

Andrea F. Huberty · Robert F. Denno

Trade-off in investment between dispersal and ingestion capability in phytophagous insects and its ecological implications

Received: 11 July 2005 / Accepted: 18 January 2006 / Published online: 10 February 2006
© Springer-Verlag 2006

Abstract In population ecology, dispersal plays a fundamental role, but is potentially costly. Traditionally, studies of phenotypic trade-offs involving dispersal focus on resource allocation differences between flight and reproduction. However, investments in dispersal may also result in reduced allocation to other “third-party traits” (e.g. compensatory feeding) that are not directly associated with reproduction. Such traits remain largely uninvestigated for any phytophagous insect despite their importance for performance and survival. Using two wing-dimorphic, phloem-feeding planthoppers, *Prokelisia dolus* and *Prokelisia marginata* that differ dramatically in dispersal abilities, we sought evidence for a trade-off between investments in dispersal (flight apparatus) and ingestion capability (allocation to the esophageal musculature governing ingestion). Dispersal allows species to meet nutrient demands by moving to higher-quality resources. In contrast, enhanced investment in esophageal musculature increases ingestion capacity and allows phloem feeders to compensate for deteriorating plant nutrition on site. Our objectives were to compare differences in flight and feeding investment between *P. dolus* and *P. marginata* and between the wing forms of both species, and to compare ingestion capacity between the two species and wing forms. Morphometric and gravimetric measures of investment in flight versus feeding indicate that the sedentary *P. dolus* allocates more muscle mass to feeding whereas *P. marginata* invests more heavily in flight. Likewise, brachypters invest more in feeding and

less in flight than macropters. The greater esophageal investment in *P. dolus* is associated with enhanced ingestion capacity compared to *P. marginata*. As a consequence, *P. dolus* is better equipped to meet on-site nutrient demands when faced with deteriorating plant quality than *P. marginata*, which must migrate elsewhere to do so. Notably, such third-party trade-offs place constraints on how insect herbivores cope with changing resources and set the stage for fundamental differences in population dynamics.

Keywords Cibarial musculature · Feeding compensation · Flight dimorphism · Life history strategy · *Prokelisia* planthopper

Introduction

Dispersal by flight provides organisms the opportunity to synchronize reproduction with favorable resources across spatially diverse landscapes, and thus plays a key role in the evolution of insect life history strategies (Roff 1986; Roff and Fairbairn 1991; Denno 1994; Zera and Denno 1997; Denno et al. 2001). Dispersal also acts as a stabilizing process in meta-population dynamics (den Boer 1981; Hanski 1999), influences species interactions (Denno et al. 2000), and directly affects gene flow and the genetic structure of populations (Peterson and Denno 1997, 1998; Mun et al. 1999). Moreover, a high incidence of dispersal is characteristic of many severe agricultural and forest insect pests (Berryman 1988; Pedgely 1993; Kisimoto and Rosenberg 1994). Thus, dispersal has widespread consequences for both population ecology and pest management (Cappuccino and Price 1995).

Dispersal, however, does not occur without costs, costs that are often imposed on life history traits associated with reproduction (Roff 1986; Roff and Fairbairn 1991; Zera and Denno 1997; Zera and Harshman 2001). Wing-dimorphic insects such as planthoppers, aphids, and crickets have proved invaluable for investigating

Communicated by John Reeve

A. F. Huberty · R. F. Denno
Department of Entomology, University of Maryland,
College Park, Maryland 20742, USA

A. F. Huberty (✉)
USDA/APHIS/BRS, 4700 River Road, Unit 147, Riverdale,
Maryland 20737, USA
E-mail: ahuberty@terpalum.umd.edu
Tel.: +1-301-7340659
Fax: +1-301-3149290

trade-offs between dispersal and other life history traits because flight-capable and flightless forms are easily recognized (Denno et al. 1991; Roff and Fairbairn 1991; Tanaka 1993; Dixon 1998; Zera and Brink 2000). Populations of most wing-dimorphic insects contain both flightless adults (brachypters with reduced wings or wingless apterae) and flight-capable adults (macropters or alates) that possess fully developed wings and can disperse long distances (Denno 1994; Kisimoto and Rosenberg 1994; Dixon 1998). Traditionally, dispersal costs have been evaluated by comparing reproductive traits between flight-capable and flightless morphs with the expectation of reduced reproductive effort in the flight-capable morph (Zera and Denno 1997). Indeed, for females, there is widespread evidence that macropters have reduced fecundity, extended age to first reproduction, or reduced offspring size compared to their flightless counterparts (Roff 1986; Denno et al. 1989; Roff and Fairbairn 1991; Denno 1994; Zera and Denno 1997). Similar trade-offs between dispersal and siring capability have been found in males (Langellotto et al. 2000; Langellotto and Denno 2001). Underlying antagonistic trade-offs between dispersal and reproduction are differences in resource allocation between macropters and brachypters, given a limited energy budget. For example, in macropters, relatively more resources are allocated to flight muscles and the biochemistry associated with muscle maintenance and flight, whereas in brachypters assimilated and synthesized nutrients are allocated more to reproductive effort (Zera et al. 1998; Zera and Brink 2000; Zera and Harshman 2001; Zhao and Zera 2002).

Historically, phenotypic trade-offs involving dispersal have focused almost exclusively on differences in allocation between flight and reproduction (Zera and Denno 1997). However, resource investments in dispersal may also result in reduced resource allocation to other so-called third-party traits (e.g., compensatory feeding) that are not directly associated with reproduction (sensu Zera et al. 1998). Such traits, however, remain largely uninvestigated for any insect despite their potential importance for performance and survival. In this study we provide evidence that investment in the musculature associated with ingestion, and thus the ability to compensate for nutrient-poor food resources, trades off functionally with dispersal capability in two wing-dimorphic planthoppers (*Prokelisia marginata*, *Prokelisia dolus*: Hemiptera, Delphacidae). Clues to identifying a potential trade-off between dispersal and ingestion capability lie with differences in dispersal, response to nutrient limitation, competitive ability, and population dynamics between these two phloem-feeding insects. For example, *P. marginata* invests far more in dispersal than *P. dolus*, as evidenced by the much higher frequency of macropterous adults in populations (Denno et al. 1991, 1996). Despite its greater investment in flight capability, *P. marginata* performs and survives far worse on nutrient-deficient host plants, and is less able to regulate its own macronutrient composition (nitrogen and

