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Does phenotypic integration constrain sexual size dimorphism in eastern lubber grasshoppers (*Romalea microptera*)?

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Abstract

Conspicuous sex differences in size, shape, color and behavior are pervasive throughout both the animal and plant kingdoms. Although previous work has shown that sexual dimorphism can evolve purely as the result of either natural (intersexual resource competition) or sexual selection (fecundity selection, male-male combat), a handful of studies have also shown that these mechanisms need not be mutually exclusive and may even act synergistically to enhance dimorphisms. More recent studies have focused on the factors that act to constrain the evolution of sexual dimorphism. For example, a high genetic covariance among traits between the sexes is thought to retard adaptive sexual differentiation or place an upper limit on the degree of intersexual divergence. However, high genetic correlations themselves are often the result of selection for functional coherence amongst traits (integration), and thus divergent selection between the sexes could theoretically drive sexual dimorphism in the genetic variance-covariance matrix (**G**). To address this issue, we consider the phenotypic variance-covariance matrix (**P**), within the context of the evolution of sexual dimorphism in the eastern lubber grasshopper (*Romalea microptera*). We show that: 1) adult female lubbers have relatively wider heads than adult males; 2) most morphological traits show significant integration with one another, but males show a higher degree of integration than females; 3) **P** in lubbers is not strongly correlated across the sexes. These results suggest that phenotypic integration does not constrain the evolution of sexual dimorphism in *R. microptera*. Hence, sex-related traits can evolve separately from other traits.

Key words

adaptation, body size, ecological dimorphism, orthoptera, grasshopper

Introduction

The concept of adaptation as a multivariate phenomenon was only recently formalized by Lande (1979), but biologists have long realized that organismal traits seldom evolve in isolation, and that selection on a given phenotype frequently results in correlated changes in others (*e.g.*, Simpson 1953). The pattern of functional, genetic or developmental correlations among different traits within an organism (likely facilitated by pleiotropy or linkage disequilibrium among suites of genes: Falconer 1989, Schluter 2000) is broadly defined as phenotypic integration (Pigliucci 2003), and is thought to arise initially as a result of selection for functional coherence among traits.

Although phenotypic integration may theoretically enhance the adaptive process (Berg 1960, Wagner 1988), tight functional interrelationships among traits might also bias or constrain phenotypic evolution (Arnold 1992, Wagner & Schwenk 2000). For example, Schluter (2000) showed that a high degree of phenotypic or genetic covariation amongst traits can bias evolutionary transformations in wild populations, due to a lack of additive genetic variation for individual traits (also see Schluter 1996); this is so especially during the early stages of diversification, although this bias should decay over time. Despite this work, relatively few empirical studies have examined integration as either a form of adaptation or as a constraint (but see *e.g.*, Vincent *et al*. 2006).

The sexes of numerous animal species differ dramatically in their external phenotype (Blankenhorn 2005, Butler *et al*. 2007), and recent studies have begun to test whether phenotypic integration can constrain the degree of sexual dimorphism within a species (Parker & Garant 2004, Delph 2005, Fedorka *et al*. 2007, Foerster *et al*. 2007). Surprisingly however, researchers have generally failed to find compelling evidence that genetic correlations between the sexes hinder the evolution of sexual dimorphism (Slatkin 1984, Fedorka *et al*. 2007, Foerster *et al*. 2007, but see Jensen *et al*. 2003) — though this may depend on the trait in question (Parker & Garant 2004). Instead these few studies have found evidence that genetic correlations among traits within one sex (but not the other) may facilitate the evolution of dimorphism (*e.g.*, Reusch & Blanckenhorn 1998). Simply put, natural or sexual selection can act differently between the sexes on suites of functionally interdependent traits, leading to stronger patterns of integration in one sex compared to the other for a given set of traits. This is likely to be especially true for sexually selected traits such as ornaments or armaments which are typically greatly exaggerated in males relative to females (Andersson 1992). Divergent selection between the sexes would therefore be expected to result in distinct genetic and phenotypic variance-covariance matrices (**G** & **P** respectively) within each sex, although much work remains to be done to test this possibility.

