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A Change in Grain? Diet Induced Plasticity in the Generalist Grasshopper Melanoplus differentialis

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A Change in Grain? Diet Induced Plasticity in the Generalist Grasshopper Melanoplus differentialis

A Thesis

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Table of Contents

List of Figures

Abstract:

Phenotypic plasticity is favored in heterogeneous environments in which alternative phenotypes can exploit alternative resources. However, it's not clear whether phenotypic plasticity is useful in environments that become more homogenous over an organism's life cycle. I studied a population of grasshopper *Melanoplus differentialis* that experiences high resource diversity as nymphs but low resource diversity as adults to determine if individuals can undergo diet-induced morphological plasticity in head shape to increase biting ability and ingestion of hard diets. Insects on a soft diet were larger and had greater bite force than those on a hard diet. Head structures related to chewing ability changed shape with mass, heads became taller and narrower. Scaling relationships among body parts suggested that there wasn't evidence for tradeoff in allocation to chewing vs. locomotor performance. Results are consistent with the idea that essential adult feeding morphology constrains the advantage of plasticity in feeding structures among nymphs.

Introduction:

Genetic adaptation and phenotypic plasticity represent alternative evolutionary outcomes of selection in stable and variable environments (West-Eberhard 2003). Adaptation is favored when organisms encounter consistent directional or stabilizing selection, and optimal trait values for a given selective regime may become strongly canalized, or resistant to modification (Waddington 1942). In contrast, phenotypic plasticity allows organisms to exploit a wide range of environments by producing alternative phenotypes in response to proximate environmental cues to future environmental conditions (Agrawal 2001, Pigliucci 2001, Schlichting & Smith, 2002, West-Eberhard 2003). Historically, research on adaptation through selection on individual alleles or quantitative traits dominated evolutionary thinking from the time of Darwin through most of the 20th century (Wright 1931, Simpson 1953, Williams 1966). Phenotypic plasticity was not widely recognized as a significant mechanism for shaping organismal traits until the mid-20th century (Bradshaw 1965), but plasticity and its consequences have become major topics of research in modern evolutionary biology (Pigliucci 2005).

Much effort has been devoted to understanding the occurrence and significance of morphological plasticity in insects. Insects are characterized by a rigid exoskeleton and highly integrated, discrete developmental stages (Chapman 1998), and shifting allocation patterns during development may significantly modify adult morphology, allowing insects to exploit a wide variety of ecological niches (Whitman & Agrawal 2009). Abiotic factors such as temperature and photoperiod regulate expression of long- and short winged morphs of *Gerris* waterstriders (Vepsalainen 1974b, 1978, Zera 1985) and seasonal color polyphenisms in *Papilio polyxenes* and other butterfly species (Hazel 2002, Hazel & West 1979, 1983). A response to social factors, such as mate competition and crowding, regulates resource allocation to wings and flight muscles vs. ovarian growth in *Gryllus* species (Zera & Denno 1997; Zera 2004, 2005), and the complex phase polyphenisms of migratory locusts (Simpson and Sword 2009). Food type and quality regulate horn and body size dimorphism in dung beetles (Moczek & Emlen 1999, Shafiei et al. 2001), and alternative cryptic morphs of *Nemoria* caterpillars (Greene 1989).

Although diet-induced morphological plasticity in insects is well-known, only a few studies have documented its expression in traits that are directly related to feeding efficiency. Caterpillars of the noctuid moth *Pseudaletia unipunctata* reared on tough grasses displayed greater allometric growth of the head than when fed a diet of soft food (Bernays 1986). Larvae of the butterfly *Pieris napi* fed tough diets developed larger heads than those fed soft diets (Ohata et al. 2011). *Melanoplus femurrubrum*

grasshoppers also responded to hard diets by significantly increasing allocation to head mass (Thompson 1992). In each case increased allocation to head mass resulted in greater consumption of tough diets, indicating that morphological plasticity can be an important adaptive response to diet characteristics (Bernays 1986, Thompson 1992, Ohata et al. 2011).

The fitness advantage of phenotypic plasticity depends on the diversity of environmental conditions experienced by an organism, often termed environmental grain (Levins 1968). In fine-grained environments, a diversity of environments favors the evolution of plastic responses allowing organisms to exploit a diversity of resources, while coarse-grained environments select for fixed adaptation to the dominant set of environmental conditions (Hollander 2008, Baythavong 2011). However, it is unclear whether plastic or fixed responses will predominate when organisms experience changes in environmental grain during different life stages. Rapid and reversible strategies such as induced behavioral or physiological phenotypes may offer significant fitness advantages in early life stages without imposing opportunity costs on later ones. In contrast, irreversible developmental responses such as investment in morphological structures may enhance fitness at one stage while producing phenotypes ill-suited to later stages.

Previous studies of diet-induced morphological plasticity have focused on organisms that experience consistent environmental grain throughout the life cycle. Although *P. unipunctata* and *P. napi* may exploit a variety of resources, lepidopteran larvae are relatively sessile and close association between an individual larva and its host plant is common. *M. femurrubrum* studied by Thompson (1992) were derived from a population that originated in a mesic environment where relatively benign environmental conditions might be expected to maintain a variety of food sources throughout the growing season; once diet-induced morphological responses to a specific host plant occur these grasshoppers are mobile enough to seek out additional host plants of the same or similar species. In contrast, insects inhabiting harsh or seasonal environments may at times experience limited food diversity and availability, which may select for canalized morphology that can reliably cope with limited food diversity or availability at critical stages of the life cycle. For example, the Australian spur-throated locust, *Austracris guttulosa*, requires ephemeral grasses and forbs for nymphal development, while adults subsist on trees and shrubs such as *Eucalyptus* and *Acacia* (Farrow 1977). Breeding is tightly linked to the rainy season, and nymphs must complete development before high-quality resources disappear. Under these conditions phenotypic plasticity of nymphal stages may not confer significant

2

fitness gains and may even interfere with the development of adult morphology required to complete the life cycle (Schlichting & Smith 2002).

