## CHAPTER ONE

# Flight-fecundity tradeoffs in wing-monomorphic insects

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## Contents

## Abstract

Winged insects often spend considerable amounts of energy in flight, searching for food, escaping predators, and dispersing. In females, flight is hypothesized to reduce resources available for egg production, thus leading to a tradeoff between flight and fecundity. Yet, the generality of a flight-fecundity tradeoff in insects may have been

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overestimated, given that empirical validation of such a tradeoff has largely relied on studies in wing-polymorphic insects. In this review, we evaluate evidence of a flight-fecundity tradeoff in wing-monomorphic insects by conducting a systematic literature search. We compiled information from studies on migratory and non-migratory insects, testing for an association between flight and fecundity and using a number of different methods—phenotypic and genotypic correlations, manipulation of resource availability, and manipulation of either flight or fecundity. Although most studies indicated a negative association between flight and fecundity in wing-monomorphic insects, evidence for a tradeoff between the two traits was less prevalent. In several contexts, there were species that showed none or a positive association between both traits. Importantly, flight and fecundity in wing-monomorphic insects was related in a number of ways: via physiological constraints—resource-based tradeoffs—as well as via biomechanical constraints—when egg loads affected take-off performance—, due to adaptive negative correlations—when switching from flight to egg production if appropriate conditions to reproduce were encountered—and, due to adaptive positive correlations—when optimal flight and high fecundity were favoured for colonizing new habitats.

## 1. Introduction

Organisms have finite amounts of resources to use for reproduction, growth, metabolism, and maintenance. Increased allocation of resources to any one of these functions necessarily reduces the amount available for the others. Such resource allocation tradeoffs directly affect fitness and underlie the evolution of life histories in all organisms (Roff, 1992; Stearns, 1992).

Insects utilize a significant portion of their energy budget in building, maintaining, and operating their flight system. Their flight muscles, for instance, are known to exhibit the highest mass-specific rates of oxygen consumption of any locomotory tissue (Marden, 2000). As a consequence, the energetic and material costs required to fly are likely to divert resources away from other fitness-related processes. Especially in females, flight is expected to impact egg production, which also is energetically costly and is often limited by available resources (Papaj, 2000; Wheeler, 1996). Indeed, some of the strongest empirical evidence of resource allocation tradeoffs involves the allocation of limited resources between flight muscles and fecundity in wing-dimorphic insects (Guerra, 2011; Mole and Zera, 1993; Roff, 1986; Roff and Bradford, 1996; Tanaka and Suzuki, 1998). Overall, winged females exhibit developed flight muscles and reduced ovaries, whereas wingless morphs allocate more resources to reproduction and have reduced flight muscles and wings.

While the idea that a flight-fecundity tradeoff underlies the life history of insects has been widely accepted, a growing number of studies suggest that the generality of such a tradeoff might have been overestimated (Guerra, 2011; Guerra and Pollack, 2007; Rankin et al., 1986; Roff, 1995; Sappington and Showers, 1992). These studies have argued that a negative correlation between flight and fecundity has not been observed in some insect species, whereas in others, flight actually appears to stimulate reproduction. A recent meta-analysis showed that although a flight-fecundity tradeoff was likely to occur across wing-dimorphic insect species, the strength and direction of it varied substantially with the insect order (Guerra, 2011). Importantly, much of the evidence of flight-fecundity tradeoffs has been drawn from studies in wing-polymorphic species. Yet, most insects are wing-monomorphic, and the extent of flight-fecundity tradeoffs among this group of insects is much less known. In this review, we explore the generality of flight-fecundity tradeoffs among wing-monomorphic species. We focus on studies that compared flight-fecundity tradeoffs between- and within-populations, rather than between species comparisons (but see Duthie et al., 2015; Stevens et al., 2012).

## 2. Review methods

Our search for evidence of a flight-fecundity tradeoff (or lack thereof) was based on a systematic literature search using the Web of Science database and Google Scholar, as well as review of references from those papers. The key search terms we used were: flight × fecundity, reproductive cost × flight, dispersal × fecundity, and fecundity × tradeoff. We included studies that specifically tested the existence of a tradeoff between flight and fecundity, as well as studies that provided information about an association between these traits (positive, negative, or none), even when these did not aim at assessing a tradeoff. For consistency, we use the term "association" to refer to the link between flight and fecundity, identified by different statistical methods (e.g. correlation, regression, ANOVA, etc.). Studies were considered if they used one of the following methods to examine a flight-fecundity association: (1) *Manipulation of resources*: when quantity or quality of available resources was manipulated (e.g. low quality diet) and the correlated response of flight and fecundity measured. (2) *Manipulation of flight or fecundity*: one of the life-history traits was manipulated (e.g. whether or not an individual was flown), to measure the response in the other variable (e.g. number of eggs produced). (3) *Phenotypic correlation between flight and fecundity*: here associations were measured as the correlation between flight and fecundity of various individuals or populations. (4) *Genotypic correlation between flight and fecundity*: these studies included a quantitative genetic estimate of the correlation between flight and fecundity-related traits as well as comparison of fecundity between genetic strains that had been selected for high dispersal activity by flight. We identified a total of 68 studies (covering 51 insect species) that reported an association between flight and fecundity (Appendix). From these studies, we examined what factors—e.g., method used, traits measured, variation in life history—were likely to influence the occurrence, and/or detection, of a flight-fecundity tradeoff in wing-monomorphic insects.

## 3. Empirical evidence of a flight-fecundity tradeoff

We found that out of the 68 surveyed studies, including 51 different insect species, 39 studies and 35 species —which constitute 57% of studies and 69% of species—provided evidence of a negative association between flight and fecundity. Sixteen studies found no evidence (13 species), and nine detected a positive association (seven species). Note that for a number of the surveyed species, detection (either positive or negative) or not of an association between flight and fecundity depended on the specific study, population, and the context (e.g. temperature, ontogenic stage).

In general, the study of resource-allocation tradeoffs has posed many empirical challenges (Agrawal et al., 2010; Saeki et al., 2014) and evidence of a tradeoff often relies solely on the identification of a negative association between traits that are thought to compete for a limited resource (Zera and Harshman, 2001). However, a negative association between traits does not necessarily reflect a resource-related tradeoff. A tradeoff can occur as an "adaptive negative correlation"—when expressing the two traits simultaneously brings a fitness benefit—or a "one-trait tradeoff"—when one trait is under opposite selection—(definitions from Agrawal et al., 2010). Thus, in the following sections, we discuss the extent to which the observed negative association may result from allocation of limited resources between flight and fecundity, and under which circumstances a neutral or positive association may arise instead.

## 4. Methods used to assess the association between flight and fecundity

Empirical studies on resource allocation tradeoffs have relied on a number of different methods to detect potential tradeoffs between life history traits. These include, among others, examining phenotypic correlations, manipulations of the available resources, evaluation of genetic correlations and correlated responses to artificial selection. However, the ability to detect a potential tradeoff between flight and fecundity may be influenced by the method used to evaluate the relationship between the two traits. Reznick (1985) addressed this issue by comparing how frequent were tradeoffs (between female reproduction and lifespan) identified by different methods. Here, following a similar approach, we evaluated if the proportion of studies detecting a negative association between flight and fecundity differed among the different methods. Specifically, we compared the three most commonly used methods: manipulation of available resources, increased cost of flight by encouraging (or forcing) insects to fly, and testing for a genetic correlation between flight and fecundity. In contrast to Reznick's (1985) findings, which indicated that genetic correlation was the most likely method to detect a tradeoff, we found that studies that manipulated available resources seemed more likely to detect a negative association (Table 1).