Here we consider the phenotypic variance-covariance matrix (**P**) within the context of the evolution of sexual size dimorphism in the generalist-feeding grasshopper *Romalea microptera*. In particular, we examine the differences in **P** for several ecologically important morphological traits in adult male and female *R. microptera* to test the hypothesis that phenotypic integration constrains the evolution of sexual size dimorphism in this species. For example, the trophic apparatus of numerous animal species has proven to be a model system for testing hypotheses relating to ecological dimorphisms, due to the highly integrated and specialized nature of most feeding systems, particularly those of snakes (Shine 1989, Vincent & Herrel 2007). In this respect, lubbers are ideal for the current study because previous work has shown that adult males and females differ both in trophic morphology and in the type and thickness of plants consumed (Vincent 2006). Specifically, Vincent (2006) showed that adult females have relatively wider heads than their (smaller) males and consume thicker grasses as well. Additionally, preliminary field work suggests that male kicking performance is a sexually-selected trait in lubbers (Vincent & Lailvaux unpub.), allow-

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Table 1. Means ± 1 $s_{\bar{x}}$ of morphological variables for adult male and female lubber grasshoppers (*R. microptera*) sampled in this study. See Methods section for explanation of variables.

	Size (mm)	
Variable	Males (n = 42)	Females (n = 47)
HL	6.60 ± 0.08	7.20 ± 0.08
HW	8.00 ± 0.06	9.30 ± 0.08
PL	17.7 ± 0.24	20.2 ± 0.19
PW	10.4 ± 0.13	12.8 ± 0.13
ML	15.6 ± 0.21	17.7 ± 0.19
MW	12.4 ± 0.27	17.2 ± 0.33
FL	29.2 ± 0.62	31.7 ± 0.29
TL	30.1 ± 0.61	31.9 ± 0.35
EL	27.1 ± 0.30	27.9 ± 0.25
EW	9.40 ± 0.14	10.5 ± 0.14

ing us to examine patterns of integration in hindlimb morphology (particularly hindlimb length) in males in comparison to females. Such a comparison is particularly meaningful in *R. microptera* because jumping performance is unlikely to be under strong natural selection in this chemically defended, slow-moving grasshopper (Jones *et al*. 1989, Hatle & Faragher 1998, Vincent & Lailvaux unpub.).

Although studies of genetic constraints should ideally consider the additive genetic variance-covariance matrix (**G**), estimating **G** can be problematic for most species. In these cases, **P** is often used as a proxy for **G** (see Revell *et al*. 2007 for a recent example). Although the circumstances under which **G** and **P** will resemble each other are the subject of some debate, empirical evidence suggests that they are often highly correlated, particularly for morphological traits (Cheverud 1988, Roff 1995, Reusch & Blanckenhorn 1998). Furthermore previous authors have shown that phenotype is canalized in the final instar within lubbers (Hatle *et al*. 2003, Juliano *et al*. 2004) and hence, **P** should be a strong surrogate for **G** in this species.

Methods

Grasshopper sampling and morphometrics.—We collected 150 adult eastern lubber grasshoppers from a brackish marsh in St. Charles Parish, Louisiana, on July 7th, 2007. To test for sexual dimorphism and phenotypic integration in lubbers, we used only a subset of this larger sample, consisting of the individuals in the best physical condition (*i.e.*, elytra fully grown and intact; all legs present, etc.) (Table 1). For each individual in this subset, we recorded ten linear morphological measurements using Mitutoyo digital calipers (± 0.01 mm): head length (**HL**), maximum head width (**HW**), pronotum length (**PL**) and (maximum) pronotum width (**PW**), metapleuron length (**ML**) and (maximum) metapleuron width (**MW**), length of the femur (**FL**) and tibia of the right hindlimb (**TL**), and elytra length (**EL**) and maximum width (**EW**) (Table 1). Each measurement was recorded 3× and the average of these measurements used in the analysis in order to minimize measurement error.

Statistical analysis.—We used SPSS (version 11.5, SPSS Inc.) for all statistical analyses. We $\log_{10}$ transformed all morphological variables to meet the assumption of normality for regression analyses (Sokal & Rohlf 1981, Kachigan 1991) and verified these transformations using Lillifors tests. To examine whether males and females are morphologically distinct, we performed a discriminant function analysis using the $\log_{10}$ -transformed morphological variables as the dependent variables and sex as the grouping variable. To test for morphological integration *within* each sex in head/body size, we calculated Pearson correlation matrices for the $\log_{10}$ -transformed morphological variables. Additionally, we tested for morphological integration *within* each sex in head/body shape. To do so, we regressed all morphological variables against protonum length for each sex separately, using ordinary least-squares regression to generate 'size-adjusted' residual values. These size-adjusted variables were subsequently, used to calculate a shape correlation matrix for each sex. Finally, we applied a matrix-wide Bonferonni correction factor to adjust for multiple comparisons for both the size and shape matrices, respectively.

