of flight on ovarian development

Two days after treatment, individuals were dissected to inspect their flight muscles and weigh their ovaries. Unflown animals were examined at equivalent ages, i.e., 5-7 days after the adult moult. As an allometric control, we divided the combined fresh weight of both ovaries by the pre-dissection weight of the female. Flight muscles were classified as functional or non-functional according to colour and size (large and pink, or small and white, respectively; Shiga et al 1991; Guerra & Pollack 2007).

We log-transformed measurements of both body weight and ovarian weight before statistical tests, to fulfill assumptions for normality. Normalized ovary weight remained non-normal even after transformation (arcsine), so we analyzed these data using non-parametric tests.

Effect of flight on male courtship behaviour

We tested only long-winged males (5-13 days after last molt), as Guerra & Pollack (2007) previously found that flight-capable males had lower courtship propensity than short-winged individuals. The courtship protocol was identical to that described by Guerra & Pollack (2007). Briefly, a single male was placed in an arena with a single long-winged female (aged 7-9 days after the moult to adulthood). If no contact occurred within 6 minutes, the trial was discontinued. Otherwise, the trial continued either until the male began to court the female, as indicated by the production of courtship song, or until 5 minutes elapsed with no courtship display, in which case the male was scored as non-courting. Trials were performed under dim red illumination.

To determine the effect of flight on male courtship behaviour, flown males were tested in courtship trials either immediately following flight, i.e., during the first 4 hours of scotophase, or 10 hours later, shortly before subjective dawn. This delay was introduced because field studies show that flight is most common early in the evening, but mating is most common at around dawn (Cade 1979a). Handling controls were treated according to the same time regimes. Flight-muscle condition of the males was determined following the courtship trials. We used two-tailed Fisher's exact tests (Bonferroni-corrected when necessary) to compare frequencies of courtship behaviour.

RESULTS

There were no differences among the different types of control, i.e., handled vs. unhandled females (raw ovary weight: t_{21}=-.093, p=0.9267; normalized ovary weight: t_{21}=-.175, p=0.8627), and males that were unhandled, handled and then tested immediately, or handled and tested after a delay (Fisher's exact test, $p>0.99$). We therefore combined data from the control groups within each of these experiments.

Effect of flight on ovarian development

Body weight, measured at ages 5-7 days, did not differ between experimental groups ($F_{2,44}=1.78$, $p=0.180$; mean ± 1 SD: control long-winged=447±81 mg; flown long-winged=471±92; short-winged=410±91). All long-winged females ($n=33$), regardless of treatment, had functional, pink flight muscles. All short-winged females ($n=14$) had non-functional, white flight muscles.

We measured ovarian weight as an indicator of investment into reproduction. Earlier work (*Gryllus firmus*; Zera et al 1997) showed that this is a reliable proxy for the number of post-vitellogenic eggs, and we confirmed this for *G. texensis:* four out of five unflown long-winged females had no mature oocytes (defined as length of 0.5 mm or more) and the fifth had only two, whereas all of five flown females had mature oocytes, with counts ranging between 22 and 140. Ovary weight varied with treatment (Figure 3.1a; $F_{2,44}=69.78$, $p<0.0001$). Short-winged females had larger ovaries than long-winged controls, and flight caused an increase in ovarian weight (flown vs control long-winged females, Tukey HSD, $p<0.05$ for both comparisons), such that by 2 days after the flight, ovary weight was similar between long-winged females that had flown and short-winged females (Tukey HSD, $p>0.05$).

The same result was found when ovary weight was normalized by body weight (Kruskal-Wallis: $X^2=35.55$, $df=2$, $p<0.0001$; Figure 3.1b). A *post hoc*

Dunn's test ($\alpha=0.05$) showed that the normalized ovary weight of short-winged and long-winged, flown females were similar, and that both were greater than that of controls.

Effect of flight on male courtship behaviour

All males had functional, pink flight muscles. Flown males courted with higher probability than controls, whether tested immediately after flight or 10 hours later (Figure 3.2; Bonferroni-corrected Fisher's exact tests, $\alpha=0.017$, $p<0.0001$in both cases). There was no difference between males tested immediately after flight and those tested 10 hours later ($p>0.99$).

DISCUSSION

We show that in *G. texensis*, a species in which there is an oogenesis-flight trade-off in females (our data) and a lower probability of courtship behaviour in flight-capable males relative to flight-incapable males (Guerra & Pollack 2007), a single, short flight bout can mitigate the reproductive penalty of being flight-capable. In males, this effect can last at least overnight, in accord with the delay in mating relative to flight that has been observed in the field (Cade 1979a,b). The enhancement of reproductive output can occur without any obvious changes in flight muscle condition; both males and females still had functional flight muscles when reproductive enhancements were demonstrated, at least as indicated by muscle colour and size. This suggests that energy resources are sufficient to support both reproduction and flight ability, at least in our well fed, lab reared animals. It remains to be seen whether flight would accelerate reproduction under less favorable dietary conditions. Indeed, earlier work has shown that the trade-off between flight capability and investment in reproduction is amplified under conditions of dietary restriction (Zera et al., 1998).

Whether our findings relate to the occurrence of a trade-off between flight and reproduction in the field is unclear. Virtually nothing is known about the age of onset, frequency, or duration of flights in the field. However, our results for males are consistent with previous work on *G. texensis*, which showed that calling behaviour is enhanced in males that were observed to have flown, relative to flight-incapable males (Bertram 2007). Similarly, our findings for females are consistent with those for other insect taxa, where reproduction commences after a dispersal flight (e.g., aphids: Kennedy & Booth 1963; ants: Hölldobler & Wilson 1977; migratory grasshoppers: McAnelly & Rankin 1986; water striders: Kaitala & Huldén 1990; see Roff & Fairbairn 2007 for review). In contrast to these examples, Zera et al. (2007) found that field-collected, flight capable females of *G. firmus* had smaller ovaries than short-winged females or long-winged females with histolyzed muscles. Although these results are intriguing, flight history (as distinct from flight capability) was not known for most animals, nor was it known whether the captured animals had already oviposited. Additional field data are required to determine the impact of flight on reproductive output in crickets.

Evolutionary biologists have considered flight dimorphism to result from a balance in costs and benefits to each of the alternative flight morphs (Roff 1986). Much of the evidence supporting this view comes from studies on crickets, in which flight ability is assumed to carry the benefits of dispersion (e.g., moving to a more suitable habitat), at the cost of decreased reproduction relative to flight-incapable individuals. Our findings suggest that the reproductive penalty of flight ability may have been overestimated. We suggest that other potential costs associated with flight (as opposed to merely being flight-capable) require further investigation, most importantly under field conditions.

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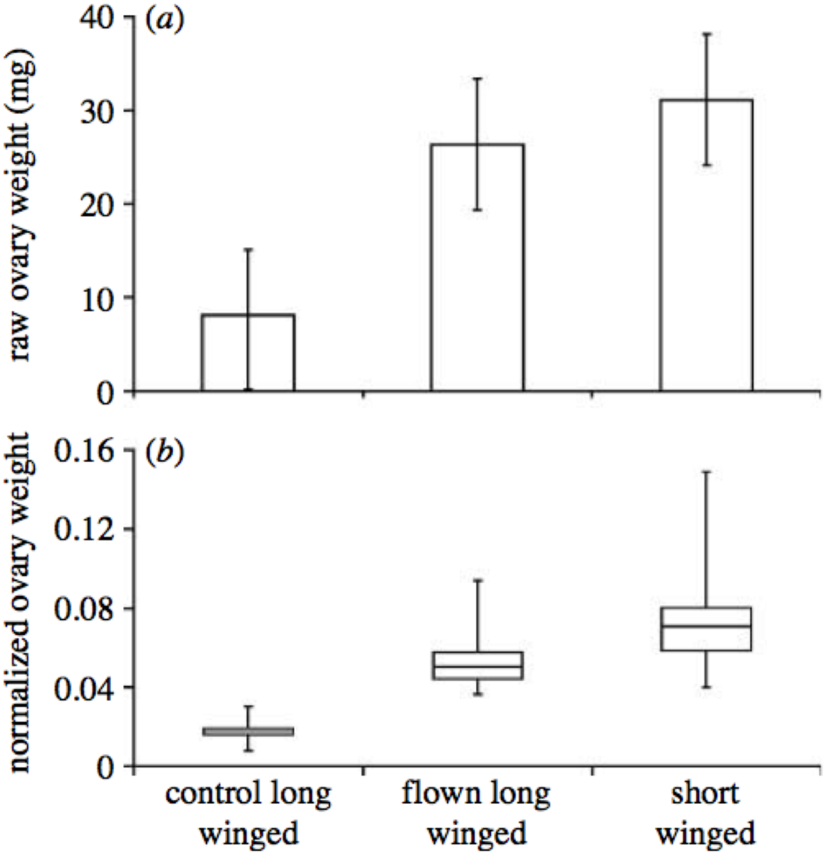

Fig. 3.1 (*a*) Raw ovarian weights of the different treatment groups (mean ± SD). (*b*) Normalized ovarian weights for the different experimental groups. The line across the middle of each box is the median value; ends of the boxes represent quartiles; vertical lines show ranges of values.