In this study I asked whether a population of the generalist grasshopper *Melanoplus differentialis* is capable of expressing morphological plasticity in feeding structures in response to diet. The study population is from a semi-arid grassland that provides many potential food resources to nymphal stages but relatively few suitable food resources to adults. In addition, nymphal resources are generally soft ephemeral annual forbs while adult resources are tough perennial forbs and shrubs. I compared insects reared on hard and soft diets to determine if this population was capable of altering resource allocation to head morphology and biting performance in response to the physical challenges posed by rearing diet. I also compared allometric relationships among body parts to search for potential tradeoffs in allocation that might account for phenotypic plasticity in head morphology. I hypothesized that the conditions under which this population evolved would select for fixed rather than plastic morphology, and that insects would show little morphological plasticity compared to previous studies.

Materials and Methods

Study species and source population

      The differential grasshopper, *Melanoplus differentialis*, is a widespread generalist species that ranges across North America from central Mexico to southern Canada and from the Pacific coast to the Atlantic coast, except in the southeastern United States (Pfadt 1994). *M. differentialis* is highly polyphagous and has been recorded feeding on over 200 different plant species (Pfadt 1994). It is notorious as a pest of cultivated species (Pfadt 1994) and is capable of maintaining high levels of survival, growth, and reproduction on both mixed diets and single host plants (Howard, unpublished), suggesting that phenotypically plastic responses to diet may contribute to homeostasis in performance. However, the degree to which behavioral, physiological, or morphological plasticity plays a role in these responses is currently unknown.

      The experimental population was derived from a source population from Sonoran Desert upland grassland between Elgin and Sierra Vista, about 50 km SE of Tucson, Arizona. The grasslands of southern Arizona between Tucson and the San Pedro River are dominated by perennial bunchgrasses such as *Boutelous gracilis, Aristida divaricata* and *Hilaria mutica*, with scattered mesquite (*Prosopis velutina*) and numerous shrub species including *Gutierrizia sarothrae*, *Ericameria nauseosa,* and *Ambrosia dumosa* (Humphrey 1958). The area experiences unpredictable and highly variable summer precipitation (McDonald 1956, Eder 1989) and the phenology of numerous annual plants is tightly linked to precipitation patterns (Humphrey 1958*, Ehleringer 1985). Summer annuals germinate in response to summer rainfall, and *M. differentialis* hatching is also cued by rainfall, so that emergence of hatchlings coincides with the availability of the diverse ephemeral summer annual flora. However, ephemeral summer annuals rapidly disappear by the time grasshoppers reach adulthood in August and September (Stromberg 2007, Crimmins et al 2008), leaving adults with resources that are predominantly perennial, tougher, and of lower quality than nymphal food plants.

Culture conditions

      The culture was started from approximately 50 egg pods collected from randomly caught individuals in 2011 and supplemented with individuals collected in 2016. The culture was maintained with a 12L:12D cycle with a maximum temperature of 30°C and a minimum of 23°C, and fed a diet of seedling wheat, romaine lettuce, and wheat bran. Hoppers were fed ad libitum, and housed in 30x30x30

cm wire mesh cages (BioQuip Inc., Rancho Dominguez, CA). Each cage was provided with a 72-watt light bulb for basking, and food was replaced, and cages cleaned daily.

Experimental Populations

Newly hatched first instar grasshoppers were randomly assigned to hard (leaves of the cultivated shrub *Photinia x fraseri*) or soft (romaine lettuce; *Lactuca sativa*) diets, supplemented with wheat bran, and small amounts of carrot and sweet potato shavings to avoid nutritional deficiencies. Hatchlings of both treatments were also provided leaves of kale for the first three days to enhance initial survival on the hard diet, which was difficult for first instars to consume. Although differing dramatically in both leaf specific mass and toughness, both Romaine lettuce and *Photinia* are known to supply complete nutrition, and individuals can successfully reach adulthood raised on a monospecific diet of either species. The relative difficulty of consuming each diet was established by measuring mass of a known leaf area (leaf specific mass) and by measuring leaf toughness. Leaf toughness was estimated as shear force required to punch through leaves (kg/cm^2) using a penetrometer (Chatillion Co.) (n = 20). *Photinia* had a mean leaf specific mass of 14.5 ± 0.8 mg/cm^2 and mean shear force of 878.98 ± 52.28 kg/cm^2, while Romaine lettuce had mean leaf specific mass of 2.6 ± 0.4 mg/cm^2 and mean shear force of 176.22 ± 49.62 kg/cm^2.

Analysis of bite force and morphology

Grasshoppers were weighed within 12 hours of molting to adulthood using a subset of individuals that were known not to have fed prior to weighing and in which all body parts were intact and undamaged. Bite force was measured using a Tekscan FlexiForce wireless ELF system (Tekscan Inc., Boston, MA), after which insects were sacrificed and mounted on pins for morphological analysis. Morphological measurements (Table 1) were obtained from digital images acquired using a Leica E3 camera and Leica Digital Suite software. Digitized images were measured using Image J software (National Institutes of Health; https://imagej.nih.gov/ij/).

I measured external head dimensions related to chewing and the volume of muscle required to drive mandibles: head width, height and depth (measured as the width of the gena, the lateral sclerite of the head), and used these measurements to estimate head volume. I also measured structures related to locomotion to determine if they scaled isometrically or allometrically with head measured. I measured thorax length, width and height and used these

Table 1. Morphological measurements of adult *Melanoplus differentialis* analyzed from digital images.