Table 2. Loadings of morphological variables on the canonical discriminant function. High loadings (>0.70) are indicated in bold. See Methods section for explanation of variables.

Variable	CV 1
HL	0.54
HW	**0.92**
PL	-0.21
PW	0.14
ML	0.20
MW	0.54
FL	0.28
TL	-0.65
EL	**-0.72**
EW	-0.02

To examine whether the nonsize-adjusted p-matrix is significantly correlated across the sexes, we first calculated **P** for each sex separately, using common principle components analysis (CPC). These variance-covariance matrices were subsequently exported and compared using Mantel's tests with 9999 permutations (Manly 1991). Finally, we also compared the size-adjusted p-matrices using the residual morphological variables in the same manner as the nonsize-adjusted variables.

Results

The discriminant function analysis was highly significant (Wilks' Lambda = 0.11, df = 10, 79, $p < 0.0001$) and correctly classified 100% of the individuals as being either male or female based on their external morphology. Inspection of the variable loadings on canonical variate 1 (CV1) showed that maximum head width was the variable that loaded most highly (Table 2) and female lubbers had higher loadings than males. Hence, absolute head width is larger in females than males, enabling clear differentiation between the sexes in lubber grasshoppers.

The nonsize-adjusted correlation matrix for male lubbers showed that morphological traits across the matrix are significantly integrated with one another after Bonferonni correction (Bartlett Chi-square statistic = 426.5, df = 45, $p < 0.0001$; Table 3). However, head length and pronotum width exhibited the least amount of integration with other morphological traits (Table 3, Fig. 1a). In a similar manner, the nonsize-adjusted morphological traits for female lubbers also exhibited significant integration across the matrix after Bonferonni correction (Bartlett Chi-square statistic = 298.7, df = 45, $p < 0.0001$; Table 3). Even so, most female morphological traits tended to be correlated with substantially fewer traits than those of male lubbers (Table 3, Fig. 1b).

Male size-adjusted morphological traits were once again significantly correlated across the matrix (Bartlett Chi-square statistic = 240.1, df = 36, $p < 0.0001$; Table 4). Even so, inspection of the columns revealed that far fewer male traits were correlated with one another after size adjustment (Table 4). For example, pronotum

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Table 3. Pearson correlation matrix, adult male (above the diagonal) and female (below the diagonal) lubber nonsize-adjusted morphological traits. Significant correlations after matrix-wide Bonferonni correction are indicated in bold. See Methods section for explanation of variables.

	HL	HW	PL	PW	ML	MW	FL	TL	EL	EW
HL	-	**0.54**	0.39	0.19	0.41	0.27	**0.67**	**0.71**	**0.53**	0.33
HW	0.01	-	**0.64**	**0.56**	**0.70**	**0.67**	**0.63**	**0.61**	**0.66**	**0.55**
PL	0.09	**0.61**	-	**0.73**	**0.80**	**0.78**	**0.60**	**0.58**	0.42	**0.71**
PW	-0.14	**0.69**	**0.77**	-	**0.79**	**0.77**	0.47	0.45	0.28	**0.56**
ML	-0.03	0.26	**0.65**	**0.56**	-	**0.84**	**0.69**	**0.68**	**0.50**	**0.71**
MW	-0.11	0.42	**0.74**	**0.71**	**0.69**	-	**0.58**	**0.56**	0.47	**0.68**
FL	-0.21	0.43	**0.55**	**0.52**	0.33	0.44	-	**0.98**	**0.55**	**0.69**
TL	0.00	0.43	**0.78**	**0.58**	**0.72**	**0.71**	0.43	-	**0.56**	**0.71**
EL	0.17	**0.46**	**0.62**	**0.53**	0.27	0.42	**0.51**	0.32	-	**0.69**
EW	-0.11	**0.57**	**0.71**	**0.62**	0.29	**0.47**	0.43	**0.53**	**0.53**	-

and metapleuron widths showed no correlation with other traits after size-adjustment. Interesting, however, the lengths of the tibia and femur in males still exhibited a near perfect correlation (0.97) with one another after size adjustment (Fig. 2a).