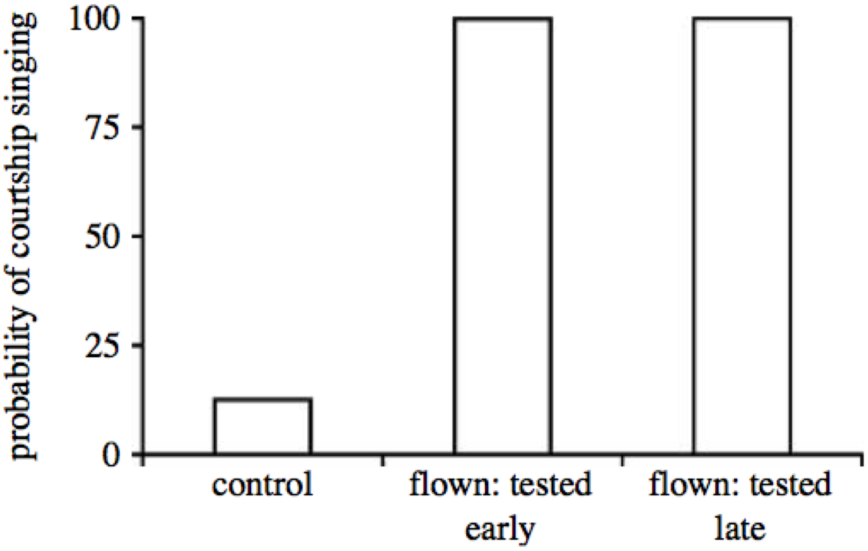

Fig. 3.2 Effect of flight on male courtship singing propensity. Sample sizes: control, n=24; experimental groups, n=8 for each.

Bridge from 3 to Chapter 4

Chapter 3 found that flight eliminated the trade-off between flight capability and reproduction in male and female *G. texensis*. This suggests that previous work may have overestimated the trade-off in wing dimorphic insects, as animals used in studies did not fly. Moreover, the enhancement of reproduction of flight-capable individuals after flight, suggests for the existence of a reproduction-flight syndrome, where flight initiates reproduction.

In Chapter 4, we determine whether or not flight-capability trades-off with aggression in males of wing dimorphic insects. In field crickets, males can fight intensely with another, where males will fight over mates or resources that might help them with acquiring a mate. As fighting can be a costly activity, in terms of its energetic cost, and the risk of injury or death, fighting behaviour might trade-off with flight-capability in male *G. texensis*. We tested for the occurrence of this trade-off by comparing the fighting behaviour of males of the different flight-morphs, in paired encounters with a common rival. We also test for an effect of flight on fighting in flight-capable males, in relation to the potential trade-off.

Chapter 4

Colonists and Desperadoes: different fighting strategies in wing dimorphic male Texas field crickets

Patrick A. Guerra & Gerald S. Pollack

ABSTRACT

In many species, males fight one another for mates or resources. Fighting can vary among males, however, such that some males are highly aggressive whereas others are not. We observed that fighting was negatively associated with flight capability in the wing dimorphic field cricket, *Gryllus texensis*. Long-winged males capable of flight had a significantly lower fighting propensity and displayed lower levels of aggression than short-winged, flight-incapable males in staged contests. Long-winged males no longer able to fly as a result of the histolysis of their flight muscles were more aggressive than long-winged males that had functional flight muscles, but were still less aggressive than short-winged males. Long-winged, flight-capable males were more aggressive after a brief flight just prior to an interaction with a rival, but only in contests with other flight-capable males. Flight capability and flight itself had no effect on the outcome of fights. Our results support the existence of an aggression-flight syndrome in flight dimorphic insects.

INTRODUCTION

In many species of animals, males compete with one another for mates or resources that facilitate mate acquisition (Shuster & Wade 2003). Fighting is an important component of this competition (Archer 1988; Huntingford & Turner 1987). Intriguingly, although fighting is a key way in which a male can enhance his own reproductive success, males vary in their propensity to fight. A possible reason for this variation is that fighting can be negatively associated with other traits, such as flight capability. Some males are highly aggressive and fight at the expense of flight capability, while other males are non-aggressive and do not fight, but can fly and are therefore more mobile (Crespi 1988; Short & Balaban 1994).

Field crickets (Orthoptera; Gryllidae) have been used extensively to examine both the dynamics of male fighting (e.g., Alexander 1961; Adamo & Hoy 1995; Hofmann & Schildberger 2001; Jang et al. 2008), and life history trade-offs that occur between traits (e.g., flight capability versus reproduction – Roff 1986; Dingle 1996; Zera & Denno 1997). Using the wing dimorphic cricket, *Gryllus texensis*, we studied whether fighting and the ability to fly are negatively associated in males. In male *G. texensis*, flight capability and reproduction are negatively associated. Long-winged, flight-capable individuals (LWF) invest heavily in flight wings, muscles, and fuels (Zera & Denno 1997), but engage in reproductive behaviour with low probability. In contrast, short-winged, flight-incapable (SW) individuals more frequently engage in reproductive behaviour, relative to flight-capable individuals (Guerra & Pollack 2007). The LWF morph may, later in life (Zera et al. 1997), lose the ability to fly via flight-muscle histolysis (LWH males), which is accompanied by an increase in reproductive behaviour to a level similar to that of SW males (Guerra & Pollack 2007). In addition, flight itself increases the reproductive behavior of LWF males, as males who flew had a greater probability of engaging in courtship than LWF males who did not fly (Guerra & Pollack 2009). This suite of traits in *G. texensis* constitutes a reproduction-flight syndrome (Johnson 1969; Sih et al. 2004).

Fighting can increase the probability of acquiring mates, both directly and through the acquisition of resources important for mate attraction (Simmons 1986;

Loher & Dambach 1989), and thus reflects a key aspect of male reproductive investment in field crickets. Therefore, consistent with the reproduction-flight syndrome, we predicted that fighting and flight capability would also be negatively associated in male *G. texensis*. Specifically, we predicted that LWF males would be less aggressive than SW males, and that agonistic behaviour of LWF males would increase after they underwent flight-muscle histolysis. As flight enhances courtship propensity in LWF *G. texensis* males (Guerra & Pollack 2009), and increases agonistic behaviour in other field cricket species (wing monomorphic *Gryllus bimaculatus* – Hofmann & Stevenson 2000; Stevenson et al. 2005), we also predicted that LWF males would become more aggressive after flight. Finally, we examined whether fighting in *G. texensis* is affected by differences between rivals in body mass (Arnott & Elwood 2009) and relative investment into gonads (Neat et al. 1998), factors that are known to influence fighting in males of many other species (Maynard Smith 1982).

METHODS

Experimental Animals

Male *G. texensis* were obtained from an eight-year-old laboratory colony (G. S. P., McGill University, Montréal, Quebec). Animals were reared under controlled conditions (12:12 L/D; 27°C; 50% humidity), and given *ad libitum* access to Purina cat chow and water. Crickets were reared communally in 80 litre Rubbermaid storage containers, and were segregated by sex as nymphs. Newly eclosed adults were collected and isolated individually in inverted mesh-covered plastic cups every other day. We tested socially naïve, virgin adult males, as previous experience with conspecifics can influence male fighting in crickets (e.g., agonistic encounters – Alexander 1961; mating – Killian & Allen 2008). As fighting might covary with reproductive state, we used crickets between 5 and 17 days of adulthood as this age range encompasses the time at which males are sexually mature (spermatophore production begins on day 5 and the mean of the onset of calling is at 6.9 ± 3.3 days; Cade & Wyatt 1984). In other *Gryllus* species, this range includes the age at which males are most aggressive (2-4 weeks in *G. bimaculatus*; Hofmann & Schildberger 2001) and when muscle histolysis typically begins for long-winged males (*G. firmus*; Zera et al. 1997). Individuals were tested only once.