Measurement	Description
Head width	Maximum width of head in frontal view.
Head height	Distance from fronto-clypeal suture to top of the vertex.
Gena width	Distance between the anterior and posterior margins of the sclerite in lateral view
Thorax height	Maximum dorso-ventral distance in lateral view
Thorax width	Lateral distance measured at median sulcus in dorsal view
Thorax length	Anterior-posterior distance from the back of the head to the first abdominal segment in lateral view
Femur length	Distance from tibial articulation to the trochanter articulation (in lateral view)
Wing length	Distance from end of pronotum to the edge of the posterior forewing wing tip

measures to estimate thorax volume as an index of potential development of flight muscles. I also measured wing and femur length as indicators of investment in locomotion.

Statistical Analysis

I analyzed the effect of diet and sex on each measured or calculated variable using 2-way Analysis of variance (ANOVA) with diet and sex as fixed effects. ANOVA was carried out in SYSTAT v. 13 (SYSTAT Software Inc, San Jose, CA). I investigated scaling relationships among morphological measures using standardized major axis (SMA) regression, which is recommended for analysis of variables in which allometric scaling of relationships is expected (Warton et al. 2006). SMA regressions were carried out in R version 3.5.0 using the smatr package version 3.4-8. An overall regression line was first fit for all data, and then the equality of slopes among groups within the data was tested. Allometry among measurements was assessed using expected isometric scaling exponents for measures of varying dimension. For measurements with the same dimensional measure (linear:linear or cubic:cubic) I compared scaling exponents to the expected value isometric exponent of 1.0; when comparing

measurements differing in dimensional measure (linear:cubic) scaling exponents were compared to the

expected isometric relationship of 0.33.

Results:

Effects of diet and sex

Two-way ANOVA found that diet had a significant effect on bite force and all morphological variables except for mass and gena width (Table 2). Sex also had significant effects on most variables except bite force, head width, and gena width (Table 2). A significant diet x sex interaction was found only for head height ($F_{1,148}$ = 5.56, P < 0.05); no other interaction terms were found to be significant for any variable (Table 2). In all cases where a significant diet effect was found, insects on the lettuce treatment were larger and had greater bite force than those on the *Photinia* treatment (Figures 2-4). Similarly, females were uniformly larger than males in all cases where a significant sex effect was found. The significant diet x sex interaction in head height was due to the greater difference between lettuce and *Photinia* diets in males than in females (Figure 3). However, in both sexes insects fed *Photinia* had smaller head heights than those fed lettuce.

Scaling relationships between mass and morphological measurements

Six out of the ten morphological measures analyzed showed significant scaling relationships with body mass (Table 3). Head height, thorax width, femur length, and wing length all showed positive scaling relationships with mass, and scaling exponents ranged from 0.30-0.36, indicating that these measures scaled approximately isometrically with body mass. Head height, femur length and wing length showed a strong relationship with mass, with r^2 values greater than 0.40, while thorax width showed a much weaker but still significant relationship to mass with r^2 of only 0.08 (Table 3).   In contrast, head width and gena width scaled negatively with body mass, and their exponents indicated that they decreased nearly isometrically as mass increased (Table 3). As with thorax width, these were both relatively weak relationships with r^2 of 0.09 and 0.06, respectively. In no case was a significant difference in scaling relationships detected among diet treatments, indicating that diet did not alter the way that morphological variables scaled with mass.

Table 2. F-ratio and level of significance of two-way ANOVA effects for body dimensions and bite force of *Melanoplus differentialis* reared on hard (*Photinia* x *fraseri*) and soft (*Lactuca sativa*) diets.

Variable	F ratio for ANOVA effect		
	Diet	Sex	Diet x Sex
Mass ($F_{1,77}$)	0.18	54.77***	0.33
Bite force ($F_{1,77}$)	9.87**	2.67	1.87
Head width ($F_{1,148}$)	4.17*	1.48	0.13
Head height ($F_{1,148}$)	27.76***	81.74***	5.56*
Gena width ($F_{1,148}$)	0.17	0.07	0.01
Head volume ($F_{1,148}$)	8.17**	13.30***	0.10
Thorax height ($F_{1,148}$)	21.66***	17.25***	2.44
Thorax length ($F_{1,148}$)	22.29***	4.66*	0.66
Thorax width ($F_{1,148}$)	13.63***	44.98***	1.02
Thorax volume ($F_{1,148}$)	25.17***	23.93***	1.69
Wing length ($F_{1,148}$)	35.85***	14.53***	2.60
Femur length ($F_{1,148}$)	22.20***	77.48***	2.28