Female size-adjusted morphological traits were also correlated across the matrix (Bartlett Chi-square statistic = 75.8, df = 36, $p < 0.0001$; Table 4). However, inspection of the columns in the matrix showed that only head width and metapleuron length exhibited significant correlations (albeit weakly) with any other traits after size adjustment. Therefore, male lubbers exhibit stronger patterns of integration in both nonsize and size-adjusted morphology compared to females.

Mantel's tests showed that the nonsize-adjusted p-matrices are only weakly correlated across the sexes ($r_m = 0.43$, $p < 0.05$), whereas the size-adjusted p-matrices are not significantly correlated between the sexes in lubbers ($r_m = 0.17$, $p < 0.20$). The p-matrix between the sexes in lubbers specifically, and phenotypic integration in general, therefore do not appear to be a modern-day constraint on the evolution of sexual dimorphism.

Discussion

Identification of constraints on the potential for males and females of the same species to respond to divergent selection pressures is an important step in understanding the evolution of sexual size dimorphism and other ecological dimorphisms. We tested the hypothesis that phenotypic integration constrains the evolution of sexual size dimorphism by comparing **P** matrices for males and females in the final instar of lubber grasshoppers. Our data show that males and females differ clearly in all morphological variables studied, with trophic and limb morphology correctly classifying individuals to sex in every case. Consistent with previous work (Vincent 2006), males and females differed significantly in overall head shape, with females exhibiting relatively wider heads than males. Moreover, examination of **P** matrices within each sex shows that males exhibit an overall higher degree of phenotypic integration for both absolute (Fig. 1) and size-corrected morphological variables (Fig. 2). Furthermore, the lack of a significant correlation between male and female size-corrected **P** matrices (and the generally weak correlation between the absolute matrices), strongly suggests a similar lack of correlation between the **G** matrices, given the previously demonstrated high correlation between **P** and **G** for morphological traits (Roff 1996). Even in the absence of genetics data, however, our findings here suggest that phenotypic integration does not act as a current constraint on the evolution of sexual size dimorphism in *R. microptera;* indeed, the stronger patterns of integration within males compared to females may even facilitate intersexual morphological divergence (Lande & Arnold 1983).

The fact that phenotypic and genetic covariances evolve is well established (Roff 2000, Steppan *et al*. 2002), but the nature of the variation in **P** and **G** matrices is less well understood. Our findings here that phenotypic integration is apparently stronger in males relative to females, is therefore an important counterpoint to studies examining interpopulational variation in **P**, because it suggests that divergent selection on the sexes can affect phenotypic variation to different degrees in males and females (Cheverud 1985, Jensen *et al*. 2003, Fedorka *et al*. 2007). In this respect, our findings are at least qualitatively in accord with those of Roff and Mousseau (2005), who showed that **P** matrix variation within species can be even greater than that among species in the grasshopper genus *Melanoplus*, as well as with those of Reusch and Blanckenhorn (1998), who showed that the sexes differed in degree of genetic variation in the dung fly *Sepsis cynipsea*. Thus, while several studies to date have demonstrated differential variation in **P** and/or **G** matrices between males and females (see also Guntrip *et al*. 1997, Coltman *et al*. 2001, Fedorka *et al*. 2007), whether such variation is a general feature of sexual dimorphism is an open issue.

Previous authors have hypothesized that the lengths of the hindlimb elements in orthopterans should be under selection as defensive adaptations against potential predators (*e.g.*, Burrows & Morris 2002, 2003). Specifically, longer hindlimbs should enable grasshoppers to either rapidly escape predation via jumping or aid in warding off an attack by kicking at the predator with its spiked hindlimbs. Indeed, many grasshopper species are superb jumpers (Bennet-Clark 1990), and some, such as the powerful *Brachystola magna*, can kick with enough force to draw blood in human fingers (D. Whitman, pers. comm.). We suggest that the ecological and evolutionary significance of hindlimb elements in eastern lubber grasshoppers are categorically different from other grasshoppers, however. Specifically, previous work has shown that lubbers do not employ jumping as their primary antipredator behavior, but instead use slow movements, coupled with toxic secretions, to avoid predation (Yosef & Whitman 1992, Hatle & Faragher 1998). As a result, hindlimb length in lubbers should not be under mortality selection as is believed to be the case for many other grasshopper species.