## 4.1 Limited available resources

A tradeoff among traits is dependent on their sharing the same resource and the quantity of that resource is not sufficient for both traits (Zera and Harshman, 2001). Expression of resource allocation tradeoffs, therefore, depends on the amount of resources available to supply the different traits (van Noordwijk and de Jong, 1986). In theory, reduced amounts of energy or nutrient input should magnify the tradeoff between flight and fecundity, whereas increased nutrients may obviate it (Blanckenhorn et al., 1995; Zera and Brink, 2000). Thus, experimental manipulation of resource availability, including food limitation and host plant quality, has been widely used to

**Table 1** Comparison of different methods commonly used to assess a flight-fecundity association.

| | Flight–fecundity association | | | |
|---|---|---|---|---|
| | **Negative** | **Positive** | **NA** | **Dual effect** |
| 1. Limited resources | 16 | | 5 | 2 |
| 2. Forced flight | 5 | 1 | | 1 |
| 3. Genetic correlation | 7 | 1 | 4 | |

Entries in the "Negative", "Positive", and "NA" columns refer to number of studies finding a negative, positive, or no association between flight and fecundity, respectively. "Dual effect" indicates that the association can be either negative or positive, depending on the context.

study resource allocation tradeoffs in insects. Overall, 76% of studies (Table 1) showed a negative association between flight and fecundity when resources were manipulated. We identified studies on 12 and 10 species, for which available resources (most frequently diet) were reduced in the larval or adult stage, respectively (Table 2). However, a negative association between flight and fecundity was not detected in a number of species (seven), and when detected, it did not always reflect a resource allocation tradeoff (e.g. *Tribolium castaneum*; Table 2). Thus suggesting that flight and fecundity were either not competing for the same limited resource, or that the resource itself was not limited, which is unlikely given that in all cases pupal size was reduced under resource limitation.

Some interesting patterns emerged when characteristics of the different taxonomic groups were taken into account, and whether flight and fecundity were affected differently when resources were limited during the larval vs. the adult stage. A number of studies, mainly in Lepidoptera (e.g. Boggs, 1997; Jervis et al., 2005; Levin et al., 2016, 2017b), have demonstrated that insects that feed as both larva (or nymph) and adult, can support flight and reproduction with a ratio of larval- and adult-derived resources.

Effects of limited resources during the larval stage carried on into the adult by reducing body size as well as by changing allometric relations among body parts (Fig. 1A). Seven out of 12 insect species exhibited a flight-fecundity tradeoff (Table 2A). Interestingly, these studies revealed that when developing under food constraints (Table 2A), most Lepidoptera females appeared to change allocation strategies to their adult bodies in a way that would improve their flight performance: by allocating more to wings and thorax, or by decreasing wing load—smaller bodies with relatively larger wings. For example, *Plutella xylostella* larvae that developed on low quality host plants, allocated less to fecundity and more to wing size, which resulted in females with increased flight activity (Bayoumy and Michaud, 2015; Begum et al., 1996). In theory, available resources during larval development should be preferentially allocated to the body parts or functions that have the greatest effect on fitness (Nijhout and Emlen, 1998). Indeed, flight ability in Lepidoptera is likely to impact female fitness in many ways, as flight is necessary to mate, feed (nectar), oviposit, and disperse. In contrast, reduced larval resources in Trichoptera, insects that do not feed or live long as adults and for which flight might be less important, did not favour female flight (Table 2A).

When experiencing food limitation as adults, nine out of 10 species exhibited a negative association between flight and fecundity (Table 2B). These effects, however, appeared to occur via different pathways: either by increasing the reproductive cost of flight or by triggering female flight,

**Table 2** Studies examining a flight-fecundity tradeoff by limiting available resources (e.g. food quality) to females during (A) the larval stage, or (B) the adult stage.

**(A) Larva–Resource limitation**

| | **Species** | **Treatment** | **Fecundity** | **Thorax/ wings** | **Flight performance** | **Negative association** | **Effect** | **Citation** |
|---|---|---|---|---|---|---|---|---|
| Hymenoptera | *Trichograma* | Food quality | Down | Down | Down | No | Fecundity and wing area decrease. High wing loading | Kishani Farahani et al. (2016) |
| Trichoptera | *Agrypnia deflate* | Resource quantity | Up | Down | Down | Yes | Allocation to fecundity increases at expenses of thorax size | Jannot et al. (2007) |
| | *Asynarchus nigriculus* | Resource quantity | Down | Down | Same | No | Overall reduction of all structures. An allometry is maintained | Wissinger et al. (2004) |
| | *Odontocerum albicorne* | Resource quantity | Up | Down | Down | Yes | Allocation to fecundity increases at expenses of thorax and wings | Stevens et al. (1999) |
| Lepidoptera | *Bactra verutana* | Food quality | Down | Up | Up | Yes | Allocation to wing size increases at expenses of fecundity | Frick and Wilson (1982) |
| | *Speyeria mormonia* | Food quantity | Same | Down | Up | No | Decreased wing size. Not change to fecundity. Low wing loading | Boggs and Freeman (2005) |

*Continued*

**Table 2** Studies examining a flight-fecundity tradeoff by limiting available resources (e.g. food quality) to females during (A) the larval stage, or (B) the adult stage.—cont'd

**(A) Larva–Resource limitation**

| Species | Treatment | Fecundity | Thorax/ wings | Flight performance | Negative association | Effect | Citation |
|---|---|---|---|---|---|---|---|
| *Phthorimaea operculella* | food quality | Down | Down | Up | No | Everything decreases. Low wing loading | Coll and Yuval (2004) |
| *Bicyclus anynana* | Food quality | Down | Up | Up | Yes | Allocation to thorax increases at expenses of fecundity. High thorax ratio buffers fecundity cost of flight | Saastamoinen et al. (2010) |
| *Plutella xylostella* | Food + Flight | Down | Up | Up | Yes | Smaller adults with larger wings and increased flight activity. Flight reduces fecundity | Muhamad et al. (1994) and Begum et al. (1996) |
| *Pieris rapae* | Food quality | Down | Up | Up | Yes | Allocation to wing size increases at expenses of fecundity | Tigreros et al. (2013) |
| *Mythimna pallens* | Resource + Flight | Same | Same | Same | No | No effect of larval crowding | Hill and Hirai (1986) |
| *Mythimna separata* | Resource + Flight | Down |  | Same | Yes | Diet does not affect flight, but low diet and forced flight reduce fecundity | Hill and Hirai (1986) |

**(B) Adult–Resource limitation**

| | Species | Treatment | Fecundity | Flight performance | Negative association | Effect | |
|---|---|---|---|---|---|---|---|
| Lepidoptera | *Bicyclus anynana* | Diet | Down | Up | No | While food limitation decreases fecundity. Improves flight by reducing wing load. Flight does not affect fecundity | Saastamoinen et al. (2010) |
| | *Spodoptera exempta* | Diet + Flight | Down | | Yes | Flight decreases fecundity in starved adults | Gunn et al. (1989) |
| | *Pseudoplusia includens* | Diet + Flight | Down | Down | Yes | Flight decreases fecundity. Starvation affects fecundity more than flight | Mason et al. (1989a) |
| | *Heliothis virescens* | Diet + Flight | | Up | Yes | Flight decreases fecundity in starved adults | Willers et al. (1987) |
| Coleoptera | *Tribolium castaneum* | Diet | Down | Triggered | Yes | Food limitation triggers flight. Flight reduces fecundity independent of diet | Perez-Mendoza et al. (2011) |
| | *Leptinotarsa decemlineata* | Diet-overwinter | Down | Up | Yes | Low quality plants reduced oviposition and increased flight | Weber and Ferro (1996) |
| | | Diet-summer | Down | Down | No | Low quality plants reduced both oviposition and flight | Weber and Ferro (1996) |
| Hemiptera | *Neacoryphus bicrucis* | Diet | Down | Triggered | Yes (threshold) | Food limitation triggers flight. Fecundity increases with diet while flight is maintained constant until threshold, when muscles are histolized | Solbreck and Pehrson (1979) |