Observing Cricket Fights

Fights were staged between randomly chosen focal and rival males. Trials were conducted under dim red light in an anechoic chamber at a temperature of 26-28°C in an open-topped, circular mesh arena (height: 10.5 cm; diameter: 15 cm), with a ring of acetate surrounding the top 4 cm of the arena to prevent escape. The arena sat on a polyurethane foam base that was covered with a paper towel. Between trials, the arena was washed with 100% ethanol, and the paper towel was replaced, to remove any potential olfactory cues left from the previous trial (Crnokrak & Roff 1995). We recorded trials onto DVD (Pioneer 533-Hs) using a camera (Panasonic BD-400) mounted above the arena.

We controlled for variability in the motivation and potential pay-off of fighting for our experimental males by standardizing interactions in the following ways. We age-matched the focal and rival males (±1 day), as the performance of reproductive behaviour (which might affect the expression of fighting) varies with age (Guerra & Pollack 2007). We conducted trials during the first six hours of scotophase, to minimize possible daily fluctuations in male aggression (Kortet & Hedrick 2007). We also provided males with *ad libitum* access to food and water while housed, in order not to impose differences in hunger between the males (Nosil 2002). We provided a barren arena void of resources that males might fight over (e.g., food – Nosil 2002; shelter – Simmons 1986; mates – Tachon et al. 1999, Guerra & Mason 2005), and this arena was unfamiliar to both males, to preclude pre-established territoriality from affecting the outcome of trials (Jang et al. 2008).

Are There Flight-morph Specific Differences in Fighting?

To begin a trial, both males were introduced into the arena, separated by an opaque divider. When the animals had recovered from handling, such that they calmly moved about on their side of the arena (approximately 30-60 s), we removed the divider to begin the trial. During pilot trials ($N = 24$; 12 long-winged and 12 short-winged), we determined latency criteria for the onset of contact and the onset of agonistic behaviour. Based on these, we allowed males eight minutes to come into contact. If they failed to come into contact during this time, the trial was discontinued and not counted. Otherwise, we allowed them an additional two minutes to display agonistic behaviour.

The agonistic behaviour of crickets is stereotyped and progresses through a series of well-defined stages (Alexander 1961). To score the outcome of contests, we used similar criteria as in previous work on cricket aggression (e.g., Adamo & Hoy 1995, Hofmann & Schildberger 2001; Table 4.1). We recorded whether or not the focal male fought the rival, where fighting was considered as performing any behaviour between Levels 2-7. If no fighting occurred within two minutes, we scored the focal male as non-fighting (Level 0). If the focal male repeatedly avoided contact with the rival (i.e., ran away from the rival upon contact at least three times in a row), we scored the focal male as a loser (Level -1). Similarly, if the rival male repeatedly avoided contact with the focal male, we scored the focal male as a winner, with a score of Level 1. If fighting occurred, we then scored whether or not the focal male initiated the fight (i.e., attack). During a fight, each focal male received a score for his overall level of aggression (a score between 2 to 7). We allowed trials to continue until a clear winner and loser could be identified. The loser was the male who retreated from any further interaction for at least 10 s, and/or who would no longer reengage the other male (deemed the winner), even if repeatedly challenged.

After each trial, we weighed both males and dissected them to inspect their flight muscles and remove and weigh their testes. We classified flight muscles based on their colour and size as either functional (large and pink) or non-functional (small and white) (Shiga et al. 1991; Guerra & Pollack 2007). We used the Kruskal-Wallis test to compare the flight-morphs in both body and relative testes mass.

All trials were scored by one individual (P. A. G.). To standardize comparisons of the fighting behaviour of focal males (i.e., LWF, LWH, and SW), data for each measure of fighting (i.e., the propensities to fight, attack, and win, and the overall level of aggression displayed) were pooled and analyzed separately according to the flight-morph of the rival. We used binary logistic regression to determine how the probabilities of fighting, attacking, and winning of focal males were each influenced by the flight-morph of the focal male, and by the difference in both body and relative testes mass (i.e., testes mass divided by body mass) between the contestants. Body mass and relative testes mass differences were calculated as the value of the focal male minus that of the rival male. As suggested by Jang and Greenfield (1998) and Jang et al. (2008), we used the differences in mass between males as predictors, since the mass of the rival can influence the outcome of a trial for a focal male. To compare the levels of aggression, we used the Kruskal-Wallis test. To determine whether differences in body and relative testes mass were related to the level of aggression displayed by focal males, we used a multivariate analysis of variance (MANOVA), after verifying that data satisfied the assumption of normality (Shapiro-Wilk test).

Does Flight Affect the Fighting of LWF Males?

To examine the effect of flight on fighting, we flew LWF males immediately before an interaction with a rival, as described in Guerra & Pollack (2009). Briefly, males were attached to a wooden applicator stick at the pronotum using wax and placed in front of a small fan to promote flight; flight was terminated after five minutes. Handling controls were treated as above but instead of flying, they were allowed either to remain motionless or to perform tethered walking by positioning them on an air-supported Styrofoam ball. We found no differences between the two types of control males in any of our measures of aggression (probability of fighting, attacking, or winning against all rival types, Fisher's exact tests, all $P > 0.3$; level of aggression against all rival types, Kruskal-Wallis tests: all $P > 0.2$). Therefore, we combined data from the control groups in our statistical analyses. These treatments were performed within the first four hours of the scotophase (in the anechoic chamber illuminated by red light), as this is the time when crickets most commonly fly under natural conditions (Cade 1979). Fighting behaviour was then assayed using the same protocol as described above. We used two-tailed Fisher's exact probability tests (Bonferroni-corrected when necessary) to compare frequencies of fighting, attacking, and winning of the different LWF male groups. We used Kruskal-Wallis tests to compare the level of aggression of males. For these analyses, the scores of focal males were pooled and analyzed according to the flight-morph of the rival.

RESULTS

The Flight Morphs Differ in Agonistic Behaviour

Body mass differed among the three flight morphs (Kruskal-Wallis test: $H_2 = 125.96$, $P < 0.0001$, $N = 506$; Fig. 4.1a). Body mass was similar in LWF and LWH males, and both were heavier than SW males (*post hoc* Dunn's test, $\alpha = 0.05$). The flight-morphs also differed in relative testes mass (Kruskal-Wallis test: $H_2 = 56.77$, $P < 0.0001$, $N = 506$; Fig. 4.1b). SW males had the greatest relative testes mass, followed by LWF males, and then LWH males (*post hoc* Dunn's test).

Against all rival types, the proportion of focal males that fight (levels 2-7 of Table 4.1) varied with flight-morph. Against LWF rivals, LWH and SW males fought with similar probability, which was greater than that of LWF males (Table 4.2). SW males were more likely to fight a LWH rival than were either long-winged morph, which had similar fighting propensities. Against a SW rival, SW males had the greatest probability of fighting, followed by LWH males, and then by LWF individuals. Overall, SW males fought most often, followed by LWH, and then LWF males. Differences in body and relative testes mass between focal and rival males had no effect on fighting probability no matter the rival type (logistic regression: body mass, P values range from 0.18 to 0.88; relative testes mass, P values range from 0.23 to 0.60).

Flight-morph was the only factor that significantly influenced the probability of a focal male attacking a rival. SW males initiated fighting more often than the other flight-morphs, although this effect was not significant for fights against LWH rivals (Table 4.2). The two long-winged morphs did not differ in their probability of attacking a rival. Neither difference in body mass nor in relative testes mass affected probability of attacking (logistic regression, P values range from 0.24 to 0.93).

The level of aggression displayed by focal males varied with flight-morph, body-mass difference and relative testes-mass difference. Against LWF rivals, both flight-incapable morphs reached higher levels of aggression than LWF males (SW, median level = 3, $N = 26$; LWH, median level = 3, $N = 50$; LWF, median level = 0, $N = 59$; Kruskall-Wallis, $H_2 = 34.0$, $P < 0.0001$). SW males were the most aggressive against LWH rivals (median level: 5, $N = 61$) as compared with either long-winged morph (LWH, median level 1: $N = 33$; LWF, median level 0, $N = 19$; $H_2 = 22.1$, $P < 0.001$). The two long-winged morphs did not differ in level of aggression (Dunn's *post hoc* test, $P > 0.05$). Against SW rivals, SW males were again the most aggressive (median level 5: $N = 125$). LWH males displayed intermediate levels of aggression (median level 3, $N = 62$), and LWF males were the least aggressive (median level 0, $N = 63$; $H_2 = 47.79$, $P < 0.0001$; *post-hoc* Dunn's test, $\alpha = 0.05$).