*: $P < 0.05$; **: $P < 0.01$; *** $P < 0.001$.
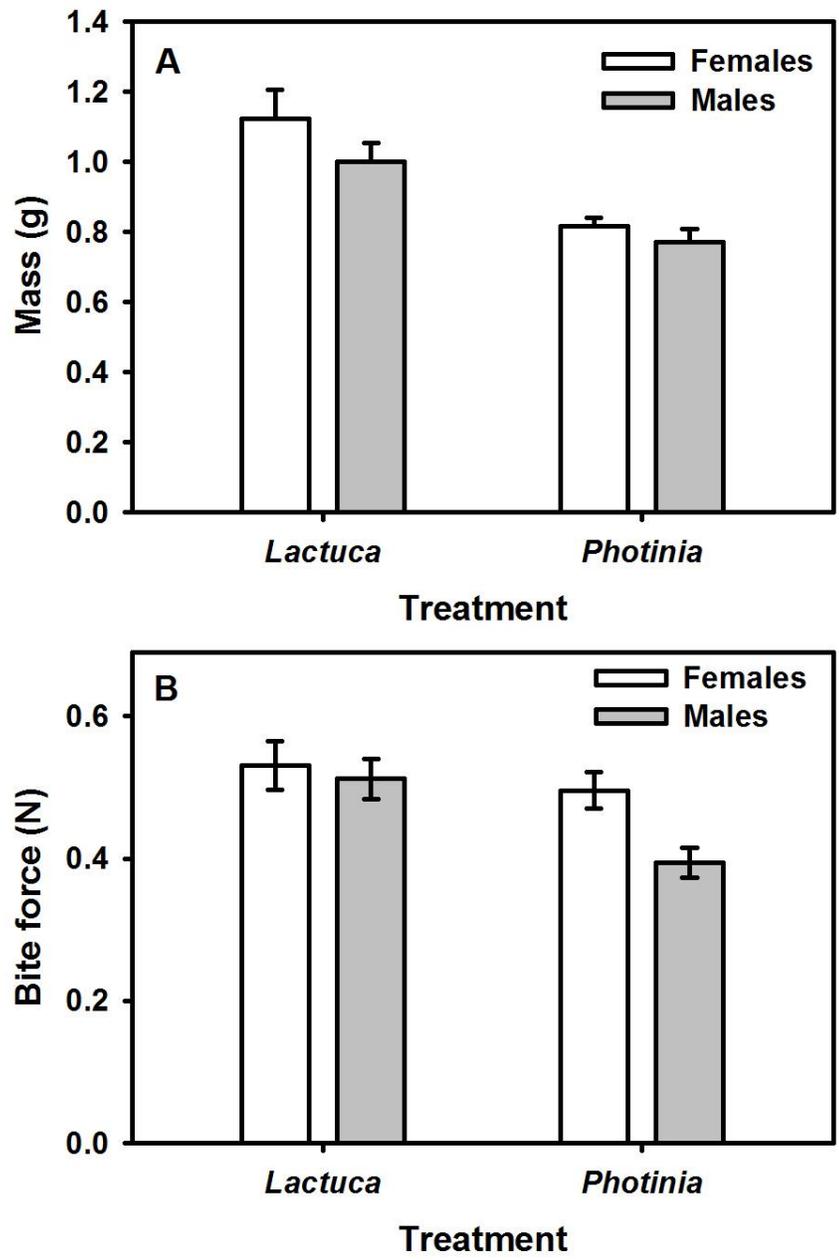
Figure 1. Mass (A) and bite force (B) of *Melanoplus differentialis* raised on soft (*Lactuca sativa*) and hard (*Photinia* x *fraseri*) diets.
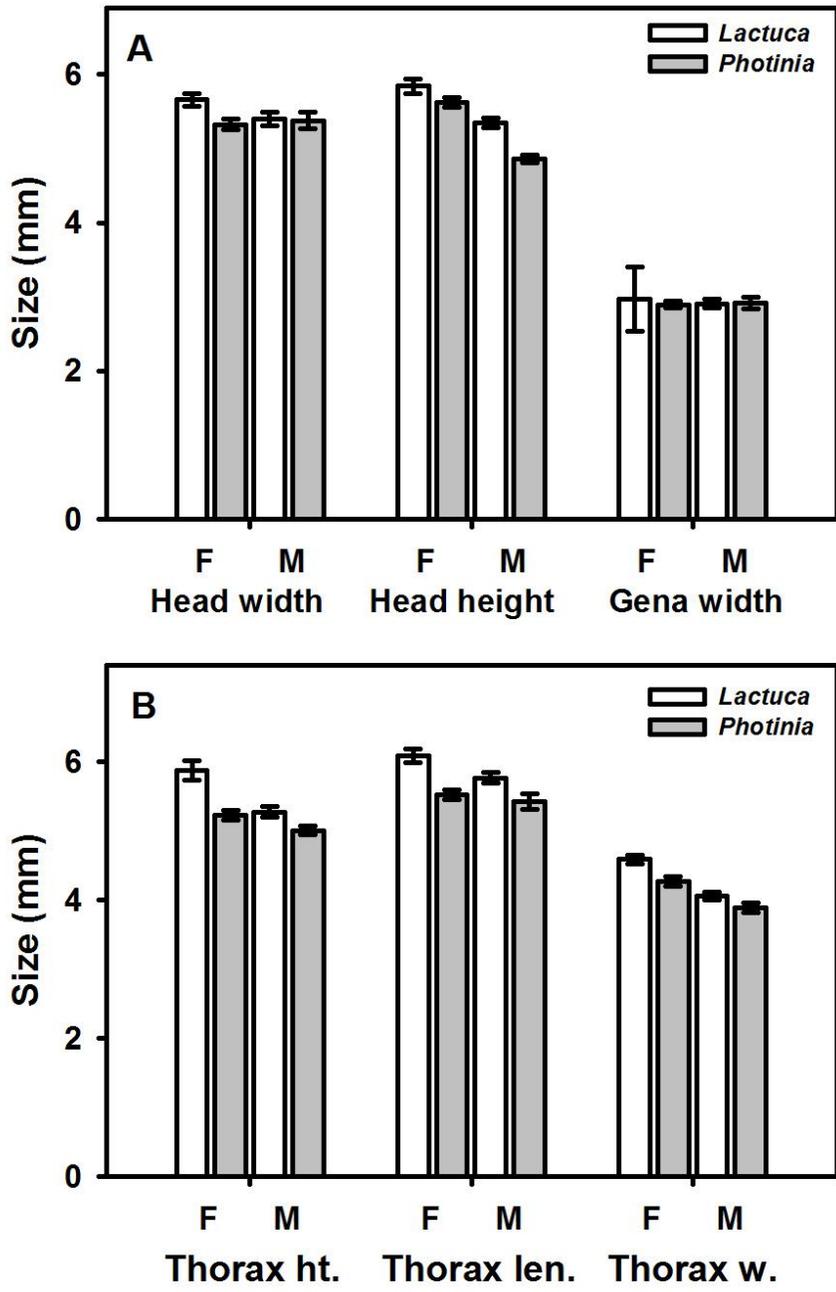
Figure 2. Head (A) and thorax dimensions (B) of Melanoplus differentialis reared on soft (*Lactuca sativa*) and hard (*Photinia* x *fraseri*) diets.
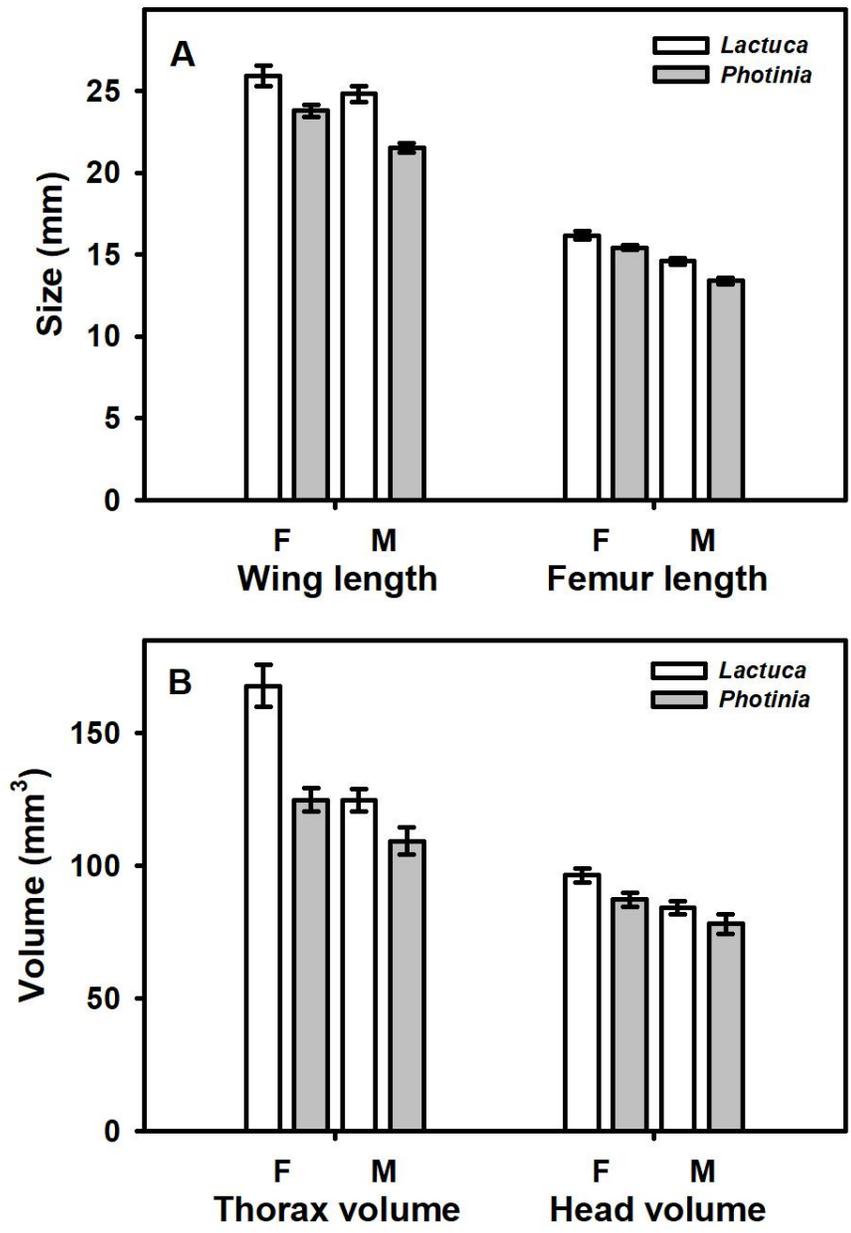
Figure 3. Wing and femur length (A) and thorax and head volume (B) of Melanoplus differentialis reared on soft (*Lactuca sativa*) and hard (*Photinia* x *fraseri*) diets.

