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Differential allocation of resources underlies the dispersal-reproduction trade-off in the wing-dimorphic cricket, *Gryllus rubens*

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Abstract

The cricket, *Gryllus rubens* (Orthoptera, Gryllidae), exists in natural populations as either a fully-winged (LW), flight-capable morph or as a short-winged (SW) morph that cannot fly. The SW morph is substantially more fecund than the LW morph. In this study we report on the physiological basis of this trade-off between flight capability and fecundity. Results from gravimetric feeding trials indicate that LW and SW morphs are equivalent in their consumption and digestion of food. However, during the adult stage, the LW morph is less efficient in converting assimilated nutrients into biomass. This may be a consequence of the respired loss of assimilated nutrients due to the maintenance of functional flight muscles in the LW morph. In both morphs the gross biomass devoted to flight muscles does not change significantly during the first 14 days of adult growth while there is a significant biomass gain in ovarian tissue mass during the same period. SW morphs have vestigial flight muscles and gain substantially more ovarian mass relative to the LW morphs. These data are consistent with a trade-off between flight muscle maintenance in the LW morph and ovarian growth in the SW form. This is the first evidence for a life-history trade-off that has a physiological basis which is limited to the allocation of acquired and assimilated nutrients within the organism.

Keywords: *Gryllus rubens*, trade-off, resource allocation, wing polymorphism, flight-oogenesis syndrome

Life history evolution has been a major focus of ecological and evolutionary research during the past two decades (Stearns 1976; Partridge and Harvey 1988). Numerous studies have documented negative associations between life-history characteristics such as elevated reproductive effort and reduced survivorship. These negative associations are referred to as trade-offs (Reznick 1985; Stearns 1989) and a major unsolved issue in life-history research concerns the factors responsible for these negative associations. Many authors have proposed that life-history trade-offs at the demographic level are the consequence of trade-offs of resources at the physiological level. That is, if resources are limited, evolutionary alterations that result in an increased allocation to one trait result in a decreased allocation to another or others. This view has been put forward at least as a partial explanation for trade-offs such as those between reproductive effort and somatic growth (Fisher 1930; Williams 1969; Calow 1979; Pianka 1981; Reekie and Bazzaz 1987).

In order to fully understand life-history trade-offs it is necessary to have information on the physiological basis of resource allocation to life history traits (Partridge and Harvey 1988; Stearns 1990). Despite considerable discus-

sion in the literature, there are few studies that have directly documented that negative trait associations result from a trade-off of resources between the tissues and organ systems that underlie these traits (Partridge and Harvey 1988; Parker and Maynard-Smith 1990). A few studies have documented a negative association between masses of somatic and reproductive tissues (Ballinger et al. 1981; Vitt and Congdon 1978; Karlsson and Wickmann 1990). However, in these cases the resource base (absorbed nutrients) for the organisms being compared has generally been ignored. Without information on the internal resource base, it cannot be determined if negative trait associations result from an internal shift in resource allocation rather than from alterations in food consumption or digestion (resource acquisition). Indeed, several field studies have identified positive associations between reproductive effort and growth that are thought to result from differences in resource availability and acquisition (Haukioja and Hakala 1978; Tuomi et al. 1983).

In this study we use wing polymorphism in the cricket *Gryllus rubens* to investigate the extent to which a trade-off of resources at the physiological level underlies the trade-off of life-history characteristics important at the demographic level (fecundity vs. dispersal