*Continued*

**Table 2** Studies examining a flight-fecundity tradeoff by limiting available resources (e.g. food quality) to females during (A) the larval stage, or (B) the adult stage.—cont'd

**(B) Adult–Resource limitation**

| | Species | Treatment | Fecundity | Flight performance | Negative association | Effect | |
|---|---|---|---|---|---|---|---|
| | *Riptortus clavatus* | Diet | Down | Triggered | Yes (threshold) | Food limitation triggers flight. Fecundity increases with diet while flight is maintained constant until threshold, when muscles are histolized | Natuhara (1983) |
| | *Oncopeltus fasciatus* | Diet + Flight | Down | | Yes | Flight decreases fecundity in starved adults | Slansky (1980) |
| Diptera | *Bactrocera oleae* | Diet + Flight | Down | | Yes | Flight decreases fecundity in starved adults | Wang et al. (2009) |

Treatment effects on allocation to fecundity and flight-morphology (thorax and wing size) are described as Down = decreased allocation, Up = increased allocation, Same = no change. Effects on flight performance refer to observed changes in flight activity or wing loading: Down = decreased performance, Up = improved performance, Same = no change, Triggered = resource limitation triggers flight. "Yes (threshold)" indicates when there is a threshold effect of diet underlying the negative association between flight and fecundity.

which then reduced available resources for egg production. For example, in *Bactrocera oleae*, *Oncopeltus fasciatus*, and most Lepidoptera, flight reduced fecundity but only when access to food was limited (Table 2B), which suggests that not enough nutritional resources to support both traits were assimilated during the larval stage. In contrast, food limitation in *Tribolium castaneum* triggered flight and indirectly impacted fecundity, as flown females produced fewer eggs.

## 4.2 Forced flight

Overall, 83% of studies (Table 1) showed evidence of a negative association between flight and fecundity under forced flight. Examples of the effects of forced flight are given below in Section 6. Components of Flight Performance.

## 4.3 Genetic correlations

We identified studies that provided information about the existence and direction of genetic correlations between fecundity and flight traits on 10 different species. Evidence of a negative genetic correlation between flight and fecundity was found for five species: *Drosophila melanoganster* (Narise, 1974), *Pararge aegeria* (Berwaerts et al., 2008) *Epiphyas postvittana* (Gu and Danthanarayana, 1992), *Spodoptera exempta* (Gunn and Gatehouse, 1993), and *Cydia pomonella* (Gu et al., 2006). In contrast, for the other five species, flight and fecundity showed either no genetic correlation or a positive correlation. No genetic correlation was found in *Pieris brassicae* (Legrand et al., 2016), *T. castaneum* (Zirkle et al., 1988), and a non-migratory population of *O. fasciatus* (Dingle et al., 1988), while evidence of a positive genetic correlation was found for migrant populations of *O. fasciatus* (Hegmann and Dingle, 1982; Palmer and Dingle, 1986) and newly established populations of *Melitaea cinxia*—although this involved clutch size rather than total fecundity (Saastamoinen and Hanski, 2008). Thus, these studies suggest that flight and fecundity are not often constrained by a negative genetic correlation, and that under some circumstances, selection may actually favour maximizing both traits simultaneously—as proposed by the colonizer syndrome (see Section 6). Further studies on the genetics of flight-fecundity tradeoffs will benefit from also addressing the environmental conditions under which genetic correlations occur. First, genetic correlations often shift depending on the environmental conditions (reviewed in Sgrò and Hoffmann, 2004) and second, negative genetic correlations can also occur when two life history traits (such as flight and fecundity) depend on the same environmental condition, but in opposite ways (e.g. Knops et al., 2007).

## 5. Flight-related morphology

Variation in flight performance can be estimated directly, based on behavioural traits or indirectly, based on flight-related morphological traits. Understanding how morphology influences performance provides important insights on the functional basis of flight-fecundity tradeoffs. Typically, flight performance is expected to improve with decreased wing loading (body mass/wing area) and increased flight muscle ratio (thorax mass/body mass) (Dudley, 1991, 2002). Both indices depend on changes in flight-related morphology as well as changes in body mass, and reflect how much work the wings and flight muscles must perform to carry the weight of the insect (Goldsworthy and Wheeler, 1989).

In this review, we identified studies on 17 different species that examined a flight-fecundity association based on flight-related morphology. Increased allocation to wing size was associated with reductions in fecundity—in *Bactra verutana* (Frick and Wilson, 1982) and *Pieris rapae* (Tigreros et al., 2013)—, as well as with increases in fecundity (e.g. *O. fasciatus*, Palmer and Dingle, 1986). Fecundity and thorax mass showed a negative association in six out of eight insect species, and no association in *Coenagrion scitulum* and *Acheta domestica* (Srihari et al., 1975; Therry et al., 2015). *Bicyclus anynana* (Saastamoinen et al., 2010) and *P. aegeria* (van Dyck and Wiklund, 2002) increased allocation to thorax at the expenses of fecundity while *Agrypnia deflate* increased allocation to fecundity by reducing allocation to thorax (Jannot et al., 2007; Stevens et al., 1999). Similarly, in *Gryllus bimaculatus* (Lorenz, 2007), and several hemiptera—*Riptortus clavatus* (Natuhara, 1983), *Neacoryphus bicrucis* (Solbreck and Pehrson, 1979), and three *Dysdercus* species (Dingle and Arora, 1973)—fecundity was increased by using resources from histolized flight muscles. In these species, however, muscles histolysis occurred when there was an abundant rather than a limited food source, indicating that degeneration of flight muscles does not reflect a resource-based tradeoff (Fig. 1B), but a response to finding the appropriate conditions to reproduce (Dingle and Arora, 1973; Natuhara, 1983; Solbreck and Pehrson, 1979). Further, a study in the wing monomorphic cricket, *A. domestica* (Srihari et al., 1975), showed, using ovariectomy, that histolysis of flight muscles and egg development appeared to be independent processes.

Studies on flight-related morphology also indicated that detection of a flight-fecundity tradeoff may often depend on the specific trait being measured. In *A. deflate* caddisflies and *P. aegeria* butterflies, females with limited resources maintained fecundity by reducing investment in thorax size without changing investment in wing size (Jannot et al., 2007; Stevens et al., 1999). In contrast, *P. rapae* butterflies maintained allocation to fecundity by sacrificing investment in wings but not thorax size (Tigreros et al., 2013).

Finally, insect body mass, although it does not represent an exclusive flight-related morphological trait, is known to have important impacts on flight performance by increasing the weight load that must be lifted and carried during flight. Female body mass increases substantially during reproduction, due to the weight of mature eggs (Jervis et al., 2005). When flight performance is constrained by the weight of egg loads, a negative association between flight and fecundity can arise, even without reducing allocation to flight morphology (wing size and thorax mass) (Fig. 1C). *B. anynana* females with limited access to nectar, decreased abdomen mass—what reduced wing loading—and showed increased flight activity (Saastamoinen et al., 2010). Similarly, in *Bemisia tabaci* whiteflies, weaker-flying females (those that flew closer to the ground) carried heavier egg loads compared to females that flew higher (Isaacs and Byrne, 1998).

## 6. Components of flight performance

Insect flight is characterized by different components of performance, including flight takeoff, endurance, and speed. Such components may differ in the underlying morphology, the energetic requirements, and the selective forces shaping them. Next, we discuss how different components of flight performance may influence the association between flight and fecundity.