Body-mass difference was related to level of aggression only for trials against LWF rivals (Table 4.3). Sorting body-mass differences according to the level of aggression reached showed that contestants differed in body mass, with the rival outweighing the focal male, only for trials in which the aggression level of the focal male was level 3 (Tukey HSD *post hoc* test, $\alpha = 0.05$). Difference in relative testes mass was associated with level of aggression in trials against LWF and SW rivals. In both cases, focal males with relatively lighter testes tended to avoid contact with a rival (level -1), whereas those with relatively heavier testes reached moderate to high levels of aggression (levels 3 and 5 for LWF and SW rivals, respectively (Tukey HSD, $\alpha = 0.05$). Regardless of their flight-morph, heavier focal males and males with heavier relative testes mass relative to a rival, were more likely to win in all three rival contexts (Fig. 4.2). In trials against long-winged rivals (LWF, LWH), both winners and losers outweighed the focal male on average, because the population of focal males included SW individuals, which are the lightest flight morph (Fig. 4.1). Nevertheless, there was an association between greater body mass and increased probability of winning. Against LWF rivals, this is reflected as a smaller difference in body mass between focal and rival males for winners than for losers, as winners were closer in body mass relative to a rival than losers (logistic regression, LWF rivals, Wald statistic, $W_1 = 9.59$, $P = 0.002$, Fig. 4.2a). Against LWH rivals, losers were lighter than their rivals, whereas winners and rivals were closer in weight ($W_1 = 15.26$, $P < 0.0005$,

Fig. 4.2b). Both winners and losers outweighed SW rivals, but by a larger margin for winners than for losers ($W_1 = 14.13$, $P < 0.0005$, Fig. 4.2c). In all three rival contexts, winners had heavier relative testes mass as compared to rivals, than losers (LWF rival, $W_1 = 10.18$, $P = 0.001$; LWH rival, $W_1 = 11.84$, $P = 0.001$; SW rival, $W_1 = 21.84$, $P < 0.0005$; Fig. 4.2d-f).

Flight Makes LWF Males More Aggressive Under Certain Conditions

Relative to control males, flown LWF males were significantly more likely to attack and to fight with LWF rivals, but there was no effect of flight on contests against LWH and SW rivals (Table 4.4). Flown LWF males also reached higher levels of aggression than controls, but again only in contests against LWF rivals. Flight had no effect on the probability of winning.

DISCUSSION

We found that long-winged males capable of flight (LWF) were less likely to fight and attack, and displayed lower levels of aggression, than SW males. Long-winged males can become more aggressive once they have either lost the ability to fly (LWH males) or have undergone a brief flight immediately before facing a rival. This increase in aggression is limited, however, as the agonistic behaviour of LWH males is typically only at an intermediate level between that of LWF and SW males, and the effect of flight is seen only against LWF rivals. Finally, if a male does fight, the probability of winning is not related to his flight-morph. Winning was influenced by differences in body mass and relative testes mass between males.

Deciding Whether to Fight: Colonists and Desperadoes

Although fighting can play an integral role in the reproductive success of males, variation in male fighting behaviour exists in several taxa such that not all males fight. Some males may adopt alternative strategies that avoid fighting, but that still allow them to access mates and gain similar success as highly aggressive and combative males (Dawkins 1980; Shuster & Wade 2003). For example, males of some species (e.g., agaonid wasps, ants, thrips) are specifically adapted for fighting, at the expense of other traits, as seen among species with fighter and migrant morphs (Short & Balaban 1994; Crespi 1988). Here, fighter males cannot fly, but are highly aggressive, adapted for combat, and will mate with females in their local areas. In contrast, migrant males can disperse by flight and will mate with females away from their natal areas, but are non-aggressive, lack developed weapons, and are not attacked by aggressive rivals (Anderson et al. 2003). Similarly, our results suggest that there are different male fighting strategies in *G. texensis*, where a reproduction-flight syndrome (Johnson 1969; Guerra & Pollack 2009) may be reflected in the probability of fighting.

Colonists: long-winged males capable of flight

The fighting strategy for long-winged males appears to shift with changes in their flight history, in parallel with a shift in reproductive behavior. Only 33% of unflown LWF males fought in our trials (N=141, all experiments pooled). This is comparable to the probability with which LWF males court females (40%, Guerra & Pollack 2007). Fighting serves to acquire mates or mate-attracting resources (Simmons 1986). As most LWF males are apparently not in “reproductive mode”, they would not enjoy the benefits of fighting, and thus they are unlikely to assume the risks of injury or death that fighting imposes (Huntingford & Turner 1987; Ewing 1967; Hamilton 1979).

Following a brief flight, courtship probability of LWF males increases to match that of SW males (Guerra & Pollack 2009). Aggressive behavior also increases, albeit not as strikingly. Nevertheless, the delay in fighting (and reproduction) until after a flight may play a role in a larger adaptive strategy, where long-winged males are well suited for the colonization of new resources.

The increase in aggression following flight was limited to fights with other LWF males. A possible explanation for this is that, as LWF males remained flight-capable after having flown, i.e., they retained the ability for dispersal, they might avoid fighting highly aggressive SW and LWH rivals, with its accompanying risks. Moreover, this result implies that males can distinguish among one another according to flight-morph status using cues other than hind-wing length (e.g., cuticular hydrocarbons; Tregenza & Wedell 1997; Kortet & Hedrick 2005).

Our results suggest that flight is a key event in the life history of *G. texensis,* affecting both reproductive and aggressive behaviours. However, little is known of the flight behaviour of crickets under natural conditions (e.g., age of onset, frequency, duration); thus additional field data are necessary to determine whether or not our results relate to an actual reproduction-flight syndrome under natural conditions.

Desperadoes: long-winged males who can no longer fly

Once long-winged males lose the ability to fly through histolysis of flight muscles, their probability of courting females increases (Guerra & Pollack 2007).

We found that flight-muscle histolysis is also associated with increased aggression. Thus, as with flight itself, both reproduction and aggression are enhanced following flight-muscle histolysis. In the field, LWH males would benefit from a greater propensity to fight, as their ability to access alternative resources, such as territories, would be limited (Cade 1981; Simmons 1986), and the cost of not fighting, e.g., decreased mating opportunities, is potentially high. Moreover, *G. texensis* can occur at high densities (Cade 1981), exacerbating competition among males.

Our results may also explain why previous studies in other cricket species have found certain males to have low levels of aggression. In wing monomorphic *Gryllus bimaculatus*, young adult males (7-10 day old adults: Adamo & Hoy 1995; Hofmann & Schildberger 2001) are significantly less aggressive than older males, and the age range of these young, less aggressive males falls within the age range where male *G. bimaculatus* are flight-capable (2-14 day old adults; Shiga et al. 1991; Gomi et al. 1995). In contrast, male *G. bimaculatus* observed to be aggressive (and therefore used in aggression experiments) are typically 14-28 day old adults (e.g., Hofmann & Schildberger 2001), and at this age range, the vast majority of males have histolyzed flight-muscles (Shiga et al. 1991; Gomi et al. 1995). As such, the negative association between flight-capability and fighting, where flight and fighting appear to be successive stages in the life history of males, may occur in both wing monomorphic and dimorphic crickets.

Desperadoes: flightless short-winged males

SW males in *G. texensis* have greater courtship propensity (Guerra & Pollack 2007) and are significantly more aggressive (this study) than LWF males, thereby giving SW males a potential fitness advantage relative to LWF males. In the field, these advantages are presumably offset by the fact that SW males cannot fly, making them less able to escape deteriorating and heterogeneous environments (Roff 1986; Zera & Denno 1997). Therefore, SW males might be adapted to be extremely aggressive relative to both LWF and LWH males, in order to better compete with rivals for limited resources in their immediate habitat. Given that SW males are restricted to the resources found in their immediate environment, their high levels of aggression and the greater propensity to fight and attack might reflect a 'desperado effect' (Grafen 1987). We argue that the fighting strategy of SW males serves to compensate for their reduced ability to find and obtain alternative resources, especially in variable habitats such as those where *G. texensis* occur (Walker & Sivinski 1986; Cade & Otte 2000).