capability). Wing polymorphism is a common feature of many insects and has evolved independently in each of the major insect orders (Harrison 1980; Roff 1986). *Gryllus rubens*, like other wing dimorphic insects, exists as alternate fully-winged, flight-capable and short-winged, flightless morphs. The flightless morph exhibits substantially elevated fecundity (25% during the first three weeks of adulthood) compared with the dispersing morph (Zera and Rankin 1989). Wing polymorphism has been extensively studied in the context of the trade-off between resources devoted to dispersal versus reproduction (Harrison 1980; Penner 1985; Roff 1986). The polymorphism is thought to represent the most extreme case of the antagonism between these two life-history characteristics (flight-oogenesis syndrome; Johnson 1969) where selection for elevated fecundity has resulted in a phenotype in which the flight apparatus (wings, flight muscle, flight fuels) does not fully develop. This blockage allows resources that would have been allocated to growth/maintenance of the flight apparatus to be allocated to egg production resulting in a more fecund short-winged (or wingless) morph. Although there is considerable indirect evidence to support this hypothesis (reviewed in Penner 1985), no studies have directly documented that such is the case. Importantly, no studies have investigated the alternate possibility that the elevated reproductive effort in the flightless morph simply results from enhanced nutrient acquisition (consumption and assimilation) rather than a differential allocation of assimilated resources.

The present study had two major goals. The first was to determine if morphs operate on the same resource base, that is, to determine if long-winged and short-winged morphs consume and assimilate the same amount of nutrients. The second goal was to determine if resource allocation differed in the two morphs. Specifically, we test the hypothesis that conversion of nutrients to biomass is greater in the flightless (short-winged) morph relative to the long-winged morph on the assumption that the flightless (short winged) morph does not have to pay the cost of flight capability (growth and maintenance of wings/flight muscles, synthesis of flight fuels).

Materials and methods

Insects

Gryllus rubens used in this study were taken from stocks that are nearly pure breeding for long (LW) or short-wings (SW). These are the same stocks that have been used in previous endocrine studies of wing morph determination and morph-specific fecundity [see Zera and Tiebel (1989) and Zera and Tobe (1990) for additional stock characteristics]. All LW and a few SW individuals came from the LW stock while most (76%) SW individuals came from the SW stock. No differences between SW individuals from the SW versus the LW stocks were detected in this or previous (Zera and Tiebel 1989) studies and so our results exclusively concern comparisons between morph classes. Stocks from which crickets were taken were maintained under standard con-

ditions (60 crickets/10 gal aquarium, 16 h :8 h light :dark photoperiod, 28 ° C, modified *Manduca* diet; see Zera and Tobe, 1990). Crickets were checked for molting into the last stadium or adult stage at 24 h intervals.

Feeding experiments

Feeding trials were conducted to estimate nutritional indices on adult and last stadium, LW and SW female *G. rubens*. In one feeding trial, nutritional indices were measured for the entire last stadium. The experiment was started with 45 individuals for which a full data set was obtained for 41. Of these individuals, nutritional indices were also measured on 8 LW and 9 SW adult crickets during the first 14 days after adult eclosion (referred to as first experiment on adults). In a second experiment on adults, an additional 7 LW and 18 SW females were also studied during the first 14 days after adult eclosion. Nutritional indices were measured during the first two weeks of adulthood since this is the time when morphs differ dramatically in egg production (Zera and Rankin 1989). In all feeding trials crickets were fed the same standard diet used in the rearing of *G. rubens* (Zera and Tiebel, 1988).

Newly molted crickets were withdrawn from group-reared stocks at the beginning of the feeding trials and placed individually in 16 oz containers with a fresh piece of food. To ensure normal egg development in adults, crickets were mated by placing them in a separate container without food with 2-5 males for 1-4 hours on each of the first four days of adulthood. In both experiments, fresh moist gauze was placed in the 16 oz container as an oviposition substrate, beginning on the fifth day of the experiment, and was changed every other day until the termination of the experiment. Gauze was removed and any eggs laid were counted using a dissecting microscope.