### 6.1 Flight endurance

Flight endurance, typically estimated as the distance or duration of flight, is perhaps the most widely studied component of flight performance in insects (Dudley, 2002; Goldsworthy and Wheeler, 1989). This aspect of flight is particularly important during dispersal and migration and is thought to increase with low wing loading and high thorax ratio (Davis and Holden, 2015).

We identified 33 studies on 26 different species that tested a causal effect of flight on fecundity (Table 3). A majority, used the tethered flight technique (Minter et al., 2018) to measure duration and/or distance of flight within a determined amount of time or until exhaustion (Table 3). Overall,

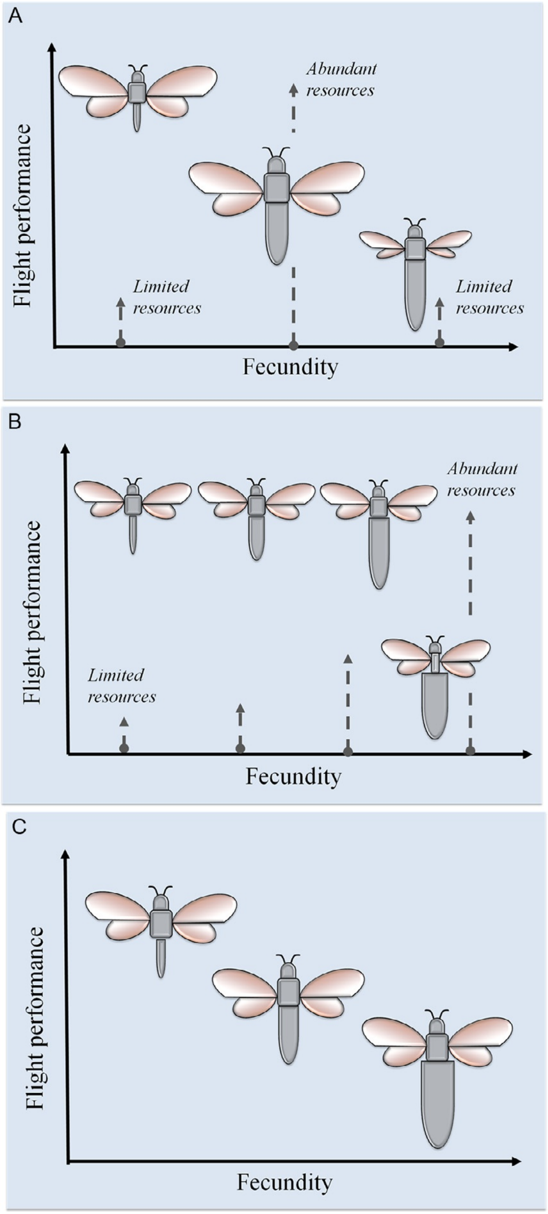

**Fig. 1** A negative flight-fecundity association can result from (A) resource-based tradeoffs: when available resources are differentially allocated to reproduction (lower right) or flight (upper left), (B) facultative flight muscle histolysis: fecundity does not compete with flight; but when available resources for reproduction are optimal (e.g. abundant host plants) flight is no longer needed, and resources from flight muscles are histolized and reallocated to fecundity (lower right), or (C) biomechanical constraints: when high egg loads (lower right) decrease flight performance, or low egg loads (upper left) increase flight performance. The relative size of wings and abdomen (and thorax in B) represents the relative investment of resources to the structure.

these studies provided some evidence of a fecundity cost of flight; long-flights reduced female fecundity in 15 out of 26 species, while increasing or not having an effect on four and seven species, respectively. As expected, species varied on how sensitive they were in terms of the strength of the effect that long flights had on fecundity. For example, in *P. aegeria* butterflies, 5 min of flight were sufficient to reduce female fecundity, and 10 min were lethal (Gibbs and van Dyck, 2010). In contrast, fecundity in *Oscinella frite* (Rygg, 1966), *Pseudoplusia includens* (Mason et al., 1989a) and *Rhodnius prolixus* (Oliveira et al., 2006), was only affected if females flew until exhaustion for several days. Also, in some species (e.g. *O. fasciatus*, *S. exempta),* the fecundity cost of long-flight was only observed when females had limited nutritional resources (Gunn et al., 1989; Slansky, 1980).

Interestingly, the impact of long-flight on fecundity was often age-dependent. For example, in *Cnaphalocrocis medinalis* (Zhang et al., 2015) and *Mythimna separata* (Luo et al., 1999), flying on days 1–2 after emergence increased fecundity, while flying later on (e.g. day 4) decreased it. In *S. exigua*, total fecundity was only reduced when females flew before and after an inter-oviposition period (days 2–7). Finally, independent of the effect on fecundity, long flights conveyed a reproductive benefit in several species, by accelerating the onset of egg maturation and oviposition (Table 3).

## 6.2 Flight takeoff

Flight initiation or takeoff is the most energetically expensive part of insect flight and yet, it has received much less attention than other components of flight performance (Bimbard et al., 2013), especially in the context of flight-fecundity tradeoffs. During takeoff, insects spend significant amounts of energy to generate the necessary force to lift up their body weight (Marden, 1987). The three studies (Almbro and Kullberg, 2012; Berrigan, 1991; Berwaerts et al., 2008) we identified that focused on takeoff flight performance, indicated that decreases in performance were associated with increases in weight loads during ovarian development. High egg loads impacted female takeoff by reducing lift production in *Neobellieria bullata* flies (Berrigan, 1991), and decreasing takeoff angle in *Pieris napi* butterflies (Almbro and Kullberg, 2012). Also, a negative genetic correlation was found between flight takeoff performance and abdomen mass in *P. aegeria* females (Berwaerts et al., 2008), suggesting the occurrence of a genetic tradeoff between flight and fecundity. Selection to improve takeoff performance

**Table 3** Effect of flight duration and distance on female fecundity.

| Species | Experiment | Flight performance | Effect on fecundity | Comments | Citation |
|---|---|---|---|---|---|
| *Amyelois transitella* | Tethered flight (up to 2 h) | Duration | 0 | | Rovnyak et al. (2018) |
| *Aphis glycines* | Tethered flight (up to 2 h) | Distance | – | | Zhang et al. (2009) |
| *Aphis phabae* | Tethered flight (0–80 s) | Duration | + | Stimulates early reproduction | Johnson (1958) |
| *Bactrocera oleae* | Tethered flight (24 h) | Duration/ Distance | – | If starved | Wang et al. (2009) |
| *Chrysoperla sinica* | Tethered flight ($1-3h$) | Duration | – | | Khuhro et al. (2014) |
| *Cnaphalocrocis medinalis* | Tethered flight | Duration | –/+ | Age-dependent and Stimulates early reproduction | Zhang et al. (2015) |
| *Drosophila melanogaster* | Tethered flight (1 h) | Flown vs. unflown | – | | Roff, (1977) |
| *Drosophila subobscura* | Tethered flight (1 h) | Flown vs. unflown | – | | Inglesfield and Begon (1983) |
| *Heliothis virescens* | Tethered flight (2 h/daily) | Flown vs. unflown | – | If starved | Willers et al. (1987) |
| *Leptinotarsa decemlineata* | Tethered flight (1 h) | Duration | –/+ | Summer generation: positive and Overwintered generation: negative | Weber and Ferro (1996) |