phosphorus content) than *P. dolus* (Huberty 2005). *P. marginata* is also a poorer inter-specific competitor than *P. dolus*, an ability that is mediated by tolerance to feeding-induced reductions in plant quality (Denno et al. 2000). The common denominator underlying differences in performance and competitive ability between the *Prokelisia* species may be the ability to increase ingestion rate as food quality decreases and thus compensate for nutrient reductions (Slansky and Feeny 1977; Raubenheimer and Simpson 1993; Cook and Denno 1994; Lavoie and Oberhauser 2004). Compensatory feeding may be particularly critical given that phytophagous insects in general face a food resource that is extremely deficient in nutrients (nitrogen and phosphorus) compared to their own body composition, a nutrient mismatch that imposes tremendous nutrient demands on consumers with potentially drastic consequences for growth (McNeill and Southwood 1978; Mattson 1980; White 1993; Cook and Denno 1994; Ayres et al. 2000; Elser et al. 2000; Schade et al. 2003; Denno and Fagan 2003; Huberty and Denno 2004).

For planthoppers, compensatory feeding occurs when ingestion rate is increased as the concentration of macronutrients in the host plant decreases (McNeill and Prestidge 1982; Prestidge 1982; Backus 1985; Cook and Denno 1994). Perhaps this is made possible by a large commitment to the musculature associated with ingestion. Planthoppers feed by inserting their stylets into phloem tissues (Backus 1985; Cook and Denno 1994). Then using a cibarial pump (modified esophagus), cell sap is ingested. The cibarial pump is driven by a series of dilator muscles that insert on the interior of the face (clypeus), and face size is positively related to the cross-sectional mass and thus the power of the cibarial muscles to ingest cell sap (Backus 1985).

Although dispersal and compensatory feeding have been discussed as alternative strategies for coping with deteriorating plant nutrition and meeting nutrient demands (McNeill and Southwood 1978; Cook and Denno 1994), they have never been linked by virtue of a phenotypic trade-off. If a third-party trade-off indeed exists (sensu Zera 1998), then dispersal ability should constrain compensatory feeding and vice versa. In this context, the objectives for this study were to: (1) compare differences in investment in the flight and feeding morphology between *P. dolus* and *P. marginata*, and between the brachypters and macropters of both species; and (2) compare ingestion capability between the two species and their wing forms. Differences in flight and feeding musculature were measured by comparing head metrics (face areas and head dry masses), cibarial muscle area, and thoracic metrics (area and dry mass) between the two planthopper species and wing forms. Differences in ingestion capability between the species and wing forms were assessed by measuring honeydew production (liquid excretory product). In phloem-feeding insects such as planthoppers, ingestion and excretion rates are positively related (Prestidge 1982; Brodbeck et al. 1996);

thus, honeydew production was used as a surrogate for ingestion capacity.

If a trade-off between dispersal and compensatory feeding exists, we expected *P. marginata* to show a relatively greater investment in flight than cibarial apparatus, and *P. dolus* to show the reverse. Likewise, with a presumed greater investment in cibarial musculature and thus enhanced compensatory feeding, we predicted *P. dolus* to exhibit greater honeydew production than *P. marginata*. We predicted that macropters compared to brachypters would exhibit a greater investment in flight than feeding morphology and would produce less honeydew. By examining patterns of investment in dispersal and feeding apparatus between the species and wing forms of *Prokelisia* planthoppers, we aim to identify a third-party trait, namely compensatory feeding, that may be negatively associated with flight capability. Identifying such a trade-off between dispersal and a non-reproductive trait should mandate a broader view of life history theory and elucidate the constraints associated with the evolution of particular life history strategies that allow insect herbivores to cope with changing resources.

Study system

P. marginata and *P. dolus* are the most abundant herbivores on Atlantic coastal marshes where they feed exclusively on *Spartina alterniflora* (Denno et al. 2002; Denno et al. 2003). Both species are wing dimorphic with flight-capable macropters (adults with fully developed wings) and flightless brachypters (adults with vestigial hind wings) present in the same population (Denno et al. 1991; Denno et al. 1996). However, most adults of *P. marginata* are macropterous (>90%) whereas those of *P. dolus* are primarily brachypterous (>90%), a difference that reflects a marked disparity in dispersal and population dynamics between the two species (Denno et al. 1996). *P. dolus* is a relatively sedentary species that is restricted primarily to high-marsh meadows of *Spartina*. By contrast, *P. marginata* is a highly mobile species along the Atlantic coast and undergoes annual inter-habitat migrations between over-wintering sites on the high-marsh and more favorable low-marsh habitats where development occurs (Denno et al. 1996).

Although both *P. marginata* and *P. dolus* exhibit population increases on nitrogen-enriched *Spartina*, all evidence suggests that the two species cope with nutrient-deficient *Spartina* differently (Cook and Denno 1994; Denno et al. 2002; Denno et al. 2003; Huberty 2005). For instance, even though both species select the most nitrogen-rich plants on which to feed and oviposit, the macropters of *P. marginata* colonize nitrogen-rich plants at tremendously high densities compared to *P. dolus* (Denno et al. 2002). Moreover, both species exhibit enhanced survival and performance on nitrogen-fertilized *Spartina* (Cook and Denno 1994; Olmstead et al. 1997), but *P. marginata* shows a much stronger response

(Denno et al. 2002, Huberty 2005). *P. dolus*, however, has the ability to withstand nitrogen-deficient plants better than *P. marginata* (Huberty 2005). Thus, existing data suggest that nitrogen is limiting for both *Prokelisia* species, but that *P. marginata* copes with spatial changes in host-plant quality by dispersal to more favorable habitats, whereas *P. dolus* is able to remain on site and persist through periods of inadequate plant nutrition (Cook and Denno 1994; Denno et al. 2000).