Table 3. Standardized major axis regression scaling exponents and confidence intervals relating body dimensions to mass. All variables were $\log_{10}$ transformed.

SMA regression (y~x)	Scaling exponent	95% CI	r^2	Regression *P*-value
Head width ~ Mass	-0.32	-0.40 - -0.26	0.09	<0.01
Head height~ Mass	0.30	0.25 – 0.35	0.52	<0.001
Gena width ~ Mass	-0.29	-0.36 - -0.23	0.06	<0.05
Head volume ~ Mass	0.47	0.38 – 0.58	<0.01	0.385
Thorax height ~ Mass	0.31	0.25 – 0.38	<0.01	0.954
Thorax length ~ Mass	-0.28	-0.35 - -0.23	0.01	0.352
Thorax width ~ Mass	0.31	0.25 – 0.38	0.08	<0.01
Thorax volume ~ Mass	0.70	0.56 – 0.87	<0.01	0.430
Femur length ~ Mass	0.36	0.30 – 0.42	0.44	<0.001
Wing length ~ Mass	0.35	0.30 – 0.41	0.46	<0.001

Scaling relationships between bite force and head morphology

Bite force showed a significant scaling relationship with mass and head height, but not with head width, gena width, or head volume (Table 4). The scaling exponent of 1.01 between bite force and mass (a cubic measure) indicates that bite force scaled isometrically with mass. The exponent of 3.4 between bite force and head height (a linear measure) is extremely close to the exponent of 3.03 predicted by the significant scaling relationship between mass and head height of 0.30 (Table 3).