| | | | | | |
|---|---|---|---|---|---|
| *Locusta migratoria* | Tethered flight (exhaustion) | Flown vs. unflown | − | | Highnam and Haskell (1964) |
| *Loxostege sticticalis* | Tethered flight (12h) | Distance | 0 | Stimulates early reproduction | Cheng et al. (2012) |
| *Melanoplus sanguinipes* | Tethered flight (>2 h) | Flown vs. unflown | 0 | Stimulates early reproduction | McAnelly and Rankin (1986) |
| *Mythimna pallens* | Tethered flight (24 h) | Flown vs. unflown | 0 | Stimulates early reproduction | Hill and Hirai (1986) |
| *Mythimna separata* | Tethered flight (24 h) | Flown vs. unflown | −/+ | Age-dependent and Stimulates early reproduction | Hill and Hirai (1986) |
| *Oncopeltus fasciatus* | Tethered flight (30h) | Flown vs. unflown | − | If starved and Stimulates early reproduction | Slansky (1980) |
| *Oscinella frite* | Tethered flight (exhaustion) | Duration | − | Increases rate of oviposition but decreases clutch size | Rygg (1966) |
| *Pararge aegeria* | Tethered flight (5 min) | Flown vs. unflown | − | | Gibbs and van Dyck (2010) |
| *Pieris brassicae* | Tethered flight (exhaustion) | Duration | 0 | | Legrand et al. (2016) |
| *Plutella xylostella* | Tethered flight (30 min) | Flown vs. unflown | − | | Muhamad et al. (1994), Shirai (1995) and Begum et al. (1996) |
| *Pseudoplusia includens* | Tethered flight 2 h/daily | Flown vs. unflown | − | | Mason et al. (1989a) |

*Continued*

**Table 3** Effect of flight duration and distance on female fecundity.—cont'd

| Species | Experiment | Flight performance | Effect on fecundity | Comments | Citation |
|---|---|---|---|---|---|
| *Rhodnius prolixus* | Tethered flight (exhaustion) | Flown vs. unflown | − |  | Oliveira et al. (2006) |
| *Riptortus clavatus* | Tethered flight (exhaustion) | Duration | 0 |  | Natuhara (1983) |
| *Schistocerca gregaria* | Forced (exhaustion) | Flown vs. unflown | + |  | Highnam and Haskell (1964) |
| *Spodoptera exempta* | Flight balance | Duration | − | If starved | Gunn et al. (1989) |
| *Spodoptera exigua* | Tethered flight (exhaustion) | Duration/ Distance | 0/+ | Age-dependent | Han et al. (2008) |

The "Experiment" and "Flight performance" columns, provide information about experimental methods (use of tethered flight and duration) and variables used to measure flight performance. Additional information on results is provided under "Comments"; for example, when effects are observed if females were starved or, if effect changed with female age.
No effect = 0; Negative effect = −; Positive effect = +.

in these species is likely imposed by the risk of predation; most insects have to avoid predators throughout their life, and fast takeoffs can improve their survival to a predator's attack (Berrigan, 1991; Marden and Chai, 1991). Yet, frequent takeoffs may indeed lead to resource allocation tradeoffs, due to the high energy cost involved in this component of flight. *B. anynana* females that were forced to repeatedly takeoff within a period of 5 min, showed reduced fecundity (Saastamoinen et al., 2010). In nature, however, females may avoid such costs by performing longer flights with less frequent takeoffs, compared to conspecific males (Berwaerts et al., 2008).

### 6.3 Other components of performance

How other components of flight performance, including flight speed, acceleration, and hovering (e.g. during nectaring), affect female fecundity remains largely unexplored. Yet, resource-based tradeoffs specific to these aspects of flight are likely, given their high energetic cost. A recent study in *Manduca sexta*, for example, showed that the energetic cost of flight depends on speed, with the greatest amount of energy utilized when flying either very slow or very fast (Warfvinge et al., 2017).

## 7. Behavioural types of movement

Insect flight is often driven by different behavioural motivations, or "behavioural types of movement" (Kennedy, 1985). The terminology and definitions separating behavioural types of movement have been extensively discussed elsewhere (Dingle, 2014; van Dyck and Baguette, 2005) and are outside the scope of this review. In general, insect flight can be broadly categorized into two types of movement: station-keeping and migration (following Dingle, 2014). While the causes and consequences linked to station-keeping and migratory flights have been the topic of much attention, little is known about how these influence flight-fecundity tradeoffs. Resource allocation decisions are based on the relative fitness advantage obtained by favouring one trait over the other. Behavioural types of movement provide information about the function of flight or the relative advantage that flight has on fitness of a given species or population, at a given time. Below, we discuss how the different behavioural motivations may explain variations in how flight and fecundity relate.

## 7.1 Station-keeping

Station-keeping—also known as trivial or appetitive types of movement—refers to local flights that are stimulated by the organism's "appetite" for a resource, such as food, mates, egg laying sites, and shelter (Dingle, 2014). Even though station-keeping flights are exhibited by most insects at some point in life, the triggers of this behavioural type of movement vary depending on the organism's internal and external environments. In females, flight is typically related to searching for two types of resources, food and oviposition sites. When flight is triggered by the absence of food, a flight-fecundity tradeoff is likely to arise. Food limitation stimulates flight in many insect species (Perez-Mendoza et al., 2011; Weber and Ferro, 1996), which often results in reduced fecundity (e.g. Table 2B). In *T. castaneum*, for example, flight was triggered in the absence of food, and females that flew showed a reduced fecundity (Perez-Mendoza et al., 2011). In contrast, flight may be less likely to reduce fecundity, when it is linked to the female reproductive status. In *Amyelois transitella* for example, mated females, ready to lay eggs, flew longer than unmated females and did so, without diminishing fecundity (Rovnyak et al., 2018).

## 7.2 Migration

Migratory flight is a specialized behaviour, characterized by a directional, undistracted flight during which the organism's regular "appetites" for food, mates, etc., become suppressed (Dingle, 1996; Dingle and Drake, 2007). Insect migratory flight is typically triggered by internal clock mechanisms and environmental cues (e.g. shortening of daylight hours), and it can entail journeys of a few hundreds of meters to several thousands of kilometres (Dingle, 1996; Dingle and Drake, 2007). At a simplistic level, it would seem that there should always be a tradeoff between migratory flight and fecundity. But evidence of such a tradeoff has historically relied on Johnson's idea of an "oogenesis-flight syndrome" (Johnson, 1963); this suggests that migration and reproduction are alternate physiological states, with the onset of one state suppressing the other. Even though many migratory insects are known to perform their long journeys in a pre-reproductive stage—before females mate and fully develop oocytes—the generality of the oogenesis-flight syndrome remains controversial (Rankin et al., 1986; Sappington and Showers, 1992).

To determine the incidence of an oogenesis-flight syndrome in migratory insects, and if this actually reflected a reproductive cost of migratory flight, we conducted a second literature search using The Web of Science database and Google Scholar, including the following terms: "oogenesis-flight syndrome" and "migration". We only included studies that identified migratory flight in the field (under natural conditions), or in the lab, when insects were subjected to conditions that simulated those occurring in the field, during migratory flights (e.g. reduced temperature and length of days). We identified 28 studies (Table 4) covering 22 insect species and four orders: Hemiptera (three species), Lepidoptera (15 species), Coleoptera (two species), and Orthoptera (two species). These studies indicated that an oogenesis-flight syndrome was indeed observed in several migratory insects —15 out of 22 species. Yet, the other migratory species (seven) showed migratory flight while being reproductively active, and six out of the 15 species that exhibited an oogenesis-flight syndrome were also able to migrate, in some generations, while carrying fully developed oocytes (Table 4).