Material and methods

Investment in flight versus feeding morphology in *Prokelisia* planthoppers

Head and thorax metrics

Patterns of investment in flight and feeding morphology (head and thorax metrics) in the *Prokelisia* species (both wing forms) were determined from laboratory-reared planthoppers. Planthoppers for this experiment were maintained in pure species cultures in the laboratory (Huberty 2005). Upon emergence, adults were sorted to species and wing form and were stored in ethyl alcohol (70%) prior to measurement of head and thorax features using an optical micrometer. Following measurement, adult bodies were separated into heads and thoraces (wings removed) that were dried at 60°C for 48 h and then weighed individually. In all, measurements and weights (dry mass) were made on 15 adult females of *P. dolus* (five macropters and ten brachypters) and 20 females of *P. marginata* (ten macropters and ten brachypters).

Investment in feeding musculature was assessed indirectly by measuring two head metrics: face (clypeus) area (width×length in mm²) as an index of the surface available for cibarial muscle attachment, and head dry mass (mg) as a surrogate for cibarial muscle mass. Investment in flight morphology was determined from two thorax metrics: thorax area [average thorax width (mesothorax width + metathorax width/2)×entire thorax length (prothorax + mesothorax + metathorax)] and thorax dry mass (prothorax + mesothorax + metathorax in mg). The prothorax was included in the determination of thorax length (despite lacking wings) because it is small compared to the other thoracic segments and yet allows for a more precise estimate of thorax length. Because many planthopper metrics scale with body size (Denno et al. 1989), individual tibia lengths (mm) were also measured and used to control for differences in body size among individuals.

Area (face and thorax) and dry mass (head and thorax) measurements were also used to calculate two indexes of relative investment in flight versus feeding capability: face area:thorax area (entire thorax length×average thorax width) and head-dry mass/thorax-dry mass. Higher ratios suggest a greater investment in feeding relative to flight morphology.

Cibarial musculature

Investment in feeding musculature was compared directly between species and wing forms by measuring the cross-sectional area of the cibarial dilator muscles. Because the cross-sectional area of a muscle is directly proportional to power (Gullen and Cranston 2000), cross-sectional area of the dilators should reflect the ability to maintain or enhance phloem intake under conditions of lowered turgor pressure (plant stress) or reduced plant nutrition (Huberty and Denno 2004).

The cross-sectional area of cibarial dilators was assessed using standard histological techniques (Barbosa 1974). Briefly, living individuals were chilled and then transferred to 70% ethanol prior to running them through a dehydration series. Planthopper heads were then removed, cleared, stained with hematoxylin and eosin (muscle stains), embedded in Paraplast, sectioned with a microtome, and the sections placed in Permount on slides. For each individual, the head section exhibiting the maximum cibarial area was selected, measured, and its cross-sectional area determined (mm^2). The cibarial dilators appear as a mass in the center of the head underlying what was the clypeal region of the face. Measurements were made on the macropters and brachypters (females only) of *P. dolus* and *P. marginata* ($n=7, 7, 8,$ and $10,$ respectively).

Honeydew production in planthoppers
as an index of ingestion rate

Honeydew production

Ingestion rate in sap-feeding insects can be measured indirectly as excretion rate (honeydew production) (Prestidge 1982; Brodbeck et al. 1996). Honeydew production was determined for both *Prokelisia* species by feeding them on greenhouse-cultured *Spartina* (Huberty 2005). Potted *Spartina* plants (3–5 plants/pot) were grown from seed in flats (two flats, 80 pots/flat) and were fertilized with ammonium nitrate at a rate of 10 g/m^2 per year of nitrogen (5 g ammonium nitrate/flat every 3 weeks from April until June 2003). Nitrogen content of *Spartina* was determined by harvesting all aboveground living biomass from six pots prior to the onset of the honeydew-production experiment (15 August 2003). Foliar nutrient content was used as an index of the phloem nutrients available (Youssefi et al. 2000). Leaves were oven dried for 48 h at 60°C , ground in a Wiley mill and subsequently analyzed for %N using a Perkin–Elmer 2400 CHN analyzer.

Honeydew production was determined from planthoppers confined in clip cages on plants. After adult emergence from cultures, cohorts consisting of ten females of a single species and wing form combination were placed into small cylindrical clip cages (1.5 cm in diameter \times 6 cm in length and made of clear cellulose butyrate plastic) that contained a cup-shaped piece of

pre-weighed filter paper. Because few brachypterous females of *P. marginata* emerged during the rearing process, only macropters (14 replicates) of this species were available for testing. Both wing forms of *P. dolus* (13 replicates of each) were sufficiently abundant for assessment of honeydew production.

Leaves were positioned in the tops of clip cages to ensure that honeydew fell down and collected on filter paper below. After 48 h of feeding, cohorts were removed and the filter paper was re-weighed. Honeydew production ($\text{mg}/48 \text{ h}$) was measured as the difference between pre-feeding and post-feeding filter paper weight. Eleven planthopper-free “control cages” were also placed onto plants for 48 h and the filter paper was re-weighed to ensure that any change in filter paper weight in the treatment cages was due to honeydew accumulation.

Statistical analysis

The effects of species, wing form, and their interaction on head metrics, thorax metrics, cibarial muscle area, and investment indices were determined using analysis of covariance with tibia length as the covariate (SAS 2002). Honeydew production was compared between the two *Prokelisia* species and between the wing forms of *P. dolus* using ANOVA (SAS 2002). To confirm that changes in filter paper weight were due to honeydew production, filter paper weight in planthopper-free controls was compared to that in the planthopper-containing treatment (averaged across species, wing forms) using ANOVA. For the control treatment, change in filter paper weight over the 48-h experimental period (initial versus final weight) was compared using a *t*-test. Prior to each analysis, data (residuals) were assessed for normality and homogeneity of variances (SAS 2002). If residual variances were heterogeneous, variance partitioning was conducted and the best model was chosen using the Bayesian information criterion; *df* were calculated using the Kenward–Roger method (SAS 2002). All means' comparisons were conducted using a Tukey adjustment to account for inflated comparison-wise error rates.