Table 4. Standardized major axis regression scaling exponents and confidence intervals relating bite force to head dimensions and body mass. All variables were $\log_{10}$ transformed.

SMA regression (y~x)	Scaling exponent	95% CI	r^2	Regression *P*-value
Bite force ~ Mass	1.01	0.83 – 1.22	0.26	<0.001
Bite force ~ Head width	3.11	2.49 – 3.89	<0.01	0.959
Bite force ~ Head height	3.40	2.75 – 4.20	0.10	<0.01
Bite force ~ Gena width	-3.49	-4.36 - -2.80	<0.01	0.743
Bite force ~ Head volume	2.16	1.73 – 2.68	0.03	0.110

Potential tradeoffs between head height and locomotor performance

If greater investment in head structures is important to feeding efficiency and requires less investment in other body structures, then allometric rather than isometric scaling between head measures and other structures would be expected. Head height was the only head dimension that showed significant positive scaling relationships with both mass and bite force, and I investigated its relationship with morphological measures related to locomotion. Head height showed a significant positive scaling with thorax volume, but the scaling exponent of 0.33 indicated an isometric relationship (Table 5). Head height also showed significant positive scaling with femur length and wing length (Table 5). However, in both cases the scaling exponent was <1.0, indicating that head height increased at a slower rate than either femur length or wing length (Table 5).

Table 5. Standardized major axis regression scaling exponents and confidence intervals relating head height to body structures related to locomotion. All variables were $\log_{10}$ transformed.

SMA regression (y~x)	Scaling exponent	95% CI	r^2	Regression *P*-value
Head height ~ Thorax volume	0.33	0.29 – 0.38	0.38	<0.001
Head height ~ Femur length	0.91	0.83 – 1.01	0.63	<0.001
Head height ~ Wing length	0.80	0.72 – 0.89	0.56	<0.001

Discussion:

The results suggest that the study population of *Melanoplus differentialis* shows little capacity for phenotypic plasticity in feeding structures, and instead displays a relatively canalized morphology. This is consistent with the idea that the requirement for head morphology required to cope with a relatively tough, low diversity diet in the adult stage limits the potential advantage of morphological plasticity in nymphs despite the availability of a diversity of soft resources. Although nymphs could still show plastic responses to diet toughness, individuals investing less in head structures as nymphs would have to devote far more resources to differential head growth once ephemeral annuals disappeared than those that maintained a fixed trajectory toward the appropriate adult morphology. This would likely result in frequent mismatch between adult morphology and available food plants, and even a small difference in mean fitness would likely impose strong selection for fixed allocation. While a number of authors have identified mismatch between phenotype and environment as one important cost of phenotypic plasticity, they generally emphasize mismatch as a phenotypic cost resulting from imperfect information gathering or a plasticity cost due to limited ability of plasticity to generate phenotypes equivalent to those produced by genetic adaptation (DeWitt et al. 1998, Agrawal 2001, Callahan et al. 2008). This system is of particular interest because potential mismatch arises for a different reason: a predictable change in environmental grain experienced by different life stages. I suggest that changing environmental grain across developmental stages may be an important and generally unappreciated constraint on the evolution of phenotypes in insects whose development is keyed to favorable larval or nymphal conditions in seasonal environments.

The annual phenology of the Sonoran Desert grasslands likely plays an important role in selecting for fixed rather than plastic feeding morphology in the study population. While heterogeneous environments may select for phenotypic plasticity, the value of an induced phenotype depends on continued association between the individual and the environment that induced it. Insects that exhibit

diet-induced changes in feeding morphology in previous studies (Bernays 1986, Thompson 1992, Ohata et al. 2011) may experience heterogeneous environments in the form of alternative food resources, but would be expected to be able to maintain an association with food plants that induced a specific feeding morphology.   Lepidopteran larvae often complete development on a single host plant, while grasshoppers in mesic habitats may be able to locate similar plants by dispersing only short distances. In contrast, the Sonoran desert grasslands from which this study population was collected undergo a general loss of annual plant diversity at the end of the summer rainy season across the entire biome (Stromberg 2007, Crimmins et al 2008), and there is little potential for dispersal to new habitats in which annuals are still available. As a result, adult grasshoppers must be able to cope with whatever resources are still available in their natal habitat, and should experience strong stabilizing selection on feeding morphology.

In this study females were larger than males in most body measurements, a result consistent with the general pattern that females are typically larger than males in most insect species (Stillwell et al. 2010). In addition, both males and females raised on the soft lettuce diet were also generally larger in most body dimensions than those raised on the hard *Photinia* diet. This suggests that *Photinia*-reared individuals experienced nutrient limitation mediated by reduced food intake on the tougher diet. Although females often display greater morphological plasticity than males in insects (Stillwell et al. 2010) the general lack of diet x sex interactions in this study indicates that both sexes had similar responses to restricted nutrition and grew uniformly smaller on the tougher diet. The inability of insects raised on *Photinia* to alter head dimensions and bite force likely contributed significantly to nutritional limitation on the hard diet. This lack of flexibility stands in stark contrast to similar studies of *Melanoplus femurrubrum*, which was able to increase allocation to biting structure and thereby increase consumption of hard diets (Thompson 1992).

Head height was the morphological measure most strongly related to bite force. This is likely

due to the attachment of mandibular muscles at the vertex of the head; taller heads would permit

longer muscles supplying greater leverage to the mandible, resulting in greater bite force (Clissold 2008).

Head height increased isometrically with body mass, while gena width and head width decreased with

body mass, such that larger individuals had taller but narrower heads. This suggests that muscle length

rather than cross sectional area may be of greater importance in biting performance in this species.