Nutritional indices. Gravimetric nutritional index experiments (Waldbauer 1968) were conducted on individually housed females of each morph. Crickets were maintained in 16 oz containers kept in an incubator at 28 ° C with a 16 h:8 h light:dark photoregime. At the beginning of each experiment, each individual cricket was weighed and placed in a container with a pre-weighed piece of moist diet. Every other day (i) the cricket was weighed, (ii) frass and the remaining food were removed and separately lyophilized and dry-weighed, and (iii) fresh pre-weighed food was provided. A fresh weight versus dry weight calibration curve was constructed to estimate the dry weight of the food provided to the crickets. The same batch of food was used within each experiment and care was taken to store it refrigerated and without loss of water. Water contents of the food, measured directly during the experiment or calculated from the weights of dry ingredients and added water, agreed with each other to within 0.5%. For every two day feeding period the difference in dry weight between the food provided and that remaining was calculated. Food consumption (CR, Table 1) over the whole experiment was estimated as the sum of these differences. Final instars consumed 45% of the added food while adults consumed 55% of the added diet. The use of a moist diet, together with the fact that frass is a darker color than the diet, allowed the accurate separation of food and frass. By summing the total (lyophilized) weight of frass collected per individual, the approximate digestibility of food (AD, Table 1) was estimated on a dry weight basis. Samples of dry food and frass were also analyzed for their total nitrogen content by the Kjeldahl method to estimate AD on a nitrogen basis. In order to determine growth (GR) and ECD values (see Table 1), a separate but identically fed group of individuals from the same stocks was weighed alive and then after lyophilization. To span the weight range of the feeding trials, both adult and final instar crickets were used. This curve was then used to estimate the dry weights of the crickets in the experiment from their live weights, so as to estimate their dry weight gain (GR) during the experiment and their ECD.

Table 1. Equations defining terms used to analyze the consumption and utilization of food, adapted from Waldbauer (1968)

1. Growth (GR) = Weight Gain of cricket (during the experiment)
2. Consumption (CR) = Feed Ingested (during the experiment)
3. Efficiency of conversion of ingested food to body matter (ECI) is calculated as:

$$ECI = (\text{Weight gain} / \text{Feed Ingested}) \times 100\%$$
 Where all weights are made on a dry weight basis GR can be expressed in terms of CR and ECI, i.e., $GR = CR \times ECI$.
4. Approximate Digestibility (AD) is calculated as:

$$AD = (\text{Weight of Feed Ingested} - \text{Weight of Feces}) \div \text{Weight of Feed Ingested} \times 100\%$$
5. Efficiency of conversion of digested food to body matter (ECD) is calculated as:

$$ECD = \text{Weight Gain} \div (\text{Weight of Feed Ingested} - \text{Weight of Feces}) \times 100\%$$
 Where all weights are made on a dry weight basis ECI can be expressed in terms of AD and ECD, i.e., $ECI = AD \times ECD$ and thus $GR = CR \times AD \times ECD$.

Equations defining terms used to analyze the consumption and utilization of nitrogen are similar, thus...

6. $AD(N)^a = (\text{Nitrogen Ingested} - \text{Nitrogen in Feces}) \div \text{Nitrogen Ingested} \times 100\%$
7. Relative growth during the experiment (RGR) can be defined as $GR / \text{initial body weight}$.

^a Termed Nitrogen Utilization Efficiency (NUE) by Slansky and Feeny (1977)

Statistical analyses

Means and standard errors are presented for all measurements made directly and for the nutritional indices calculated from them. Because of the potential for the magnification of experimental errors in calculated ratios (Schmidt and Reese, 1986) we have followed the analysis of covariance approach recently suggested by Raubenheimer and Simpson (1992) in hypothesis testing, rather than the direct analysis of the indices by ANOVA. In essence, the numerator of each index is used as the dependent variable in the ANCOVA and the denominator is used as the covariate. We have also accepted the recommendation of Raubenheimer and Simpson (1992) that initial body weight be used as the covariate in the analysis for relative growth.

Prior to each ANCOVA a preliminary analysis was carried out to check for the absence of any interaction between the covariate and treatment (morph). None was found in any analysis. The results of the feeding trial on final instars were analyzed with individuals classified according to the adult morph into which the final instars moulted. The two separate blocks of experiments on adults were analyzed by a two way analysis, with the factors being both the adult morphs (SW, LW) and the two separate experiments. ANOVAs were used for the analysis of GR, CR and Initial body mass which are not ratios (see Table 1). Analyses were performed using DOS SYSTAT 5.1.