Results

Investment in flight versus feeding morphology
in *Prokelisia* planthoppers

Head and thorax metrics

Brachypters of *P. dolus* had a larger facial area than macropters of this species and both the brachypters and macropters of *P. marginata*, which did not differ from each other (significant species \times wing form interaction; $F_{1,30}=10.7$, $P=0.003$; Fig. 1a). In general, there was no difference in thorax area between the wing forms of

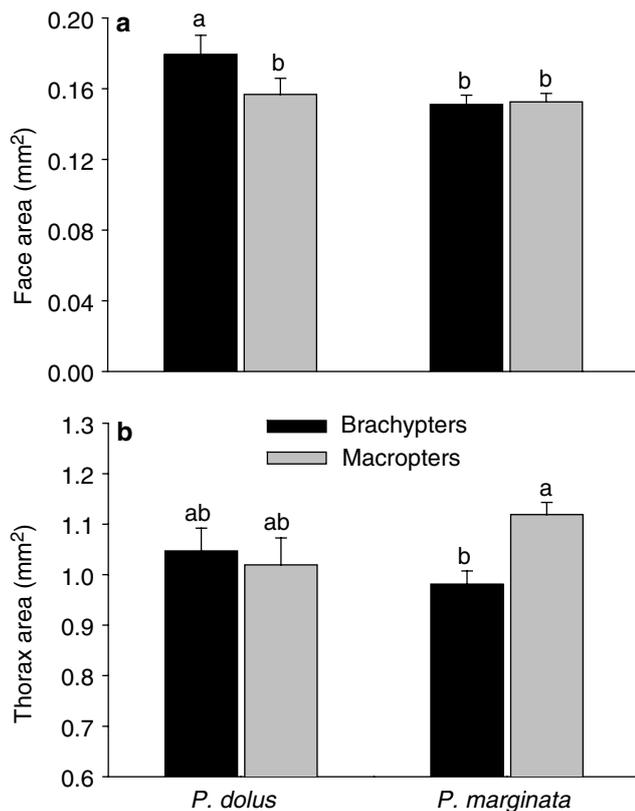


Fig. 1 a Face area (clypeus in mm²) and b thorax area (prothorax + mesothorax + metathorax in mm²) of the female wing forms (brachypters and macropters) of *Prokelisia dolus* and *Prokelisia marginata*. Least squares (LS) means (\pm SE) with the same letter are not significantly different ($P > 0.05$)

P. dolus, whereas in *P. marginata* macropters had consistently larger thoraces than brachypters (significant species \times wing form interaction; $F_{1,30} = 9.8$, $P = 0.004$; Fig. 1b). For both facial area and thorax area, tibia length was a significant covariate ($P = 0.0089$, $P = 0.001$, respectively).

Brachypters of *P. dolus* had heavier heads than macropters, a difference that was not evident between the wing forms of *P. marginata* (significant species \times wing form interaction; $F_{1,27} = 7.96$, $P = 0.009$; Fig. 2a). *P. marginata* had a heavier thorax (0.1 ± 0.004 mg) than *P. dolus* (0.09 ± 0.005 mg) when averaged across wing forms ($F_{1,30} = 3.95$, $P = 0.05$; Fig. 2b). Also, macropters (0.1 ± 0.005 mg) of both species had heavier thoraces than brachypters (0.08 ± 0.004 ; $F_{1,30} = 8.43$, $P = 0.007$), and there was no interactive effect of species and wing form on thorax dry mass ($F_{1,30} = 0.8$, $P = 0.4$; Fig. 2b). Tibia length was a significant covariate when examining head dry mass ($P = 0.009$) but not thorax dry mass ($P > 0.2$).

Indices of investment suggest differential allocation to flight and feeding morphology in the two *Prokelisia* species. As evidenced by the face-area:thorax-area index, *P. dolus* as a species exhibited a significantly greater investment in feeding (1.6 ± 0.004) than *P. marginata* (1.4 ± 0.003), which allocated more to flight

($F_{1,31} = 14.89$, $P = 0.0005$; Fig. 2c). This index also showed that brachypters allocated more to feeding morphology (0.17 ± 0.003) than macropters (0.14 ± 0.004) which invested more in flight ($F_{1,31} = 28.81$, $P < 0.0001$), a pattern that occurred for both *Prokelisia* species (no significant interactive effect of species and wing form; $F_{1,31} = 1.87$, $P = 0.2$). The head-dry mass:thorax-dry mass index indicated that brachypters of *P. dolus* allocated more to feeding than macropters of this species, whereas the wing forms of *P. marginata* showed no difference in allocation (significant species \times wing form interaction; $F_{1,26} = 4.42$, $P = 0.05$; Fig. 2d). Tibia length was not a significant covariate when analyzing the face-area:thorax-area index ($P = 0.15$) but was a significant covariate when evaluating the head-dry mass:thorax-dry mass index ($P = 0.03$).

Cibarial musculature

There was a significant effect of species on the cross-sectional area of cibarial muscles ($F_{1,28} = 9.62$, $P = 0.004$). *P. dolus*, the species with the greatest face area, had a greater cibarial muscle area (0.101 ± 0.004 mm²) than did *P. marginata* (0.082 ± 0.004 mm²), the narrow-faced species (Fig. 2e). Also, there was a non-significant trend for brachypters to have a larger cibarial muscle area than macropters (Fig. 2e). These data suggest that face area is positively correlated with the cross-sectional area of cibarial dilators.