Does habitat variability affect aggression?

A recent comparative study on the aggressiveness of different species of North American *Gryllus* field crickets showed that aggression between conspecific males differed across species (Jang et al. 2008). *G. pennsylvanicus* and *G. rubens* males displayed high levels of aggression (i.e., males engaged in grappling, a highly aggressive behaviour), while males of *G. fultoni* and *G. vernalis* were significantly less aggressive (males did not escalate to grappling). We found that *G. texensis* males are also highly aggressive during fights, as some males from all three flight-morph classes would escalate to grappling in our trials. Intriguingly, *G. pennsylvanicus*, *G. rubens* and *G. texensis* are wing dimorphic species and come from variable and temporary habitats, while *G. fultoni* and *G. vernalis* are both short-winged species that occur in areas that are more permanent

(Walker & Sivinski 1986). This suggests that habitat heterogeneity might be a selective force not only for the maintenance of wing dimorphism (i.e., the ability to move to suitable habitats; Roff 1986), but for increased agonistic behaviour as well. For example, caddisfly larvae of species that live in temporary habitats are more aggressive than larvae of species that live in long-established wetlands (Wissinger et al. 2004), possibly because the availability of contested resources can drastically change as a result of the temporary nature of the environment.

Fighting strategies in *G. texensis* appear to be different from species where there are distinct fighter and migrant morphs, as the morphs in these species possess strategies that are typically fixed (see above). Although we have not uncovered flexibility in the strategy of short-winged males, long-winged males appear to adopt different strategies during their life history that reflect changes in their flight history and in their ability to disperse.

The Effect of Differences in Body and Relative testes mass

Body mass differences appear to play a minor role in the level of aggression displayed by males, varying with level of aggression only in trials against LWF rivals, and then with no easily interpreted pattern. In contrast, differences in relative testes mass appear to have a larger influence on the level of aggression. Against both LWF and SW rivals, males who ran away from rivals (level -1) had significantly lighter testes than their rivals, compared to males that displayed agonistic behaviour, e.g., mandible flaring (level 3; LWF rivals) and mandible engagement (level 5; SW rivals), against their rival. This suggests that males are more aggressive towards rivals when they invest more into reproduction (i.e., testes) relative to their rival. Interestingly, males that ran away from rivals did so only after brief contact (e.g., antennation), suggesting that non-aggressive males might be able to assess the level of reproductive investment of their rivals in order to avoid fighting, possibly by sensing cuticular hydrocarbons (Tregenza & Wedell 1997; Kortet & Hedrick 2005).

In addition, differences in body mass and reproductive investment between males were two factors that influenced the probability of winning a fight in our trials. Surprisingly, the probability of winning was not related to a male’s ability to fly, especially given the large differences in body and relative testes mass between the flight-morphs (LW are heavier than SW, and SW have a greater proportion of their body mass as testes than LW). However, the difference in body mass, favoring LW males as winners, may be countered by the difference in relative testes mass, which favors SW males. Our results support the idea that flight-capability primarily affects the probability of fighting in males, since once males do 'decide' to fight, other factors besides flight-morph influence winning.

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Table 4.1. Agonistic behaviours scored in trials with male *G. texensis* (modified from Adamo & Hoy [1995] and Hofmann & Schildberger [2001])

Behaviour	Description	Level score
Avoidance (Focal)	Focal male avoids contact with rival after initial contact	-1
Quiescent	Focal male does not avoid contact with rival but does not display any aggressive behaviour (Level 2-7); no aggression seen between males	0
Avoidance (Rival)	Rival male avoids contact with focal after initial contact	1
Antennal fencing	Males rapidly antennate each other's antennae	2
Mandible flaring	Male hyperextends mandibles	3
Lunge and butt	Rush at conspecific and use head to hit opponent	4
Grappling	Males interlock mandibles and push/pull each other	5
Wrestling	Males wrestle with each other	6
Continuous chasing	Male repeatedly runs after the other male who avoids contact and runs away	7

Table 4.2. Propensity of the flight-morphs to fight, attack, and win in experiments.

Rival	Behaviour	LWF focal	LWH focal	SW focal
LWF	Fight	31% (18/59)*	68% (17/25)	85% (50/59)
	†$W_2 = 22.74$, $P < 0.0005$; LWF vs. LWH, $W_1 = 8.72$, $P = 0.003$; LWF vs. SW, $W_1 = 20.83$, $P < 0.0005$; SW vs. LWH, $W_1 = 2.52$, $P = 0.11$			
	Attack	45% (9/20)	41% (7/17)	86% (44/51)
	$W_2 = 11.85$, $P = 0.003$; LWF vs. LWH, $W_1 = 0.10$, $P = 0.76$; LWF vs. SW, $W_1 = 8.09$, $P = 0.004$; SW vs. LWH, $W_1 = 9.60$, $P = 0.002$			
	Win	42% (14/33)	68% (13/19)	67% (36/54)
	$W_2 = 3.18$, $P = 0.20$; LWF vs. LWH, $W_1 = 1.21$, $P = 0.27$; LWF vs. SW, $W_1 = 2.98$, $P = 0.08$; SW vs. LWH, $W_1 = 0.12$, $P = 0.73$			
LWH	Fight	21% (4/19)	48% (16/33)	90% (55/61)
	$W_2 = 27.07$, $P < 0.0005$; LWF vs. LWH, $W_1 = 2.99$, $P = 0.08$; LWF vs. SW, $W_1 = 24.74$, $P < 0.0005$; SW vs. LWH, $W_1 = 15.62$, $P < 0.0005$			
	Attack	20% (1/5)	33% (6/18)	64% (36/56)
	$W_2 = 5.41$, $P = 0.003$; LWF vs. LWH, $W_1 = 0.30$, $P = 0.58$; LWF vs. SW, $W_1 = 2.63$, $P = 0.11$; SW vs. LWH, $W_1 = 3.73$, $P = 0.05$			
	Win	40% (4/10)	72% (16/22)	38% (23/60)
	$W_2 = 3.59$, $P = 0.17$; LWF vs. LWH, $W_1 = 3.33$, $P = 0.07$; LWF vs. SW, $W_1 = 0.93$, $P = 0.34$; SW vs. LWH, $W_1 = 1.78$, $P = 0.18$			
SW	Fight	40% (25/63)	60% (37/62)	80% (100/125)
	$W_2 = 18.06$, $P < 0.0005$; LWF vs. LWH, $W_1 = 4.72$, $P = 0.03$; LWF vs. SW, $W_1 = 18.03$, $P < 0.0005$; SW vs. LWH, $W_1 = 4.62$, $P = 0.03$			
	Attack	34% (12/35)	24% (10/42)	75% (78/104)
	$W_2 = 20.67$, $P < 0.0005$; LWF vs. LWH, $W_1 = 1.27$, $P = 0.26$; LWF vs. SW, $W_1 = 8.82$, $P = 0.003$; SW vs. LWH, $W_1 = 19.04$, $P < 0.0005$			
	Win	56% (23/41)	65% (30/46)	67% (76/114)
	$W_2 = 3.24$, $P = 0.20$; LWF vs. LWH, $W_1 = 1.70$, $P = 0.19$; LWF vs. SW, $W_1 = 3.12$, $P = 0.08$; SW vs. LWH, $W_1 = 0.17$, $P = 0.68$			

*Probability to fight, attack, or win; numbers in brackets are sample sizes; fighting data consist of trials where a focal male fought (level 2-7 aggression), attack data consist of trials where the focal male attacked or was attacked; win data also include trials where focal males did not fight, but where the winner could be determined (level -1 or 1).

†Results from logistic regression analyses; W = Wald statistic. Probabilities for fighting, attacking and winning are compared pairwise among the three types of focal males.

Table 4.3. MANOVA of the relationship between the level of aggression and body (BM) and relative testes (RT) mass differences in experiments.