Several arguments have been presented to explain why, in some insect species, migratory flight and reproduction do not appear to preclude each other. First, it has been suggested that the energetic cost of flying can be mitigated when abundant food and reproductive sites are found and utilized along the migratory route; as is the case for the monarch butterfly, *Danaus plexippus* (Vargas et al., 2018). Alternatively, the energetic cost of flying can be reduced when flight is aided by the occurrence of low-level wind streams, e.g. *Agrotis ipsilon* (Showers, 1997). Finally, studies in several species (e.g. *C. medinalis, A. ipsilon*, *M. separata*, *D. plexippus,* and *Hippodamia convergens*) suggest that delaying or shutting down reproduction in migratory females depends on whether they are heading to an overwintering vs. a breeding site (Brower, 1985; Riley et al., 1995; Sappington and Showers, 1992). When these females migrate to an overwintering site in autumn, they are typically unmated and with little ovarian development. In contrast, when females fly to re-colonize breeding sites in the spring, they are often mated and have fully developed ovaries (Rankin and Rankin, 1980a). Reproductive diapause in overwintering adults is characteristic of migratory as well as non-migratory insects (e.g. Schebeck et al., 2017; Zhu et al., 2013). Thus, rechanneling reproductive energy to produce fat reserves may be more important for successful overwintering than for the migratory flight itself.

Together, these results indicate that even in species that appear to conform to a classic oogenesis-flight syndrome, shutting down reproduction is not a precondition for performing migratory flights. Also, when examining studies that directly tested for an association between flight and fecundity in 11 different migratory species (using forced flight, genetic correlations, etc.),

**Table 4** Observed occurrence of an oogenesis-flight syndrome in migratory species.

| | Species | Oogenesis-flight syndrome | Flight-fecundity association | Citations |
|---|---|---|---|---|
| Coleoptera | *Anthonomus grandis grandis* | Yes | ? | Rankin et al. (1994) |
| | *Hippodamia convergens* | Yes/No | **Positive**: Juvenile hormones stimulate both | Rankin and Rankin (1980a, 1980b) |
| Hemiptera | *Oncopeltus fasciatus* | Yes | **Negative**: if flown and starved<br>**Positive**: genetic correlation | Dingle (1965), Slansky (1980), and Palmer and Dingle (1986) |
| | *Laodelphax striatellus* | Yes | ? | Wang et al. (2008) |
| | *Bemisia tabaci* | No | **Negative**: phenotypic correlation | Isaacs and Byrne (1998) and Byrne (1999) |
| Lepidoptera | *Spodoptera exempta* | Yes | **Negative**: genetic correlation<br>**Negative**: if flown and starved | Gunn and Gatehouse (1993) |
| | *Spodoptera exigua* | No | **NA/Negative**: age dependent | Han et al. (2008) and Jiang et al. (2010) |
| | *Loxostege sticticalis* | Yes | **NA**: if flown | Cheng et al. (2012, 2016) |
| | *Cnaphalocrocis medinalis* | Yes/No | **Negative/ Positive**: age dependent | Riley et al. (1995), Huang et al. (2010), Sun et al. (2013), Fu et al. (2014c), and Zhang et al. (2015) |
| | *Agrotis ipsilon* | Yes/No | ? | Von Kaster and Showers (1982) and Sappington and Showers (1992) |

**Table 4** Observed occurrence of an oogenesis-flight syndrome in migratory species.—cont'd

| | **Species** | **Oogenesis-flight syndrome** | **Flight-fecundity association** | **Citations** |
|---|---|---|---|---|
| | *Macdunnoughia crassisigna* | No | ? | Fu et al. (2015) |
| | *Mamestra brassicae* | No | ? | Wu et al. (2015) |
| | *Choristoneura fumiferana* | No | ? | Rhainds and Kettela (2013) |
| | *Mythimna separata* | Yes/No | **Negative/ Positive**: age dependent. **Negative**: if crowded | Hill and Hirai (1986), Luo et al. (1999), and Zhao et al. (2009) |
| | *Athetis lepigone* | Yes/No | ? | Fu et al. (2014b) |
| | *Apolygus lucorum* | Yes | ? | Fu et al. (2014a) |
| | *Cydia pomonella* | No | **Negative**: genetic correlation | Schumacher et al. (1997) and Gu et al. (2006) |
| | *Pseudoplusia includens* | Yes | **Negative**: if flown | Mason et al. (1989a, 1989b) |
| | *Danaus plexippus* | Yes/No | ? | Herman and Barker (1977) and Vargas et al. (2018) |
| | *Heliothis armigera* | Yes | ? | Colvin and Gatehouse (1993) |
| Orthoptera | *Melanoplus sanguinipes* | No | **NA**: if flown | McAnelly and Rankin (1986) |
| | *Gryllus bimaculatus* | Yes | ? | Lorenz (2007) |

Yes = migratory flight and oogenesis do not overlap; No = migratory flight and oogenesis occur concurrently; Yes/No = migratory flight either overlap or not, depending on the generation (e.g. Summer vs. Winter generation). Direct evidence of a flight fecundity association is described as Negative, Positive, or none (NA). "Flight-fecundity association" column reports results from studies that directly tested for a flight-fecundity association in migratory species (via genetic correlations, resource manipulation, etc.).

we found that these were equally likely to exhibit either a positive (four species) or a negative (four species) association between flight and fecundity (Table 4). Importantly, occurrence of an oogenesis-flight syndrome did not necessarily reflect a negative association between flight and fecundity. For example, even though the migratory behaviour of *O. fasciatus* and *S. exempta* both conformed to Johnson's oogenesis-flight syndrome (Dingle, 1965; Gunn et al., 1989), the genetic correlation between flight-related traits and fecundity was negative in *S. exempta* (Gunn and Gatehouse, 1993) and positive in *O. fasciatus* (Palmer and Dingle, 1986). Thus, termination of migration and the onset of oogenesis may represent independent ontogenetic events that, for some insect species, have been selected to coincide (Baker, 1978).

## 8. The colonizer-syndrome

Insect flight can also be directed to explore new areas outside of their home range. This type of movement often results in dispersal and colonization of suitable habitats (Dingle, 1996, 2014) and thus, includes a wide-range of consequences for population dynamics in the context of global change (e.g. van Dyck and Baguette, 2005).

Some of the most significant contributions to understand potential costs associated with dispersal flights come from studies that examine dispersal as a population trait. In insects and other taxa, females from edge populations and fragmented habitats show superior flight performance when compared with those from the core of the population and continuous habitats. Like other types of flight, dispersal is energetically costly and is thought to tradeoff with female reproductive performance (e.g. Karlsson and Johansson, 2008). Indeed, in the speckled wood butterflies, *P. aegeria*, females from populations where high dispersal is favoured, such as range-expanding populations and populations from fragmented habitats, had lower fecundity than females from well-established and contiguous populations (Gibbs et al., 2010; Hughes et al., 2003).

Alternatively, the "colonizer syndrome" proposes that there should be a selective advantage for a positive association between flight and reproduction when colonizing new habitats (Bonte and Saastamoinen, 2012; Lewontin, 1965). In *M. cinxia*, female flight and fecundity were positively correlated in new populations (Hanski et al., 2006; Saastamoinen, 2007) but were not correlated in old ones. Hanski et al. (2006) showed that females from new populations were indeed more dispersive (fly more) and emerged with fewer eggs (potential fecundity); although their lifetime fecundity was not affected (Hanski et al., 2004). The colonizer syndrome may also explain the positive effect of flight on female reproduction often observed in migratory insect species (Table 4). Given that migratory flight may function as a means to escape unfavourable environments as well as a colonizing mechanism, migratory insect species can be expected to have evolved adaptations enabling them to optimize long flights and also reproduction (Lewontin, 1965; McAnelly and Rankin, 1986; Rankin and Burchsted, 1992).