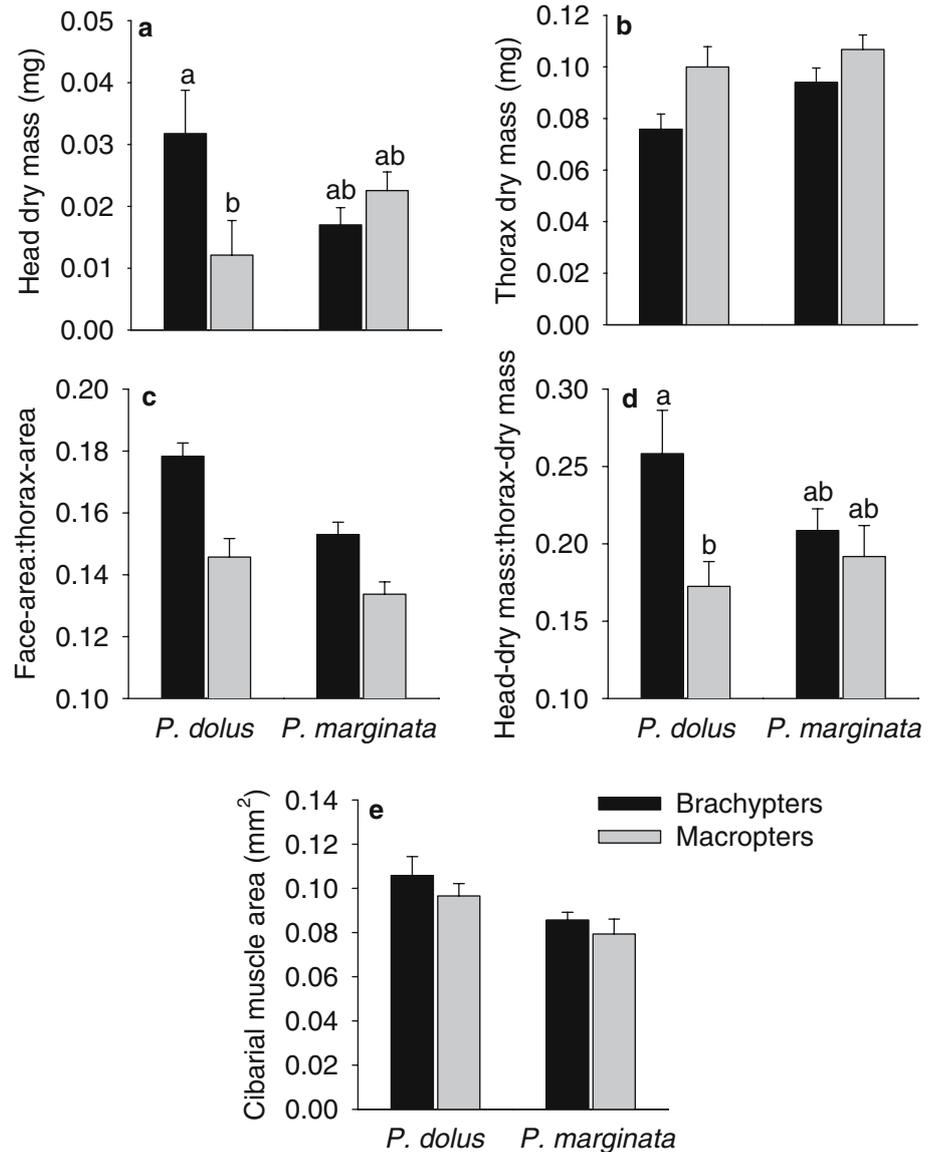
Honeydew production in planthoppers as an index of ingestion and feeding compensation

The honeydew excretion rate of *P. dolus* (0.56 ± 0.1 mg/48 h) was more than twice that for *P. marginata* (0.16 ± 0.03 mg/48 h; $F_{1,20,3} = 15.7$, $P = 0.0001$; Fig. 3a). However, honeydew production did not differ between the wing forms of *P. dolus* ($F_{1,24} = 0.26$, $P = 0.6$; Fig. 3b). Two facts suggest that honeydew excretion was accurately assessed. First, there was a significant increase in filter paper weight (the substrate on which honeydew collected) over the time course of the experiment in cages containing planthoppers ($F_{2,35} = 15.7$, $P < 0.0001$). Second, there was no change in filter paper weight in planthopper-free control cages ($t_{1,35} = 0.6$, $P = 0.6$). The nitrogen content for plants used in this experiment was $2.91 \pm 0.14\%$.

Discussion

Using wing-dimorphic *Prokelisia* planthoppers, the aim of this study was to investigate the existence of a trade-off between dispersal ability and a third-party trait, namely ingestion capacity. Overall, our results provide support for a species-level trade-off between the morphology associated with flight and that related to

Fig. 2 **a** Head dry mass (mg) and **b** thorax dry mass (mg) of the female wing forms (brachypters and macropters) of *P. dolus* and *P. marginata*. Indices of investment in feeding versus flight musculature for the female wing forms (brachypters and macropters) of *P. dolus* and *P. marginata* based on **c** face-area (mm²):thorax-area (mm²) and **d** head-dry mass (mg):thorax-dry mass (mg). **e** Cross-sectional area of cibarial muscle mass (mm²) of the female wing forms (brachypters and macropters) of *P. dolus* and *P. marginata*. **a, d** LS means (\pm SE) with the same letter are not significantly different ($P > 0.05$). **b, c, e** LS means for all species and wing forms are presented although the species by wing form interaction is not significant (see text for main effect means)



feeding. The head and thorax metrics used as surrogates for cibarial and flight musculature, and cibarial muscle area itself, indicated that *P. dolus* invests more in feeding than flight morphology, whereas *P. marginata* exhibits the reverse allocation pattern. Moreover, the same metrics suggest that investments in flight by macropters (heavy thoraces) occur at the expense of feeding morphology (light heads) and that the reverse pattern occurs in brachypters with relatively light thoraces and heavy heads compared to macropters (Fig. 2a, b). However, the allocation pattern is complex in that the discrepancy in head and thorax morphology between the wing forms is exaggerated differently between the two *Prokelisia* species. Although brachypters generally invested more in feeding morphology (larger faces and heavier heads) than macropters, this difference was relatively greater in *P. dolus* than in *P. marginata* (Fig. 2c, d). Likewise, macropters allocated more to flight (larger and heavier

thoraces) than brachypters, a difference that was generally greater in *P. marginata* than *P. dolus* (Figs. 1b, 2b). Thus, wing-form differences in head morphology, which are likely associated with feeding capability, are far greater in the sedentary species (>90% brachyptery), which must contend with on-site fluctuations in host plant quality. Similarly, wing form differences in thorax morphology are exaggerated in the migratory species, which copes with deteriorating plant nutrition via dispersal (Denno 1994; Denno et al. 2000). These latter data are consistent with the argument that selection for dispersal favors a positive correlation between the proportion of flight-capable adults in the population and the flight capability (investment in flight morphology) of the macropterous morph (Fairbairn and Desranleau 1987; Fairbairn and Butler 1990; Roff and Fairbairn 1991; Fairbairn 1994). Thus, macropters from predominantly macropterous species are better fliers