Rival	Analysis	Variable	Test statistics
LWF	MANOVA	–	Wilks' $\lambda = 0.726$, $F_{16, 266} = 2.88$, $P = 0.0002$
	Bonferroni-corrected ANOVA ($\alpha = 0.025$)	BM	$F_{8, 134} = 3.35$, $P = 0.0016$
	Bonferroni-corrected ANOVA ($\alpha = 0.025$)	RT	$F_{8, 134} = 3.42$, $P = 0.0013$
LWH	MANOVA	–	Wilks' $\lambda = 0.752$, $F_{16, 206} = 1.97$, $P = 0.02$
	Bonferroni-corrected ANOVA ($\alpha = 0.025$)	BM	$F_{8, 104} = 2.07$, $P = 0.05$
	Bonferroni-corrected ANOVA ($\alpha = 0.025$)	RT	$F_{8, 104} = 1.81$, $P = 0.08$
SW	MANOVA	–	Wilks' $\lambda = 0.871$, $F_{16, 480} = 2.15$, $P = 0.006$
	Bonferroni-corrected ANOVA ($\alpha = 0.025$)	BM	$F_{8, 241} = 2.21$, $P = 0.03$
	Bonferroni-corrected ANOVA ($\alpha = 0.025$)	RT	$F_{8, 241} = 3.19$, $P = 0.0019$

Table 4.4. The effect of flight on the propensity to fight, attack, win, and the level of aggression of LWF focal males.

Rival	Behaviour	Flown	Control	Statistical test
LWF	Fight	89% (16/18)*	17% (3/21)	Fisher's exact, $P < 0.00001$‡
	Attack	75% (12/16)	0% (0/5)	Fisher's exact, $P = 0.006$
	Aggression	3 (18)†	0 (21)	Kruskal-Wallis, $H_2 = 20.95$, $P < 0.001$
	Win	76% (13/17)	40% (2/5)	Fisher's exact, $P = 0.27$
LWH	Fight	22% (2/9)	15% (2/14)	Fisher's exact, $P > 0.99$
	Attack	0% (0/2)	0% (0/6)	Not analyzed statistically
	Aggression	0 (9)	0 (14)	Kruskal-Wallis, $H_2 = 0.07$, $P = 0.78$
	Win	0% (0/5)	0% (0/8)	Fisher's exact, $P > 0.99$
SW	Fight	28% (5/18)	19% (7/36)	Fisher's exact, $P = 0.51$
	Attack	0% (0/9)	20% (3/15)	Fisher's exact, $P = 0.27$
	Aggression	0 (18)	0 (36)	Kruskal-Wallis, $H_2 = 0.20$, $P = 0.65$
	Win	31% (4/13)	28% (5/18)	Fisher's exact, $P > 0.99$

*Probability to fight, attack, and win; numbers in brackets are sample sizes; data included for each behavioural measure as in Table 4.2

†Median level of aggression; numbers in brackets indicate sample sizes; ‡Fisher's exact tests were Bonferroni-corrected ($\alpha = 0.017$) for comparisons between the different rival-morph types made for each behavioural measure.

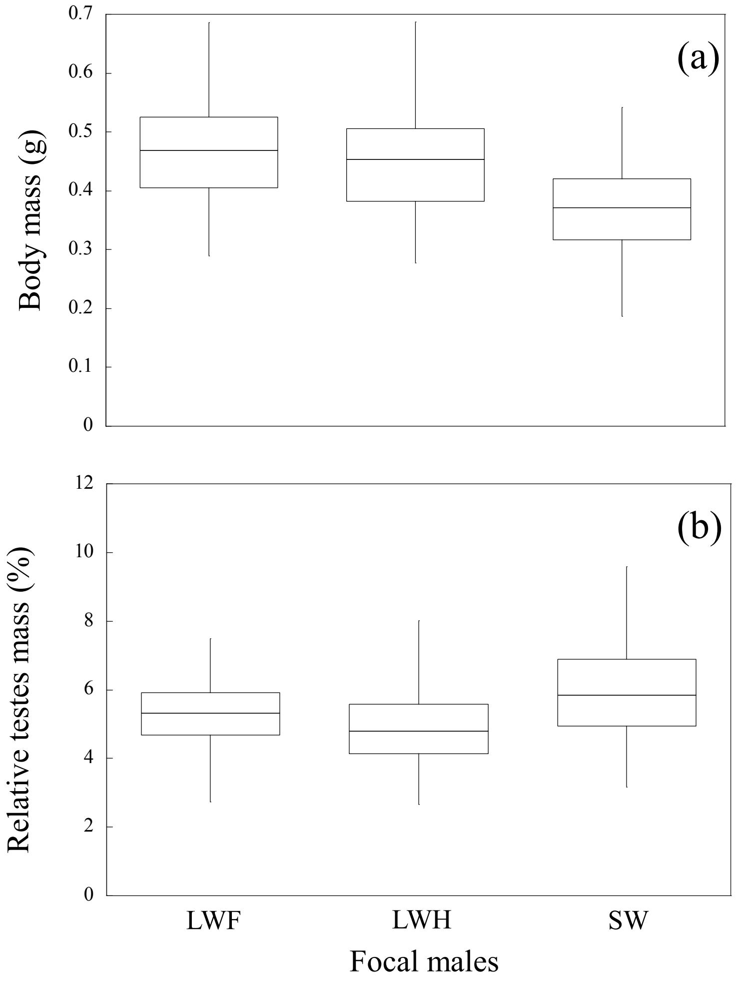

Figure 4.1. Box plots comparing the body mass (a) and relative testes mass (testes mass / body mass; b) of the different flight-morphs. The lines across the middle of the boxes are the median values, ends of boxes signify quartiles, and vertical lines show the range of values. LWF: *N* = 141; LWH: *N* = 120; SW, *N* = 245.

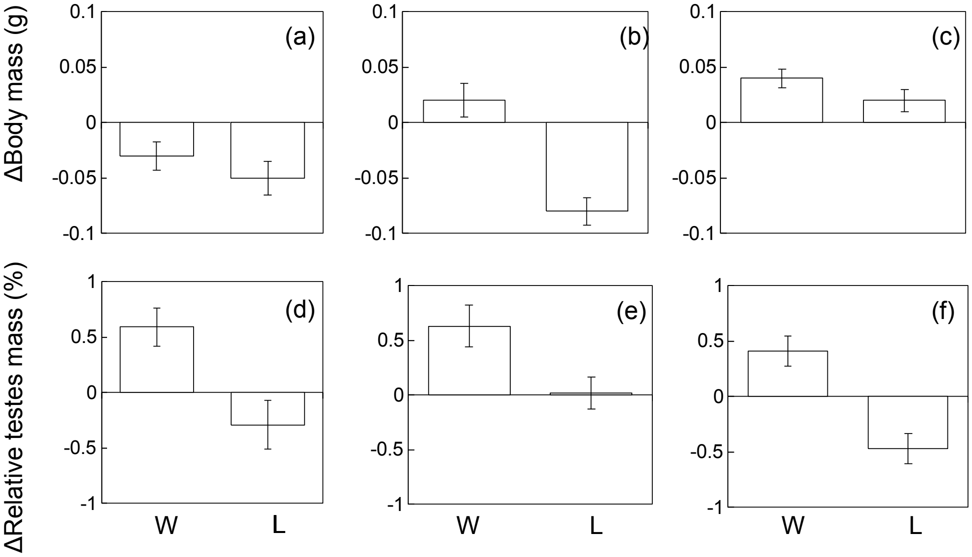

Figure 4.2. Influence of differences in body mass and relative testes mass on the outcome of agonistic contests. Graphs show mean ± SE of differences in body mass (a-c) and relative testes mass (d-f) between focal males of each of the flight morphs, and rival males (all flight morphs pooled) for winners (W) and losers (L). Focal male flight morphs were: (a, d) LWF; (b, e) LWH; (c, f) SW.

Bridge from Chapter 4 to Chapter 5

In Chapter 4, we found that flight-capable males were significantly less aggressive than males who could not fly in paired agonistic interactions. Flight-capable males had a lower propensity to fight a rival, and displayed a decreased level of aggression, relative to flight-incapable males. Once flight-capable males lost the ability to fly, they became more aggressive in trials. Flight also increased the fighting behaviour of flight-capable males, but only in certain contexts. We argue that males of the different flight-morphs might have different fighting strategies, where each strategy is influenced by the flight capability of the male.

Given this difference in male fighting behaviour, the goal of Chapter 5 was to examine for variation in weaponry between males of the different flight-morphs. In agonistic interactions, male field crickets will use their mandibles in aggressive displays, as well as weapons in overt fighting, e.g., mandible engagement and biting a rival. We found that short-winged males had larger mandibles for their body size than long-winged males. This result supports the idea that the most aggressive males invest more into weaponry, in a species where male aggression is potentially influenced by a reproduction-flight syndrome.