Dissections

At the conclusion of the feeding trials on adults (day-14), crickets were weighed and ovaries were dissected and weighed. Two additional groups of females of similar body mass were raised under the same conditions as the crickets used to estimate nutritional indices. In one group, ovaries and flight muscles were dissected out within one day after the adult moult (day-0) while in the second group flight muscles were dissected on day-14. Flight muscles (dorso-longitudinal and dorso-ventral muscles; see Figure 1 of Srihari et al. 1975) were dissected free from fat bodies and other tissues. Flight muscles plus a small amount of attached thoracic cuticle were weighed, muscle tissues were dissolved in hot aqueous KOH, the remaining cuticle was reweighed and muscle weight was determined by subtraction. Using the data for day-14 adults, a regression of flight muscle mass on cricket live weight was constructed for each morph. These data were used to estimate the flight muscle mass in the crickets from the feeding trial (day-14 crickets). Flight muscle and ovarian masses for day-0 crickets

were scaled to the initial masses of the day-14 crickets of the feeding trial.

To verify that the aqueous KOH treatment did not dissolve a significant portion of the attached thoracic cuticle leading to an overestimate of flight muscle mass, cuticle plus flight muscles were weighed and the muscles were thoroughly dissected away from a group of 7 LW and 7 SW females. The cuticle was then weighed, subjected to the KOH treatment and reweighed. Muscle mass estimated by the standard KOH treatment was greater than that estimated by direct dissection by only $5.2 \pm 0.6\%$. In a final experiment, the dry weight of a sample of counted and newly laid cricket eggs was obtained in order to convert the numbers of eggs oviposited by individual crickets in the feeding trials into dry weights.

Results

Feeding trials

The results of the gravimetric feeding trials on adults are presented in Table 2 and are considered first. SW females weighed slightly less than their LW counterparts at eclosion (see Table 2). However, during the feeding trials, SW individuals gained significantly more weight than LW individuals on both an absolute (GR) and a relative basis (RGR). This difference in biomass gain is seen irrespective of whether the weight gain of the insect is considered alone or in combination with the weight of eggs laid (see Table 2).

The food consumption (CR) by both morphs is very close and not significantly different (see Table 2). This is also the case for the approximate digestibility (AD) of the diet (see Table 2). Total nitrogen analyses of the freeze-dried frass showed a nitrogen content of 5.3% ($\pm 0.1\%$) for both morphs. Thus, the absence of any significant difference between morphs for the approximate digestibility of their diet (AD) is true on a nitrogen basis as well as on a dry weight basis. In summary, consumption and digestion are indistinguishable between morphs and so these factors do not appear to be responsible for differences in growth (GR) seen in Table 2.

Table 2. Growth analysis of female crickets on a dry weight basis

Measurement ^a	Mean (SE)		<i>p</i> ^b
	Short Winged	Long Winged	
I. Adults			
GR	52 mg (4)	36 mg (5)	0.009**
GR (plus eggs)	57 mg (4)	42 mg (5)	0.021''
CR	1057 mg (58)	1080 mg (73)	0.540
AD	70% (1.8)	68% (2.2)	0.644
ECD	8.7% (0.8)	5.2% (0.9)	0.002***
ECD (plus eggs)	9.6% (0.9)	5.9% (0.8)	0.002***
Initial Mass	128 mg (3)	140 mg (4)	0.030*
RGR	40% (2.8)	27% (3.5)	0.022**
II. Final Instar			
GR	50 mg (2)	56 mg (3)	0.145
CR	1304 mg (169)	1170 mg (196)	0.606
AD	82% (2.9)	75% (3.4)	0.811
ECD	7.5% (1.9)	12.2% (2.2)	0.116
RGR	78% (5.5)	87% (6.6)	0.153

^a See Table 1 for explanation of terms and formulae used in calculations.

^b Probabilities for between morph differences were obtained from ANOVAs for GR, Initial Mass and CR and ANCOVAs for index data, see "statistical analyses" in methods.