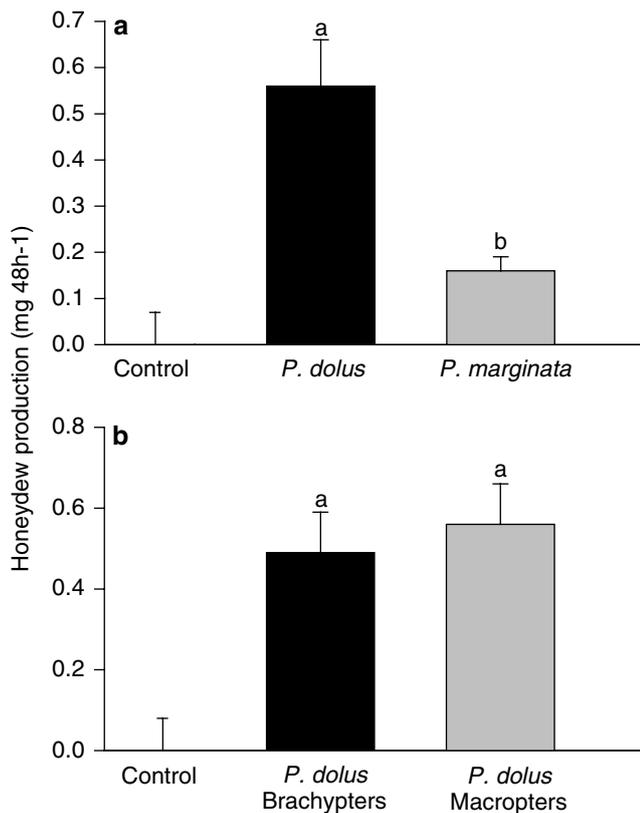


Fig. 3 **a** Honeydew production (mg/48 h) of the female macropters of *P. dolus* and *P. marginata*, and **b** of the female brachypters and macropters of *P. dolus*. Controls verify the absence of honeydew in planthopper-free treatments. LS means (\pm SE) with the same letter are not significantly different ($P > 0.05$)

than macropters from species that are largely brachypterous (Fairbairn and Desranleau 1987; Fairbairn and Butler 1990). Likewise, selection may favor a greater investment in the head morphology associated with feeding in the brachypterous morph of sedentary species, as our data suggests (Figs. 1a, 2a). Collectively, our data support the view that selection for a particular trait (e.g., dispersal) affects a suite of other associated physiological traits and patterns of allocation (Fairbairn and Desranleau 1987; Roff and Fairbairn 1991; Fairbairn 1994), and that the magnitude of the trade-off in a dichotomous trait is frequency dependent (Roff 1994).

One could argue that the head metrics we used as surrogates for cibarial musculature are in fact associated with other functions. The most obvious of these alternatives might be vision and associated eyes and optic lobes of the brain. Thus, the larger head of *P. dolus*, especially the brachypterous morph (Figs. 1a, 2a), may result from selective pressures associated with sight rather than feeding. All evidence points to the contrary, because large eyes and visual acuity in flies and bumble bees are associated with males that are extremely mobile and rely on dispersal to locate mates (Menzel et al. 1991; Hornstein et al. 2000). Accordingly, it should be the macropters of *P. marginata* that have the largest heads, which was not the case. Most convincing is that the

cross-sectional area of the cibarial muscles of *P. dolus* is larger than that for *P. marginata* (Fig. 2e). Thus, the heavy head and large facial area of *P. dolus* are indeed positively associated with a larger cibarial muscle mass. Regarding our use of thorax metrics as indicators of flight musculature, there is a positive association between thorax size and flight capability in many insects (Chai and Srygley 1990; Hill et al. 1999; Fric and Konvicka 2002). Thus, we are confident that the surrogates used to assess flight and feeding musculature were accurate indicators.

Based on its greater investment in cibarial musculature (Figs. 1, 2), the expectation was for *P. dolus* to exhibit a higher ingestion rate than *P. marginata*. Likewise, we expected brachypters to have a greater ingestion capacity than macropters. Because ingestion and excretion rates are highly correlated in phloem-feeding insects (Prestidge 1982; Brodbeck et al. 1996), we used honeydew production as an index of ingestion rate. In fact, *P. dolus* produced more than twice the amount of honeydew as *P. marginata* (Fig. 3a), suggesting a much higher ingestion capacity. At the species level, the greater ingestion capacity of *P. dolus* is likely related to its increased ability to survive, perform, and regulate its macronutrient composition on nutrient-deficient host plants compared to *P. marginata* (Huberty 2005). Notably, the species-specific difference in ingestion rate (honeydew production) was likely attributable to an allocational difference in cibarial musculature, with *P. dolus* having a greater cross-sectional area of cibarial muscles than *P. marginata* (Fig. 2e).

Within-species predictions regarding ingestion rate and feeding morphology were less well supported. For example, there was no difference in honeydew production between the wing forms of *P. dolus* (Fig. 3b), even though brachypters invest more in feeding morphology than macropters (head to thorax area and dry mass, Fig. 2c, d; trend toward greater cibarial muscle area, Fig. 2e). Admittedly, the nitrogen content of experimental plants was rather high ($\sim 3\%$), which may have masked any potential difference in ingestion rate between the wing forms that may be realized only on nitrogen-poor plants.

The physiology underlying life history trade-offs in wing-dimorphic insects has received much attention in recent years (Zera et al. 1998; Zera and Brink 2000; Zhao and Zera 2002). In the context of our study, life history strategies bear heavily on the ability of phytophagous insects to cope with the fundamental stoichiometric mismatch that exists between their nutrient composition and that of their host plants (Elser et al. 2000; Denno and Fagan 2003). Differences in dispersal ability may influence a species' response to nutrient limitation by virtue of constraints placed on third-party traits such as the ability to increase feeding rate during times of deteriorating plant quality. Notably, such a trade-off may set the stage for fundamental differences in population dynamics and competitive ability in sap-feeding insects. Nutrient demands can be met either by

dispersal to higher quality patches or by feeding compensation, but not both. Moreover, the competitive superiority of *P. dolus* over *P. marginata* is likely attributable to its greater commitment to cibarial muscle mass and increased ability to compensate for declining plant nitrogen via enhanced ingestion. For example, in mixed-species crowds, not only does *P. dolus* contribute more to feeding-induced declines in plant nitrogen but it also tolerates such declines better and experiences fewer performance and fitness costs (Olmstead et al. 1997; Denno et al. 2000). Thus, competitive superiority is associated with feeding compensation and tolerance of low plant nitrogen, whereas poor competitive ability is linked with intolerance of depleted nitrogen and high mobility (Denno et al. 2000). In fact, competitive dominance and dispersal ability are inversely related in several species of sap-feeders (Denno et al. 1995).