Chapter 5

The reproduction-flight syndrome mediates the investment into weapons in *Gryllus texensis* field crickets

Patrick A. Guerra & Gerald S. Pollack

ABSTRACT

Male crickets fight one another over mates and resources. Recent work with the wing-dimorphic field cricket, *Gryllus texensis*, showed that short-winged males, which are incapable of flight, are significantly more aggressive than long-winged individuals. Mandibles are used in agonistic displays and as weapons. We found that relative to body size, short-winged males have significantly larger mandibles than long-winged individuals. We suggest that larger mandibles are an adaptation for aggression in short-winged males.

INTRODUCTION

Flight-polymorphic insect species have been used extensively to study the evolution and physiological mechanisms of variation in life history traits. One morph invests in the development and maintenance of the flight-apparatus (long wings, powerful muscles, flight fuels), but has delayed and/or meager reproductive output, either because of limited resources (flight-reproduction trade-off) or because of a temporal separation of life-history stages, with reproduction following dispersal. By contrast, an alternative morph, which lacks the musculature and/or wings required for flight throughout life, invests more in reproduction from the outset (Zera and Harshman 2001; Roff and Fairbairn 2007). In many species of field cricket individuals may develop with either short (flight-incapable) or long (flight-capable) hindwings. The former are incapable of flight throughout life, whereas the latter may lose this ability through wing-muscle histolysis (Zera et al. 1997). Most studies of the flight-reproduction relationship focused on females, but recent work shows that this occurs in males as well.

Flight-incapable male crickets, *Gryllus texensis*, engage in courtship behavior more readily than their flight-capable counterparts (Guerra and Pollack 2007), although a brief bout of flight by the latter increases their courtship probability to match that of flight-incapable males (Guerra and Pollack 2009).

Male crickets also engage in fights, which serve to acquire mates or mate-attracting resources, and recent work with *G. texensis* showed that aggressive behavior, like reproduction, is negatively correlated with flight ability (Guerra and Pollack in review). During fights, males use their mandibles both for display and as weapons (Alexander 1961; Adamo and Hoy 1995; Hofmann and Schildberger 2001; Jang et al. 2008). Their efficacy as weapons is demonstrated by the finding that the probability of winning fights is correlated with mandible size (Judge and Bonanno 2008) or asymmetry (Briffa 2008). Given the close coupling between reproduction and aggression, we predicted that short-winged individuals would possess specializations for aggression, namely larger, more asymmetric, mandibles than long-winged males. Because aggression is less common in females, we predict that their mandible characteristics would be unrelated to wing morph.

MATERIALS AND METHODS

Morphological measurements

Virgin adult *G. texensis,* aged 5-17 days past the last molt, were obtained from an established laboratory colony in which food (Purina Cat Chow) and water were continuously available. We used Vernier calipers (Manostat Mechanic Type 6911) to measure (resolution: 0.05 mm) pronotum width and the left and right mandible lengths (from the lateral articulation to the distal tip; Judge and Bonnano 2008). We also assessed the condition of the flight muscles via dorsal dissection, classifying them as either functional (large and pink) or non-functional (small and white) (Shiga et al. 1991; Guerra and Pollack 2007). We log transformed data to fulfill assumptions of normality.

Previous studies in crickets used weight as an indicator of body size. In wing-dimorphic crickets, however, weight can be confounded by the difference between functional (heavy) and non-functional (light) flight muscles. We therefore used pronotum width as our measure of body size.

RESULTS

Body size varies with sex and flight morph (two-way ANOVA: $F_{5, 120}=11.39$, $P<0.0001$; Fig. 5.1a). Short-winged males were smaller than all other sex/flight-morph classes, which did not differ from one another (Post-hoc Tukey tests; $\alpha=0.05$). Mandible length (mean of left and right mandibles) also varies with sex and flight morph (two-way ANCOVA: $F_{2, 118}=5.34$, $P=0.006$; Fig. 5.1b). After controlling for body size, we found that short-winged males had the longest mandibles. Mandible length did not differ between flight-capable and flight-incapable long-winged males. Females of all three flight-morph classes had the shortest mandibles. Neither sex nor flight-morph affected mandible asymmetry (two-way Kruskal-Wallis test: sex, $\chi^2_1=0.73$, n=126, $P=0.39$; flight morph, $\chi^2_2=4.76$, n=126, $P=0.09$) (Fig. 5.1c).

DISCUSSION

Short-winged males are adapted to have large weapons

We found that short-winged males, although they are smaller than other conspecifics, have the largest mandibles when measurements are corrected for body size. This differs from the situation in most insect taxa, where weapons are restricted to, or larger in, the largest males. For example, in beetles, large males possess horns (Eberhard 1982; Emlen 1997; Okada et al. 2008) or have larger mandibles than small males (Shiokawa and Iwahashi 2000). In some thrips species, large males have well-developed foreleg weapons, and smaller males have underdeveloped forelegs similar to those of females (Crespi 1986). In contrast, in other thrips species, long- and short-winged males are similar in size, but short-winged males have larger foreleg weapons than long-winged males and are dominant (Crespi 1988). Similarly, among other wing dimorphic species, wingless males that fight rivals possess larger weapons than their winged counterparts that are non-aggressive (fig wasps, ants, bees – Emlen 2008).

Why should small, short-winged males possess larger weapons than large, long-winged males, especially when long-winged males will also fight? One possible explanation is that large weapons might interfere with the ability to fly, e.g., by affecting the individual's center of gravity or wing loading (Emlen 2008). However, the absence of a difference in mandible size between long- and short-winged females suggests that this explanation is unlikely. We suggest that the large mandibles of short-winged males are instead part of a larger set of adaptations to flightlessness. Unlike long-winged males that can fly, short-winged males are effectively limited to the resources that are available in their immediate habitat. They may invest more into weapons in order to be able to compete better with rivals. This would constitute a morphological complement to the greater aggressiveness of short-winged males that we demonstrated previously (Guerra & Pollack in review). The lack of difference in mandible size between flight-capable and flight-incapable long-winged males is as expected; adult mandible size is set at the final molt, following which all, or nearly all, long-winged individuals are initially flight-capable.

Mandibles as feeding structures

The difference in mandible sizes seen in *G. texensis* might also reflect adaptations for feeding. For example, small mandibles might be better at handling food and extracting nutrients than large mandibles. If so, the smaller mandibles of females (who require energy for oogenesis) relative to those of males, and those of long-winged males (who require energy for flight) relative to short-winged males, might be an adaptation for more effective food intake (see Judge and Bonanno 2008). The relationship between mandible size and feeding efficiency remains to be studied in crickets, however.

Mandible asymmetry in G. texensis: similar across groups

In another field cricket, *Acheta domesticus,* the probability of winning a fight correlates with the degree of mandible asymmetry (Briffa 2008). In other taxa, mandible asymmetry aids in feeding (e.g., water scavenger beetle larvae - Inoda et al. 2003). In *G. texensis*, we did not find any difference in mandible asymmetry between sexes or flight-morphs. Therefore, even if mandible asymmetry (whether greater or lesser asymmetry) provides some benefit in *G. texensis*, it appears to not be sex or flight-morph specific.