In contrast, the efficiency with which assimilated nutrients were converted to new biomass (ECD) by adults was substantially and significantly greater in the SW morph (see Table 2). As with GR, this difference in ECD holds true irrespective of whether the mass of oviposited eggs is or is not included in the biomass gained. The only numerical effect of including the mass of eggs laid is to increase both values for ECD as would be expected. In summary, morph specific differences in ECD, but not CR or AD, account for differences in GR in adults.

Results presented above (Table 2) are means resulting from the ANCOVA of data pooled from the two feeding trials. An example ANCOVA table for one of these analyses is given in Table 3. No significant interactions between wing morph and experiment were observed for any of the nutritional indices, i.e. differences between morphs were in the same direction in both experiments.

Table 4. Biomass^a partition between ovaries and wing muscle

Measurement	Mean ^b (SE)		<i>p</i> ^c
	Short Winged	Long Winged	
I. Measurements on 14 day old adults			
Whole body mass	569 mg (22)	553 mg (26)	0.616
Ovary mass	172 mg (12)	105 mg (15)	0.002***
Wing muscle mass ^d	31 mg (0.5)	55 mg (0.6)	0.000***
II. Measurements on newly moulted adults (Day-0)			
Ovary mass	5.4 (0.48)	5.0 (0.66)	0.409
Wing muscle mass	23.6 (1.6)	52.9 (2.9)	0.000***

^a Weighed at time of dissection

^{b,c} Least squared means and probabilities from two way analyses of variance (see Table 3)

^d Estimated from regression of muscle mass against body weight for other individuals of the same morph and from the same stock

Table 3. Example ANCOVA for the analysis of data for adults obtained from the two experiments on LW and SW morphs

Dependent variable: Weight Gain Covariate: (Food Ingested-Frass Produced)					
Source	SSQ	Df	MS	F-ratio	<i>p</i>
Morph	0.004	1	0.004	11.678	0.002
Experiment	0.003	1	0.003	11.258	0.002
Expt * Morph	0.000	1	0.000	0.625	0.435
Covariate	0.001	1	0.000	0.071	0.792
Error	0.011	34	0.000		

However, the magnitude of some indices (AD, ECD and initial differences in biomass) did vary significantly between the two experiments. Food consumption (CR), final weights and ovarian masses did not differ between experiments. The reasons for the variation between experiments are presently unknown. These differences do not affect conclusions about morph-specific differences in nutritional indices.

No significant differences were observed between last-stadium morphs for any of the factors studied (GR, CR, AD and ECD; see Table 2). Most importantly, the mean dry weight gains during the final instar (GR) were similar and since the last stadium is of equal duration in both morphs these values represent equal growth. Some differences between adults and final instars can be seen by comparison with Table 2. For instance RGR is higher in last stadium rather than in adults and this is not unusual (Waldbauer, 1968).

Dissections

Ovarian and flight muscle masses for day-14 and newly molted (day-0) LW and SW adults are given in Table 4. Ovaries were small and did not differ significantly in newly molted adults but were significantly higher in day-14 SW vs. LW adults. The proportion of whole body mass due to ovaries was also significantly higher (SW 30%, LW 19%; $p < 0.01$). Substantial qualitative differences were seen in the flight muscles. Muscles in the LW morph were pink in color, indicative of functional flight

muscle, while in the SW morph the muscles were white-translucent and substantially smaller in size, indicative of non-functional muscles. Estimated flight muscle mass was significantly greater in the LW versus the SW morph both on day-0 and on day-14 (Table 4). Muscle masses were approximately the same on days 0 and 14 within each morph, indicating no substantial change in mass with time. In contrast there was a substantial increase in ovarian mass in both LW and SW females.