Further, because habitat persistence per se influences the dispersal strategies of planthoppers and many other sap-feeding insects (Denno et al. 1996, 2001), increased investment in dispersal may arise from selective pressures associated with the overall permanence of habitats (e.g., short-lived natural and agricultural habitats) as well as the combined need to colonize nitrogen-rich host plants and escape deteriorating plant patches by virtue of a “third-party trade-off” that precludes the sedentary option of feeding compensation. Thus, such species may be locked into a mobile life history strategy for satisfying their nitrogen demands and incur all the associated constraints of dispersal, which include penalties imposed on reproduction (Denno 1994; Zera and Denno 1997; Langellotto et al. 2000), competitive ability (Denno et al. 2000) and now feeding compensation. Resource allocation differences that underlie the strategies used by phytophagous insects to cope with nutrient limitation have rarely been identified. Toward this end, this study presents the first attempt to link dispersal and feeding investments as antagonistic traits within and between species.

Acknowledgements Larry Douglass, Irv Forseth, Bill Lamp, Charles Mitter, and Tony Zera provided comments on earlier drafts of this article, and we hope to have incorporated their many insightful suggestions. Ideas for this research were stimulated by our participation in an NCEAS workshop, Ecological Stoichiometry of Plant–Herbivore Interactions, organized by James Elser and Bill Fagan in 1999–2000. Mark Fox measured cibarial musculature and Kelly Enfield assessed honeydew production. This research was supported by an EPA Science to Achieve Results Graduate Fellowship to A. F. H. and NSF grants DEB-9903601 and DEB-0313903 to R. F. D.

References

- Ayres MP, Wilkens RT, Ruel JJ, Lombardero MJ, Vallery E (2000) Nitrogen budgets of phloem-feeding bark beetles with and without symbiotic fungi. *Ecology* 81:2198–2210
- Backus EA (1985) Anatomical and sensory mechanisms of leafhopper and planthopper feeding behavior. In: Nault LR, Rodriguez JG (eds) *The leafhoppers and planthoppers*. Wiley, New York, pp 163–194
- Barbosa P (1974) *Manual of basic techniques in insect histology*. Autumn, Amherst, Mass.
- Berryman AA (1988) *Dynamics of forest insect populations: patterns, causes, and implications*. Plenum, New York
- den Boer PJ (1981) On the survival of populations in a heterogeneous and variable environment. *Oecologia* 50:39–53
- Brodbeck BV, Andersen PC, Mizell RFI (1996) Utilization of primary nutrients by the polyphagous xylophage, *Homalodisca coagulata*, reared on a single host species. *Arch Insect Biochem Physiol* 32:65–83
- Cappuccino N, Price PW (1995) *Population dynamics: new approaches and synthesis*. Academic Press, London
- Chai P, Srygley RB (1990) Predation and the flight, morphology, and temperature of neotropical rainforest butterflies. *Am Nat* 135:748–765
- Cook A, Denno RF (1994) Planthopper/plant interactions: feeding behavior, plant nutrition, plant defense, and host plant specialization. In: Denno RF, Prefect TJ (eds) *Planthoppers: their ecology and management*. Chapman and Hall, New York, pp 114–139
- Denno RF (1994) Life history variation in planthoppers. In: Denno RF, Prefect TJ (eds) *Planthoppers: their ecology and management*. Chapman and Hall, New York, pp 163–215
- Denno RF, Fagan WF (2003) Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology* 84:2522–2531
- Denno RF, Olmstead KL, McCloud ES (1989) Reproductive cost of flight capability: a comparison of life history traits in wing dimorphic planthoppers. *Ecol Entomol* 14:31–44
- Denno RF, McClure MS, Ott JR (1995) Interspecific interactions in phytophagous insects: competition revisited and resurrected. *Annu Rev Entomol* 40:297–331
- Denno RF, Roderick GK, Olmstead KL, Doebel HG (1991) Density-related migration in planthoppers (Homoptera: Delphacidae): the role of habitat persistence. *Am Nat* 138:1513–1541
- Denno RF, Roderick GK, Peterson MA, Huberty AF, Doebel HG, Eubanks MD, Losey JE, Langellotto GA (1996) Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecol Monogr* 66:389–408
- Denno RF, Peterson MA, Gratton C, Cheng J, Langellotto GA, Huberty AF, Finke DL (2000) Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology* 81:1814–1827
- Denno RF, Gratton C, Langellotto GA (2001) Significance of habitat persistence and dimensionality in the evolution of insect dispersal strategies. In: Woiwod I, Reynolds DR, Thomas C (eds) *Insect movement: mechanisms and consequences*. CABI, London
- Denno RF, Gratton C, Peterson MA, Langellotto GA, Finke DL, Huberty AF (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* 83:1443–1458
- Denno RF, Gratton C, Dobel H, Finke DL (2003) Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology* 84:1032–1044
- Dixon AFG (1998) *Aphid ecology*. Blackie and Sons, London
- Elser JJ, Fagan WF, Denno RF, Dobberfuhl DR, Folarin A, Huberty A, Interlandi S, Kilham SS, McCauley E, Schulz KL, Siemann EH, Sterner RW (2000) Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408:578–580
- Fairbairn DJ (1994) Wing dimorphism and the migratory syndrome: correlated traits for migratory tendency in wing dimorphic insects. *Res Popul Ecol* 36:157–163
- Fairbairn D, Butler TC (1990) Correlated traits for migration in the Gerridae (Hemiptera: Heteroptera): a field test. *Ecol Entomol* 15:131–142
- Fairbairn D, Desranleau L (1987) Flight threshold, wing muscle histolysis, and alary polymorphism: correlated traits for dispersal tendency in the Gerridae. *Ecol Entomol* 12:13–24
- Fric Z, Konvicka M (2002) Generations of the polyphenic butterfly *Araschnia levana* differ in body design. *Evol Ecol Res* 4:1017–1032