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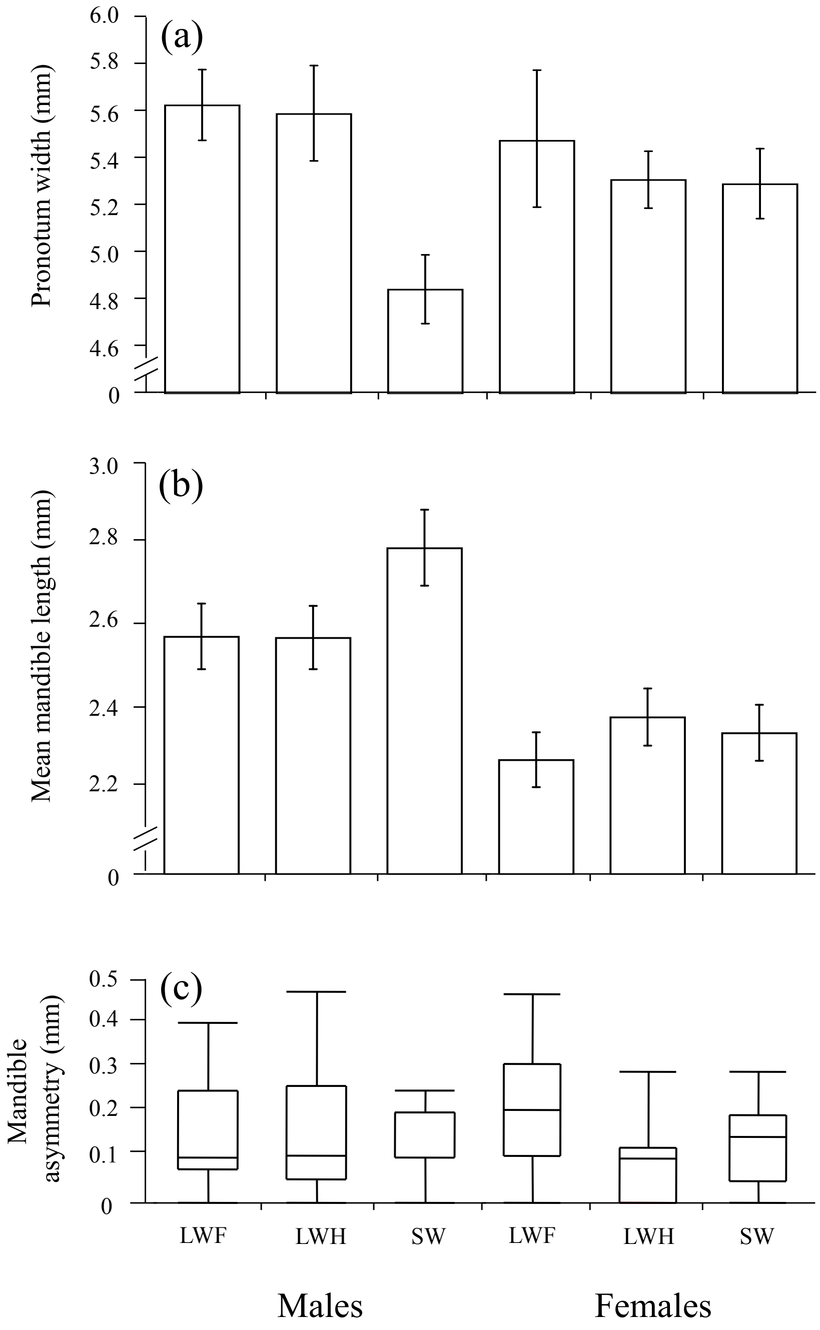

Fig. 5.1 (**a**) Mean body size (back-transformed mean ± 95% confidence intervals; mm) of crickets, as measured by their pronotum width. N=21 for each group. (**b**) Mean mandible lengths (left and right mandibles; back-transformed least-square means ± 95% confidence intervals; mm) adjusted for body size using ANCOVA.

N=21 for each group except for long-winged, flight-capable males where N=20. We omitted from the analysis a single very large (pronotum width: 7 mm) long-winged flight-capable male that was identified as an outlier first by visual inspection of the data set and confirmed as such by a Grubb's test (Z=2.80, n=21, *P*<0.05). Inclusion of this individual in the analysis resulted in a significant interaction between body size and flight morph, violating the requirement of ANCOVA of homogeneity of slopes relating factors and the covariate. When this male was omitted this assumption was satisfied ($F_{2,\,113}=3.06$, *P*=0.051). (**c**) Mandible asymmetry (left minus right; mm) of the different cricket groups. Top and bottom of boxes indicate quartiles. Lines in boxes are median values, except for short-winged males where the top of the box is also the median value. Whiskers represent interquartile ranges. LWF: long-winged, flight-capable; LWH: long-winged, flight-incapable; SW: short-winged.

General Conclusion

General Conclusion

This dissertation examined the trade-off between flight capability and reproduction in wing dimorphic insects. Using the wing dimorphic field cricket, *G. texensis*, I have demonstrated that a trade-off exists in both sexes. In females, flight capability trades-off with gonadal development, while flight capability is negatively associated with both courtship and fighting behaviour in males. I show, however, that both the loss of flight capability through flight muscle histolysis, and the act of flying itself, can attenuate the trade-off in both male and female *G. texensis*.

A reproduction-flight syndrome in wing dimorphic insects

My results support the idea that a reproduction-flight syndrome exists in *G. texensis* (Johnson 1969). Wing dimorphism in *G. texensis* possibly reflects the occurrence of two distinct groups, long-winged and short-winged individuals, which possess two different syndromes. For long-winged individuals, flight (and presumably migration) and reproduction appear to be two distinct stages in their life history. As with other insect species where reproduction begins after a migratory flight (see Roff & Fairbairn 2007), flight appears to initiate reproduction in long-winged crickets, as seen by the heavier ovaries of females and the increased probability of courtship and fighting in males, after flight. Interestingly, individuals who flew and had enhanced reproductive output were still flight-capable as indicated by the condition of their flight-muscles. This suggests that individuals had energy resources that were sufficient to support both reproduction and flight capability. It thus appears that flight dimorphism can be an adaptive strategy for colonization in *G. texensis*, and not only a bet-hedging strategy in response to unpredictable environments, as the reproductive output of flight-capable males is enhanced after flight.

Moreover, once they no longer can fly, long-winged males will also have a greater likelihood of courtship and fighting than long-winged males that still have functional flight muscles. This suggests that once the flight stage (and therefore migratory stage) of long-winged crickets has been effectively terminated, due to the eventual loss of flight capability, individuals will begin to invest into reproduction.

Short-winged crickets appear to have a suite of traits that makes them adapted for a less mobile life style. In contrast to long-winged males, short-winged males are highly aggressive, invest more into weapons that are used in combat, and readily court females. These results suggest that short-winged males have adaptations for increased competitive ability and the ability to take advantage of mating opportunities, when they are restricted to a given habitat patch where competition can be high and resources might be limited.

Flight and muscle histolysis of wing dimorphic insects in the field

The majority of studies on the trade-off between flight-capability and reproduction have been conducted under laboratory conditions. As a result, little is known about the flight behaviour (e.g., age of onset, the frequency or duration of flights) and flight muscle histolysis (e.g., age of onset, incidence level or rate of muscle degeneration) of field crickets under natural conditions, two factors that I found to mitigate the trade-off. Therefore, it is unclear whether the findings of my dissertation relate to a potential for a trade-off or a reproduction-flight syndrome in the field.

My results that suggest the occurrence of a reproduction-flight syndrome in *G. texensis* are consistent, however, with recent work with crickets collected under natural conditions. The positive effect of flight that I observed in my experiments are consistent with the results of Bertram (2007), who found that the mate attraction behaviour (i.e., calling behaviour) of male *G. texensis* observed to have flown in the field (and that still possessed functional flight-muscles) was enhanced relative to flight-incapable males. In addition, the observation that flight muscle histolysis has a positive effect on reproduction in *G. texensis*, is in accord with the results from Zera et al. (2007). Zera et al. (2007) found that the ovarian development of field-collected flight-incapable morphs was similar (long-winged females with histolyzed flight muscles and short-winged females), and was enhanced relative to flight-capable females. Therefore, additional field data are needed to confirm the existence of the reproduction-flight syndrome in crickets.

The evolution of flight dimorphism in insects

Given that understanding the evolution of variation and diversity is one of the hallmarks of research in evolutionary biology, the evolution of flight dimorphism in insects has long been of interest to evolutionary biologists. In this context, evolutionary biologists have proposed that flight dimorphism has arisen due to the balance of costs and benefits for the different morphs (Roff 1986; Zera & Denno 1997). For example, given the reproductive advantage that the flight-incapable morph has relative to the flight-capable morph, flight-capable individuals still exist in a population, as the reproductive penalty of being able to fly is presumably offset by the benefits of migration (e.g., the ability to deal with habitat heterogeneity and instability).

My study in *G. texensis*, however, suggests that the reproductive penalty of flight in flight dimorphic insect species might have been overestimated. For example, even after the enhancement of reproduction after flight, flight-capable crickets remained capable of flight. This suggests that individuals have sufficient energy resources to support both flight capability and reproductive output. It thus appears that flight-capability and reproduction are not necessarily negatively associated with one another in flight dimorphic insects. Rather, in some taxa, the decreased or postponed reproductive output measured prior to flight of flight-capable individuals can be adaptive, as it forms part of a larger strategy (e.g., a strategy for colonization). Moreover, in some wing dimorphic taxa (e.g., members of the order Coleoptera), it is the long-winged morph that has the greater reproductive output. Therefore, this implies that wing dimorphism in insects can evolve due to different adaptive regimes. For example, wing dimorphism can either reflect a possible escape strategy or a potential strategy for facilitating colonization.

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