Discussion

These results have important consequences with respect to the physiological basis of the trade-off between flight capability and reproduction in insects in general, and in wing polymorphic insects in particular. The two most important results of the feeding trials are seen for adults. First, individuals of both morphs operate on the same basis of assimilated resources even though they grow differently (differences in GR but not CR or AD, see Table 2). Second, the different growth rates of the two morphs are explicable in terms of differences in ECD and thus metabolic differences between the two morphs. There were no detectable between-morph differences in these nutritional indices for final instar crickets.

During the past two decades, numerous studies have documented the negative association between reproduction and dispersal (termed the flight-oogenesis syndrome; Johnson 1969; Penner 1985). In many monomorphic winged species, these two processes both occur during the adult stage but are temporally separated. For example, flight muscles often histolyze after dispersal, prior to the onset of egg maturation (Andersen 1973; Penner 1985). In some species, the muscles regenerate after reproduction prior to another round of dispersal (reviewed in Penner, 1985). Wing polymorphism is the most dramatic case of this negative interaction between reproduction and dispersal where the more fecund flightless morph does not even produce a functional flight apparatus (wings, flight muscles).

The dramatic association between lack of a flight apparatus and increased egg output in wing polymorphic species has given rise to widespread speculation concerning the causal linkage between these two traits. Numerous workers have speculated that this negative association is an evolved adaptation which permits the differential allocation of limited resources to either flight muscle growth and maintenance or egg production in alternate morphs (reviewed in Johnson 1969; Harrison 1980; Penner 1985; Roff 1986). However, no studies have directly tested this evolutionary re-allocation hypothesis. The energetic content of flight muscle growth and maintenance relative to egg production has yet to be quantified and so it is unclear to what extent a reallocation of resources from flight muscles to eggs can even account for the substantially greater number of eggs produced in the flightless morph.

Moreover, an alternate non-adaptive explanation for the negative flight-reproduction association can be postulated which does not involve any differential allocation of resources. Egg maturation and ovarian development are generally potentiated by the insect gonadotrophin, juvenile hormone, while flight muscle and wing development are negatively affected by this hormone (Koppe et al. 1985; Penner 1985; Hardie and Lees 1985; Zera and Tobe 1990). The negative association between flight capability and reproduction in wing polymorphic insects may simply be due to a physiological constraint due to a regulatory hormone that positively affects reproduction and negatively affects flight capability. Natural selection for increased fecundity may have resulted in indirect selection on wing and flight muscle development giving rise to a highly-fecund but flightless morph. There may be no significant or direct allocation of resources from flight muscle to eggs. It is possible that the elevated fecundity of the SW morph could be largely due to increased food consumption (CR) or assimilation (AD) over and above that in the LW morph.

Our results are important in that they discount this last possibility for adults during the first 14 days after molting. It does not appear to be the case that the evolution of a high fecundity morph has come about by altered resource acquisition (CR) or assimilation (AD).

When growth (GR) is considered along with the resource base on which growth is achieved, then the conversion efficiency ECD can be considered as an indicator of the fate of acquired nutrients. The observation that SW females attain greater biomass than their LW counterparts on the same amount of nutritional resources during the same period of time (Table 2) demonstrates that SW females more efficiently convert ingested nutrients into biomass (i.e. they have a higher ECD).

The differences in ECD between the wing morphs documents that there is differential allocation of ingested nutrients (i.e. a trade-off of resources) between the morphs, with the SW form allocating more nutrients to biomass. This is the first direct evidence that the negative association between dispersal capability and reproductive effort in wing polymorphic insects is in fact underlain by a trade-off of resources at the physiological level. The lack of morph specific differences in ECD in the final instars may indicate that the cost of maintenance of flight muscle in adults is greater than the costs of muscle growth in this juvenile stage.

The results discussed so far have been obtained from the analysis of a gravimetric feeding trial using nutritional indices following Waldbauer (1968). While this approach has become standard, there are certain pitfalls and limitations to the technique that need to be addressed (Schmidt and Reese 1986).