I found no evidence to suggest that changes in head shape required a tradeoff in allocation to

morphological structures involved in locomotion. Head height scaled isometrically with thorax volume,

indicating that investment in flight muscle mass was likely not affected by investment in head

structures. Head height showed negative allometric scaling with wing length and femur length

(exponents of 0.91 and 0.80, respectively) indicating that head height increased at a slower rate as mass

increased than either wing or femur length. This result is not unexpected, because as size increases

changes in biting performance produce a tradeoff between bite power and the size of food fragments

obtained (Clissold 2008*). As mandible size increases the size of leaf fragments obtained also increases,

and at some point large fragments require more processing than small ones to be reduced to

manageable size (Clissold 2008). There is thus a limit to the advantage gained from increased size of

feeding structures that does not appear to apply to locomotory structures such as femur and wing.

Although I found no evidence for morphological plasticity in *Melanoplus differentialis,*

behavioral and physiological plasticity may still play an important role in allowing nymphs to use a

variety of resources while permitting adults to tolerate a diet more limited in diversity. Responses to

environmental change fall into three categories: regulatory, acclimatory, and developmental (Ricklefs

1990). Regulatory and acclimatory responses such as induction of preference for host plants, digestive

enzymes in the gut, or detoxification enzymes in fat body are relatively fast and reversible, and do not

induce permanent changes in phenotype that could compromise future fitness. In contrast, developmental responses such as morphological change are both slow and irreversible, and may produce environment-phenotype mismatch in adults. It is possible that this population of *M. differentialis* displays plasticity in behavior and physiology, and that these responses would significantly enhance the fitness of nymphs feeding on ephemeral annuals.

The wide geographic range of *M. differentialis* raises the possibility that different populations of the species may vary in their degree of morphological plasticity according to the characteristics of the local environment. Interpopulation variation in phenotypic plasticity has received less attention than variation among genotypes or species, and these investigations have often been more focused on documenting varying degrees of plasticity than on relating variation in phenotypic plasticity to environmental variation (e.g., Sibly et al 1997). However, a few investigations have attempted to assess the role of phenotypic plasticity vs. adaptation in specific populations experiencing different levels of environmental variation. Wood frog tadpoles from ponds with greater variation in predator abundance exhibit greater levels of phenotypic plasticity than those from ponds with consistent predation pressure (Relyea 2002), and male soapberry bugs from populations with greater variation in sex ratio exhibit greater plasticity in mating tactics than males from populations with consistent sex ratios (Carroll and Corneli 1995). Finally, *Erodium cicutarium* populations from highly heterogeneous serpentine soils exhibit higher levels of phenotypic plasticity than those from less heterogeneous non-serpentine soils (Baythavong 2011). These studies demonstrate the relative importance of adaptation and phenotypic plasticity in permitting species to colonize environments differing in environmental grain. I suggest that interpopulation differentiation in phenotypic plasticity may be equally important in generating the wide geographical range of *M. differentialis* and many other widespread insect species.

References:

Agrawal, AA (2001). Phenotype Plasticity in the Interactions and Evolution of Species.
    Science 294: 321-326.

Baythavong, B. S. (2011). Linking the Spatial Scale of Environmental Variation and the Evolution of
    Phenotypic Plasticity: Selection Favors Adaptive Plasticity in Fine-Grained Environments.
    American Naturalist 178: 75-87.

Bernays E (1986). Diet-induced head allometry among foliage-chewing insects and
     its importance for graminivores. Science 231:495-497.

Bernays E (1991). Evolution of Morphology in Relation to Plants. Philosophical Transactions:
    Biological Sciences 333(1267):257-264.

Callahan, H. S., H. Maughan and U. K. Steiner (2008). Phenotypic plasticity, costs of phenotypes, and
    costs of plasticity. Annals of the New York Academy of Sciences 1133: 44-66.

Canfield, MR (2006). The ecology and evolution of phenotypic plasticity: case studies in Lepidoptera.
    Ph.D thesis, Harvard University, Cambridge, MA.

Carroll, S.P. and P. S. Corneli (1995). Divergence in male mating tactics between two populations of the
    soapberry bug: II. Genetic change and the evolution of a plastic reaction norm in a variable
    social environment. Behavioral Ecology 6: 45-56.

Chapman, R.F. (1998). The Insects: Structure and Function. Cambridge University Press, Cambridge,
    England.

Clissold, F. J. 2008. The biomechanics of chewing and plant fracture: mechanisms and implications.
    Advances in Insect Physiology 34: 317-372.

Crimmins, T. M., M. A. Crimmins, D. Bertelson and J. Balmat (2008). Relationships between alpha
    diversity of plant species in bloom and climatic variables across an elevation gradient.
    International Journal of Biometeorology 52: 353-366.

DeWitt, T.J., A. Sih, and D. S. Wilson (1998). Costs and limits of phenotypic plasticity. Trends in Ecology
    and Evolution 13: 77-81.

DeWitt, T.J. and S. M. Scheiner (2004). Phenotypic plasticity: functional and conceptual approaches.
    Oxford University Press, Oxford.

Eder, B. K., L. E. Truppi, and P. L. Finkelstein (1989). A climatology of temperature and precipitation
    variability in the United States. Global Climate Change Program, U. S. Environmental Protection
    Agency, Research Triangle Park, NC.

Ehleringer, J. (1985). Annuals and perennials of warm deserts. Pp. 162-180 In: B. F. Chabot and H. Mooney, eds. Physiological ecology of North American plant communities. Chapman and Hall, New York.

Emlen, DJ; Nijhout, HF (1999). Hormonal control of male horn length dimorphism in the dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). Journal of Insect Physiology 45:45-53.

Farrow, R.A. (1977). Maturation and fecundity of the spur-throated locust *Austracris-guttulosa* in New South Wales Australia during the 1974-1975 plague. Journal of the Australian Entomological Society 16: 37-29.