- Gullen PJ, Cranston PS (2000) The insects: an outline of entomology. Blackwell Science, London
- Hanski I (1999) Metapopulation ecology. Oxford University Press, Oxford
- Hill JK, Thomas CD, Lewis OT (1999) Flight morphology in fragmented populations of a rare British butterfly, *Hesperia comma*. *Biol Conserv* 87:277–283
- Hornstein EP, O'Carroll DC, Anderson JC, Laughlin SB (2000) Sexual dimorphism matches photoreceptor performance to behavioural requirements. *Proc R Soc Lond B* 267:2111–2117
- Huberty AF (2005) Nutrient limitation and its consequences for performance and the homeostatic regulation of macronutrient composition in two phytophagous insects with divergent life history strategies. PhD dissertation, University of Maryland, Department of Entomology, College Park, Md.
- Huberty AF, Denno RF (2004) Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* 85:1383–1398
- Kisimoto R, Rosenberg J (1994) Long-distance migration in delphacid planthoppers. In: Denno RF, Prefect TJ (eds) *Planthoppers: their ecology and management*. Chapman and Hall, New York
- Langellotto GA, Denno RF (2001) Benefits of dispersal in patchy environments: mate location by males of a wing-dimorphic insect. *Ecology* 82:1870–1878
- Langellotto GA, Denno RF, Ott JR (2000) A trade-off between flight capability and reproduction in males of a wing-dimorphic insect. *Ecology* 81:865–875
- Lavoie B, Oberhauser KS (2004) Compensatory feeding in *Danaus plexippus* (Lepidoptera: Nymphalidae) in response to variation in host plant quality. *Environ Entomol* 33:1062–1069
- Mattson WJ (1980) Herbivory in relation to plant nitrogen content. *Annu Rev Ecol Syst* 11:119–161
- McNeill S, Prestidge RA (1982) Plant nutritional strategies and insect herbivore community dynamics. In: Visser JH, Minks AK (eds) *Proceedings of the 5th International Symposium on Insect-Plant relationships*. Center for Agricultural Publishing and Documentation, Wageningen, pp 225–235
- McNeill S, Southwood TRE (1978) The role of nitrogen in the development of insect/plant relationships. In: Harborne JB (ed) *Biochemical aspects of plant and animal coevolution*. Academic Press, New York, pp 77–98
- Menzel JG, Wunderer H, Stavenga DG (1991) Functional morphology of the divided compound eye of the honeybee drone (*Apis mellifera*). *Tissue Cell* 23:525–535
- Mun JH, Song YH, Heong KL, Roderick GK (1999) Genetic variation among Asian populations of rice planthoppers, *Nilaparvata lugens* and *Sogatella furcifera* (Hemiptera: Delphacidae): mitochondrial DNA sequences. *Bull Entomol Res* 6:245–253
- Olmstead KL, Denno RF, Morton TC, Romeo JT (1997) Influence of *Prokelisia* planthoppers on amino acid composition and growth of *Spartina alterniflora*. *J Chem Ecol* 23:303–321
- Pedgely DE (1993) Managing migratory insect pests—a review. *Int J Pest Manage* 1:3–12
- Peterson MA, Denno RF (1997) The influence of intraspecific variation in dispersal strategies on the genetic structure of planthopper populations. *Evolution* 51:1189–1206
- Peterson MA, Denno RF (1998) The influence of dispersal and diet breadth on patterns of genetic isolation by distance in phytophagous insects. *Am Nat* 152:428–446
- Prestidge RA (1982) Instar duration, adult consumption, oviposition and nitrogen utilization efficiencies of leafhoppers feeding on different quality food (Auchenorrhyncha: Homoptera). *Ecol Entomol* 7:91–101
- Raubenheimer D, Simpson SJ (1993) The geometry of compensatory feeding in the locust. *Anim Behav* 45:953–964
- Roff DA (1986) The evolution of wing dimorphism in insects. *Evolution* 40:1009–1020
- Roff DA (1994) Evidence that the magnitude of the trade-off in a dichotomous trait is frequency dependent. *Evolution* 48:1650–1656
- Roff DA, Fairbairn DJ (1991) Wing dimorphisms and the evolution of migratory polymorphisms among the Insecta. *Am Zool* 31:243–251
- SAS (2002) *SAS/STAT user's guide*, release 8.2. SAS Institute, Cary, N.C.
- Schade JD, Kyle M, Hobbie SE, Fagan WF, Elser JJ (2003) Stoichiometric tracking of soil nutrients by a desert insect herbivore. *Ecol Lett* 6:96–101
- Slanksy F, Feeny P (1977) Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. *Ecol Monogr* 47:209–228
- Tanaka S (1993) Allocation of resources to egg reproduction and flight muscle development in a wing dimorphic cricket, *Modicogryllus confirmatus*. *J Insect Physiol* 39:493–498
- White TCR (1993) The inadequate environment: nitrogen and the abundance of animals. Springer, Berlin Heidelberg New York
- Youssefi F, Brown PH, Weinbaum SA (2000) Relationship between tree nitrogen status, xylem, and phloem sap amino acid concentrations, and apparent soil nitrogen uptake by almond trees (*Prunus dulcis*). *J Hortic Sci Biotechnol* 75:62–68
- Zera AJ, Brink T (2000) Nutrient absorption and utilization by wing and flight muscle morphs of the cricket *Gryllus firmus*: implications for the trade-off between flight capability and early reproduction. *J Insect Physiol* 46:1207–1218
- Zera AJ, Denno RF (1997) Physiology and ecology of dispersal polymorphism in insects. *Annu Rev Entomol* 42:207–230
- Zera AJ, Harshman LG (2001) The physiology of life history trade-offs in animals. *Annu Rev Ecol Syst* 32:95–126
- Zera AJ, Potts J, Kobus K (1998) The physiology of life history trade-offs: experimental analysis of a hormonally induced life history trade-off in *Gryllus assimilis*. *Am Nat* 152:7–23
- Zhao Z, Zera AJ (2002) Differential lipid biosynthesis underlies a trade-off between reproduction and flight-capability in a wing-polymorphic cricket. *Proc Natl Acad Sci USA* 99: 16829–16834