## 9. Shared resources between flight and fecundity

The potential occurrence of a tradeoff between flight and fecundity rests on the assumption that both are costly in terms of energy and resources. However, a tradeoff between two traits will exist only if those resources are utilized by both traits, and both traits compete for these resources (Zera and Harshman, 2001). In the hawkmoth *Manduca sexta*, warm-up and flight are initiated with carbohydrates as fuel (Joos, 1987; Ziegler and Schulz, 1986b) with an almost immediate switch to lipids as fuel for sustained flight (Ziegler and Schulz, 1986a). Aside from water, the largest component of *M. sexta* eggs are lipids (39%, see below) (Kawooya and Law, 1988). Thus, in *M. sexta*, egg production and sustained flight should compete for the same larval-derived lipid resources. In contrast to larval-derived fatty acids, nectar-derived fatty acids imbibed by adults are used exclusively to maintain resting metabolism and are not allocated to either flight or reproduction (Levin et al., 2017). The adult diet in nectarivorous insects, like *M. sexta*, contains not only carbohydrates but also amino acids found in the nectar (Mevi-Schütz and Erhardt, 2005). Using $^{13}$C labelled amino acids added to nectar and fed to fertilized *M. sexta* females, Levin et al. (2017a) showed that both essential (leucine and phenylalanine) and nonessential amino acids (glycine) were allocated to the flight muscle of the female as well as to her eggs. This indicates that adult-derived nectar amino acids are shared and can be involved in a resource allocation tradeoff between flight and fecundity.

### 9.1 Resource allocation to flight

Insect flight muscle is the most energetically costly mode of locomotion known: hovering hawkmoths have 170 times higher metabolic rates than they do at rest (Bartholomew and Casey, 1978). The high metabolic costs of flight also incur high levels of oxidative damage to flight muscle membranes (Levin et al., 2017). The hawkmoth *M. sexta* mitigates this oxidative damage by shunting nectar carbohydrates through the pentose phosphate pathway, which increases antioxidant potential through the production of NADPH and glutathione, two major antioxidants conserved across many taxa (Levin et al., 2017).

In addition to the metabolic cost of flight itself, the cost of maintaining flight muscle and biosynthesis of flight fuel can increase metabolic capacity 4–10-fold (Mole and Zera, 1994). Most flying insects use two sources of flight fuel: carbohydrates and lipids, although the amino acid proline is known to fuel flight in a small number of insects such as blood sucking flies (Bursell, 1975), some Hymenoptera (Teulier et al., 2016) and some Coleoptera (Weeda et al., 1979). Carbohydrates are typically used for short flights, and can be replenished from nectar meals. In species with short-duration flight such as bees, beetles, flies, butterflies, and moths (with the proline exceptions mentioned above), carbohydrates are the only source of flight fuel (Rothe and Nachtigall, 1989; Suarez, 2005; Suarez et al., 1996). In contrast, in species with long-distance flight such as hawkmoths (O'Brien, 1999; Ziegler and Schulz, 1986a, 1986b) monarch butterflies (Brown and Chippendale, 1974), dragonflies (Kallapur and George, 1973) and locusts (Pener et al., 1997; van der Horst et al., 1980), carbohydrates are used for the initial phase of flight (≈20–30 min), after which lipids are used exclusively (Chino et al., 1992).

The advantage of lipid over carbohydrate flight fuels is a function of relative energy yield and storage efficiency. Over 95% of the lipids stored in the fat body are triacylglycerides (TAG) (Arrese and Soulages, 2010; Beenakkers et al., 1985; Canavoso et al., 2001), which are highly concentrated stores of metabolic energy. Complete oxidation of fatty acids yields about 9 Kcal/g. In contrast, carbohydrates and proteins yield only about 4 kCal/g. In addition, TAG is nonpolar and stored in a nearly anhydrous form, as opposed to carbohydrates, which are stored hydrated: a single gram of glycogen binds about 2 g of water. Thus, a gram of anhydrous fat stores more than six times as much energy as a gram of hydrated glycogen. Furthermore, the net yield of the oxidation of glucose is 36 ATP and the thermodynamic efficiency of the generation of ATP from glucose is 38%. In contrast, the net yield of fatty acid (palmitate) oxidation is 129 ATP with a thermodynamic efficiency of 40%. Thus, with similar thermodynamic efficiencies, fatty acid oxidation yields 3.6 times more ATP than does glucose (Stryer, 1988).

Even though lipids are a much more efficient source of flight fuel, nectar-derived carbohydrates are immediately available for use, and can provide significant energy input for short-duration flight. For example, Raguso et al. (2003) calculated that nectar from one *Datura wrightii* flower provides *M. sexta* weighing 1.2 g with 10–15 min of hovering capability, or all that this moth needs to fly 1 km in search of a mate or oviposition site. *M. sexta* can imbibe between 20% and –60% of their body weight in nectar: the lower the concentration the more nectar imbibed (Raguso et al., 2003).

The allocation of lipid vs. carbohydrates to flight depends in part on the nutritional status of the individual and its sex. Starved or water-fed hawkmoths use lipids as flight fuels (O'Brien, 1999; Ziegler and Schulz, 1986a, 1986b), whereas moths with a steady nectar source primarily utilize carbohydrates (O'Brien, 1999). Newly eclosed females conserve carbohydrate use during flight (O'Brien, 1999) probably due to the incorporation of nectar-derived carbohydrates into eggs (O'Brien et al., 2004) whereas males use primarily carbohydrate-based fuels (O'Brien, 1999). Male *M. sexta* allocate more nectar-derived amino acids (both essential and non-essential) to flight muscle than do females (Levin et al., 2017b).

## 9.2 Resource allocation to fecundity

Oogenesis in insects is a nutrient-limited process: adult insects that feed produce more eggs than adults that are not able to feed (Papaj, 2000; Wheeler, 1996). For example, sugar-fed female *M. sexta* produced 2–3 times more eggs per day than did water-fed females (Sasaki and Riddiford, 1984). Of the total macronutrient composition in insect eggs, proteins constitute 40–50%, lipids 30–40%, and carbohydrates (sugars and glycogen) around 10–30% (Geister et al., 2008; Giron and Casas, 2003; Němec, 2002; Sloggett and Lorenz, 2008). Thus, on the surface, egg production shares common macronutrients with flight and should be involved in flight fecundity tradeoffs. While *M. sexta* eggs are 70% water, the other 30% is protein (31%), lipids (39%), and carbohydrates (2%); the remaining 28% is insoluble unidentified material (Kawooya and Law, 1988). Eggs weigh on average 1.6 mg ($n = 60$, Davidowitz, unpublished data). Over 95% of the lipids stored in the fat body are TAGs (Beenakkers et al., 1985; Canavoso et al., 2001) and the fat body contains about 55 mg TAG at peak larval size (Davidowitz and Kiley, unpublished data). From this, we have calculated that a *M. sexta* female should have enough lipids to produce 267 eggs. Yet, the average moth in a laboratory colony produces only 136 eggs (±45, $n = 292$, Davidowitz, unpublished data). Thus, it seems that 51% of the resources are held in reserve for either future reproduction or for other processes such as flight (Jervis and Boggs, 2005; Jervis et al., 2005).

The examples given above refer to the total amount of resources or energy allocated to either flight or fecundity. The geometric framework (Behmer, 2009; Simpson and Raubenheimer, 2012) shows that the amount of nutrients per se, is not always sufficient to understand allocation of resources to traits, rather the relative amounts of specific nutrients often determines trait performance (Clark et al., 2013, 2015; Lee et al., 2008; Wilson et al., 2019; Zera et al., 2016). The geometric framework has not yet been applied specifically to the flight-fecundity tradeoff and is an area ripe for future studies.