Forsman, A (2014). Rethinking phenotypic plasticity and its consequences for individuals, populations, and species. Heredity: 1-9.

Greene, E (1989). A diet-induced developmental polymorphism in a caterpillar. Science 243:643-646.

Greene, E (1999). Phenotypic variation in the larval development and evolution: Polymorphism, polyphenism, and developmental reaction norms. In: *The Origin and Evolution of Larval Forms.* B.K. Hall and M.H. Wake eds, 379-406. Academic Press, San Diego.

Hodge, C (1933). Growth and Nutrition of *Melanoplus differentialis* Thomas (Orthoptera: Acrididae) I. Growth on a Satisfactory Mixed Diet and on Diet of Single Food Plants. Physiological Zoology 6: 306-328.

Hollander, J. 2008. Testing the grain-size model for the evolution of phenotypic plasticitiy. Evolution 62: 1381-1389.

Humphrey, R. R. 1958. The desert grassland: a history of vegetational change and an analysis of causes. Botanical Review 24:193-252.

Levins, R. A. (1968). Evolution in changing environments. Princeton University Press, Princeton, NJ.

McDonald, J. E. (1956). Variability of precipitation in an arid region: A survey of characteristics for Arizona. Technical reports on the meteorology and climatology of arid regions. No. 1. University of Arizona Institute of Atmospheric Physics, Tucson, AZ.

Moczek, AP; Emlen, DJ (1999). Proximate determination of male horn dimorphism in the beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). Journal of Evolutionary Biology 12:27-37.

Ohata, M; Furumoto, A; Oshaki, N (2011). Plastic changes in head size during juvenile development of the butterfly *Pieris napi.* The Ecological Society of Japan 26: 541-546.

Pfadt, R.E. (1994). A field guide to common western grasshoppers, 2nd ed. Wyoming Agricultural Experiment Station Bulletin 912.

Pigliucci, M (2001). Phenotypic Plasticity: Beyond Nature and Nurture. John Hopkins University Press, Baltimore, MD.

Pigliucci, M (2005). Evolution of Phenotypic Plasticity: where are we going now? Trends in Ecology and Evolution 20:481-486.

Relyea, R. (2002). Local population differences in phenotypic plasticity: predator-induced changes in wood frog tadpoles. Ecological Monographs 72: 77-93.

Ricklefs, R.E. (1990). Response to Variation in the Environment, pp. 92-117. *In:* Robert E. Ricklefs, eds. Ecology. W.E. Freeman and Company, New York.

Schlichting, CD; & Smith, H (2002). Phenotypic plasticity: linking molecular mechanisms with evolutionary outcomes. Evolution and Ecology 16:189-211.

Shafiei, M; Moczek, AP; Nijhout, HF (2001). Food availability controls the onset of metamorphosis in the dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). Physiological Entomology 26:173 180.

Sibley, R. M., L Winokur, and R. H. Smith (1997). Interpopulation variation in phenotypic plasticity in the speckled wood butterfly, *Pararge aegeria.* Oikos 78: 323-330.

Simpson, S.J. & Sword, G.A. (2009). Phase polyphenism in locusts: Mechanisms, population consequences, adaptive significance and evolution. In: Whitman, D & Ananthakrishnan, T. (eds.) Phenotypic Plasticity of Insects: Mechanisms and Consequences. Science Publishers Inc., Plymouth, pp 147-190.

Stillwell, R. C., W. U. Blanckenhorn, T. Teder, G. Davidowitz, and C. W. Fox (2010). Sex differences in phenotypic plasticity affect variation in sexual size dimorphism in insects: From physiology to evolution. Annu. Rev. Entomol. 2010. 55:227–45.

Stromberg, J. C. (2007). Seasonal reversals of upland-riparian diversity gradients in the Sonoran Desert. Diversity and Distributions 13: 70-83.

Thompson, DB (1992). Consumption rates and the Evolution of Diet-Induced Plasticity in the Head Morphology of *Melanoplus Femurrubrum* (Orthoptera: Acrididae). Oecologia 89: 204-213.

Vepsäläinen, K (1978). Wing dimorphism and diapause in *Gerris*: determination and adaptive significance. In H. Dingle [ed.] . Evolution if Insect Migration and Diapause. Springer-Verlag, New York pp. 218-253.

Vepsäläinen, K (1974b). Determination of wing length and diapause in water-striders (Gerris Fabr., Heteroptera). Hereditas 77: 163-176

Waddington, CH (1942). Canalisation of development and the inheritance of acquired characters. Nature 150: 563-565.

Williams, G.C. 1966. Adaptation and Natural Selection. Princeton University Press, Princeton.

Whitman, D. W. and A. A. Agrawal (2009). What is phenotypic plasticity and why is it important?, pp. 1-63. *In*: Whitman, D. W. and A. Ananthakrishnam, eds. Phenotypic plasticity in Insects. Science Publishers, Enfield, NJ.

Zera, AJ (1985). Wing polymorphism in waterstriders: Mechanism of morph determination and adaptive significance, pp. 674-686. *In* M.A.R. Rankin [ed.] Migration: Mechanisms and Adaptive Significance. Marine Science Institute, The University of Texas at Austin, Port Aransas, TX.

Zera, AJ (2004). The endocrine regulation of wing polymorphism: State of the art, recent surprises, and future direction. Integrative and Comparative Biology 43:607-616.

Zera, AJ (2005). Intermediary metabolism and life-history trade-offs: Lipid metabolism in lines of the wing-polymorphic cricket, *Gryllus firmus*, selected for flight capability vs. early-age reproduction. Integrative and Comparative Biology 45:511-524.

Zera, AJ; Denno, RF (1997). Physiology and ecology of dispersal polymorphism in insects. Annual Review of Entomology 42:207-231.

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