Systematic errors in the determination of food consumption, especially from the consumption of a low proportion of the food ration and the incorrect estimation of

its dry weight, can lead to large errors in estimates of the nutritional indices (Schmidt and Reese, 1986). However, this should not compromise the current study because experiments were performed simultaneously on each morph and so any systematic errors in conditions will apply to each morph equally. Furthermore we have limited the major sources of these errors by providing a small ration and by preventing the desiccation of the food. Moreover, we have avoided the numerical problems inherent in working with indices (ratios) by using the analysis of covariance approach (Raubenheimer and Simpson, 1992) in our statistical analyses. In exploring this approach, we found that it yielded the same pattern of significant results when compared to ANOVAs calculated using the nutritional indices as the dependent variables.

We conducted this work with the a priori expectation that the possession of a functional flight apparatus might give rise to a between-morph difference in ECD. While the observed ECD difference is consistent with this hypothesis, it is not definitive evidence. Specifically the forgoing results only show a difference in ECD but do not directly identify the tissues responsible for the differences between morphs. For example, if the SW morph diverts resources to metabolically inactive stored reserves (e.g. in eggs) that would have otherwise have gone to flight muscle, then ECD would also be expected to relatively be high in this morph. The requirement for synthesizing large amounts of energetically-expensive lipid flight fuels by LW females may also account for the lower ECD in that morph. Most orthopterans utilize energetically-expensive lipids for dispersal (Beenackers et al. 1981) and we have recently documented that in a related species, *G. firmis*, the LW morph has a significantly greater mass of triglycerides (flight fuels) than the SW morph (Zera and Mole, unpublished). Further experiments are underway to address these possibilities for *G. rubens* by the analysis of the chemical constituents of the various tissues of crickets during their adult and final instars. Respiratory rate measurements on specific tissues are also planned to test our underlying assumption that adult flight muscle will have a high maintenance respiration rate, in proportion to its mass.

If it is assumed that functional flight muscles in adults have a high respiratory cost, then data obtained from the dissections are at least consistent with the hypothesis that there is a trade-off between flight muscle maintenance in the LW morph and egg production in the SW morph. First, flight musculature is significantly larger in the LW versus SW morph and second there is no substantial change (growth or histolysis) in muscle mass between newly hatched and 14 day old adults. Our qualitative observations on wing muscle color indicate that only the LW flight muscle is functional. Furthermore, previous studies on this population of *G. rubens* have documented that only LW adults are capable of flight (Zera and Rankin 1989). These results are con-

sistent with the idea that flight muscle maintenance is greater in LW versus SW morphs at least during the first 14 days of adult life. In contrast to flight muscles which do not change during the adult stage, there is substantial ovarian growth and development during this period and SW ovaries grow much larger than those of LW individuals. Thus ovarian development can be conceived to compete for resources with flight muscle maintenance but not with flight muscle growth.

For wing polymorphic insects, the physiological basis of the trade off between dispersal capability and reproductive effort has been discussed, both in the above scenario and by others (Harrison 1980; Roff 1986; Penner 1985), solely in terms of the exchange of resources between two components: the flight apparatus and the ovaries. However, the trade-off need not necessarily be so simple, and may involve the exchange of resources from other organismal compartments. For example, the energetic cost of the increased reproductive output of the SW morph may far outweigh the gain of resources reallocated from flight muscle maintenance. In such a situation, reserves could conceivably be drawn into egg production from storage or other non-flight, non-reproductive tissues. Furthermore, the growth and development of the flight muscles, which occurs in the final instar prior to ovarian development, adds a temporal complication to the trade-off. This is because any resources diverted from wing muscle development in the final instar of the SW morph would require storage until the onset of ovarian development at the adult stage.

In overview, the present results indicating ECD and not AD or CR differences between morphs indicate an internal physiological difference between the morphs. These data are consistent with a relatively simple physiological trade-off within the adult stage, where lower ovarian growth in the LW morph is a consequence of the cost of flight muscle maintenance. However, we cannot rule out more complex scenarios such as those discussed above. We believe this to be the first evidence for a direct relationship between a trade-off at the physiological level and one at the level of organismal characters underlying life-history differences.

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