### 9.3 Capital vs. income breeders

Life history strategies of resource accumulation are extremely diverse across insect taxa. Some insects are capital breeders: all the resources used by adults for reproduction, survival and maintenance, are acquired during the juvenile stage, and adults do not feed (e.g. *Lepidoptera*: Saturniidae and Ephemeroptera). Most insects are, however, income breeders. Income breeders feed and grow as juveniles, but resources allocated to reproduction are accumulated during the adult stage, and reproductive success is largely determined by the amount of resources acquired as adults (Papaj, 2000; Wheeler, 1996). Still, others accumulate most of their resources during the larval stage but can partially augment them as adults (e.g., Lepidoptera). We would predict a stronger tradeoff between flight and fecundity among capital breeders that have a finite amount of resources, whereas a tradeoff may or may not exist in income breeders that can acquire more resources throughout their adult life. This review found only three studies, among three species of capital breeders (Table 2: Trichoptera), looking at the effect of resource limitation on flight-fecundity tradeoffs, which showed both negative and no associations between the traits. The dearth of studies on flight-fecundity tradeoffs among capital vs. income breeders, begs the question of how this tradeoff is influenced by the different resource accumulation strategies.

## 10. Conclusions

Although, the majority of studies examined in this review showed a negative association between flight and fecundity in wing monomorphic insects, we found little support for the widespread occurrence of a resource allocation tradeoff between flight and fecundity. In all contexts, there were species or studies that found no association, or a positive association, between both traits.

As noted by several researchers (Baker, 1978; Guerra, 2011; Rankin et al., 1986), a negative association between flight and fecundity does not necessarily reflect a resource competition between both functions. A number of selective forces may act to separate flight and fecundity in wing-monomorphic insect species. Indeed, we conclude based on the reviewed literature, that flight and fecundity in wing-monomorphic insects are related in a number of ways, including (1) physiological constraints: resource-based tradeoff, (2) biomechanical constraints: when egg load affects take-off performance, (3) adaptive negative correlations: switching from flight to egg production when an appropriate place (e.g., with food, mates, and oviposition sites) to reproduce has been found or (4) adaptive positive correlations: the colonizer syndrome. It is clear that a great deal of more research is needed to understand the life history, ecological, and phylogenetic contexts where resources are allocated differentially to flight vs. fecundity in wing-monomorphic insects.

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## Appendix

List of studies examining the association between flight and fecundity in wing-monomorphic species using different methods: "A" = Manipulation of resources, "B" = Manipulation of flight or fecundity, "C" = Phenotypic correlation between flight and fecundity, and "D" = Genotypic correlation. Flight-fecundity association is described as: negative = –; positive = +; none = 0.

| Species | Method | Flight-fecundity association | Citation |
|---|---|---|---|
| *Acheta domestica* | B | 0 | Srihari et al. (1975) |
| *Agrotis ipsilon* | C | 0 | Sappington and Showers. (1992) |
| *Agrypnia deflate* | A | – | Jannot et al. (2007) |
| *Amyelois transitella* | C | 0 | Rovnyak et al. (2018) |
| *Aphis glycines* | C | – | Cheng et al. (2016) |
| *Aphis phabae* | C | + | Johnson 1958) |
| *Asynarchus nigriculus* | A | 0 | Wissinger et al. (2004) |
| *Bactra verutana* | A | 0 | Frick and Wilson (1982) |

| | | | |
|---|---|---|---|
| *Bactrocera oleae* | C | − | Wang et al. (2009) |
| *Bemisia tabaci* | E | 0 | Byrne (1999) |
| | C | − | Isaacs and Byrne (1998) |
| *Bicyclus anynana* | A | −/0 | Saastamoinen et al. (2010) |
| *Chrysoperla sinica* | B | − | Khuhro et al. (2014) |
| *Cnaphalocrocis medinalis* | C | −/+ | Zhang et al. (2015) |
| | B | − | Sun et al. (2013) |
| *Coenagrion scitulum* | A | 0 | Therry et al. (2015) |
| *Cydia pomonella* | D | − | Gu et al. (2006) |
| *Drosophila melanogaster* | D | − | Narise (1974) |
| | B | − | Roff (1977) |
| *Drosophila subobscura* | B | − | Inglesfield and Begon (1983) |
| *Dysdercus fasciatus* | A | − | Dingle and Arora (1973) |
| *Dysdercus nigrofasciatus* | A | − | |
| *Dysdercus superstitiosus* | A | − | |
| *Epiphyas postvittana* | D | − | Gu and Danthanarayana (1992) |
| *Gryllus bimaculatus* | C | − | Lorenz (2007) |
| *Heliothis virescens* | A | − | Willers et al. (1987) |
| *Laodelphax striatellus* | C | − | Wang et al. (2008) |
| *Leptinotarsa decemlineata* | A | −/+ | Weber and Ferro (1996) |
| *Locusta migratoria migratorioides* | B | + | Highnam and Haskell (1964) |
| *Loxostege sticticalis* | C | 0 | Cheng et al. (2012) |
| *Melanoplus sanguinipes* | B | + | McAnelly and Rankin (1986) |

| | | | |
|---|---|---|---|
| *Melitaea cinxia* | C | – | Hanski et al. (2004) |
| | C | + | Hanski et al. (2006) |
| | C | + | Saastamoinen (2007) |
| | D | 0 | Saastamoinen and Hanski (2008) |
| *Mythimna pallens* | A | 0 | Hill and Hirai (1986) |
| *Mythimna separata* | B | + | Luo et al. (1999) |
| | A | – | Hill and Hirai (1986) |
| *Neacoryphus bicrucis* | A | – | Solbreck and Pehrson (1979) |
| *Neobellieria bullata* | C | – | Berrigan (1991) |
| *Oncopeltus fasciatus (Iowa)* | A | – | Slansky (1980) |
| | B | + | Caldwell and Rankin (1972) |
| | D | + | Palmer and Dingle (1986) |
| *Oncopeltus fasciatus (PuertoRico)* | D | – | Dingle et al. (1988) |
| *Oscinella frite* | C | – | Rygg (1966) |
| *Odontocerum albicorne* | A | – | Stevens et al. (1999) |
| *Pararge aegeria* | D | – | Berwaerts et al. (2008) |
| | C | – | Gibbs and van Dyck (2010) |
| | C | – | Hughes et al. (2003) |
| | C | – | van Dyck and Wiklund (2002) |
| *Phthorimaea operculella* | A | 0 | Coll and Yuval (2004) |
| *Pieris brassicae* | D | 0 | Legrand et al. (2016) |
| *Pieris napi* | D | – | Almbro and Kullberg (2012) |
| | C | – | Karlsson and Johansson (2008) |
| *Pieris rapae* | A | – | Tigreros et al. (2013) |
| *Plutella xylostella* | A | – | Begum et al. (1996) |
| | A | – | Muhamad et al. (1994) |
| | B | – | Shirai (1995) |

| | | | |
|---|---|---|---|
| *Pseudoplusia includens* | A | – | Mason et al. (1989b) |
| *Rhodnius prolixus* | B | – | Oliveira et al. (2006) |
| *Riptortus clavatus* | A | – | Natuhara (1983) |
| *Schistocerca gregaria* | B | + | Highnam and Haskell (1964) |
| *Speyeria mormonia* | A | – | Boggs and Freeman (2005) |
| *Spodoptera exempta* | A | – | Gunn et al. (1989) |
| | D | – | Gunn and Gatehouse (1993) |
| *Spodoptera exigua* | C | 0 | Han et al. (2008) |
| | C | 0 | Jiang et al. (2010) |
| *Tribolium castaneum* | A | – | Perez-Mendoza et al. (2011) |
| | D | 0 | Zirkle et al. (1988) |
| *Trichogramma brassicae* | A | 0 | Kishani Farahani et al. (2016) |

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