Lubber grasshoppers typically exist at high densities (up to $9/m^2$) (Lamb *et al.* 1999), which fosters strong male-male competition for females. After copulation, males mate-guard inseminated females by riding on their backs for many days, until the female oviposits (D. Whitman, pers. comm.). Males defend access to females by

Table 4. Pearson correlation matrix, adult male (above the diagonal) and female (below the diagonal) lubber size-adjusted morphological traits. Significant correlations after matrix-wide Bonferonni correction are indicated in bold. See Methods section for explanation of variables.

	HL	HW	PW	ML	MW	FL	TL	EL	EW
HL	-	0.45	-0.17	0.26	-0.05	**0.62**	**0.65**	**0.49**	0.30
HW	0.03	-	0.15	0.44	0.35	0.42	0.40	**0.58**	0.35
PW	-0.33	**0.47**	-	0.44	0.46	0.02	0.02	0.04	0.20
ML	-0.11	-0.05	0.17	-	**0.55**	0.46	0.47	0.30	0.40
MW	-0.26	0.06	0.36	0.43	-	0.22	0.21	0.27	0.35
FL	-0.32	0.05	0.10	-0.10	-0.02	-	**0.97**	0.42	**0.57**
TL	-0.10	0.03	0.01	**0.48**	0.36	-0.08	-	0.45	**0.62**
EL	0.23	0.17	0.17	-0.05	0.05	0.16	-0.16	-	**0.62**
EW	-0.13	0.26	0.19	-0.08	0.02	-0.04	0.08	**0.18**	-

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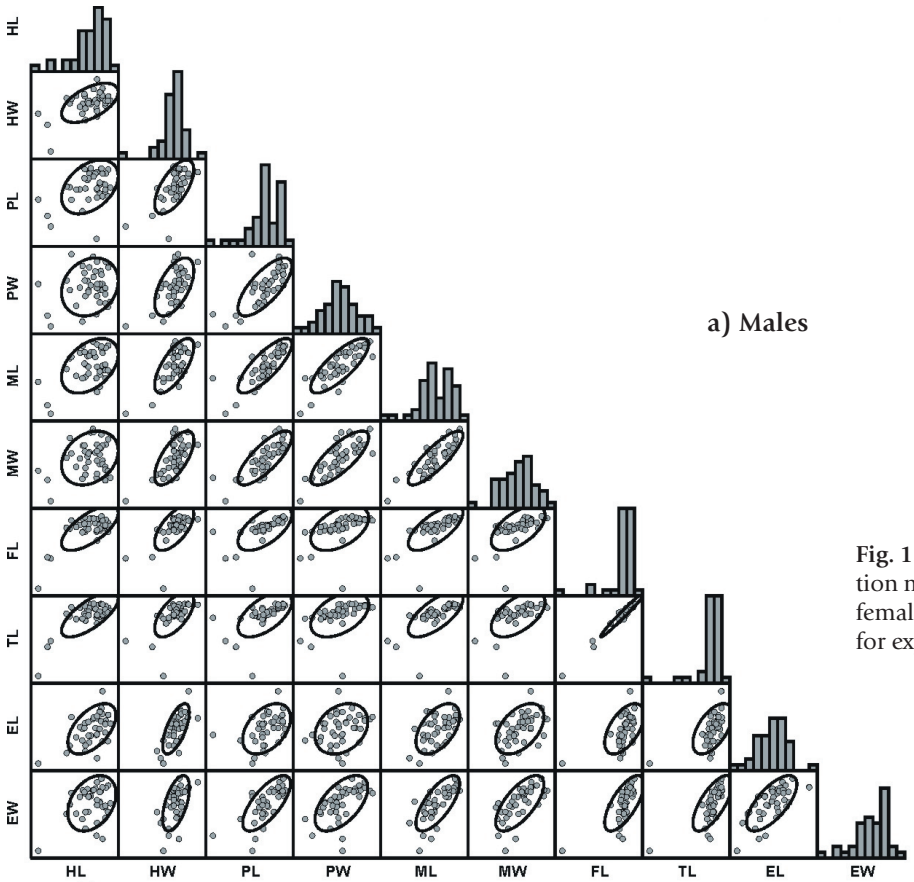

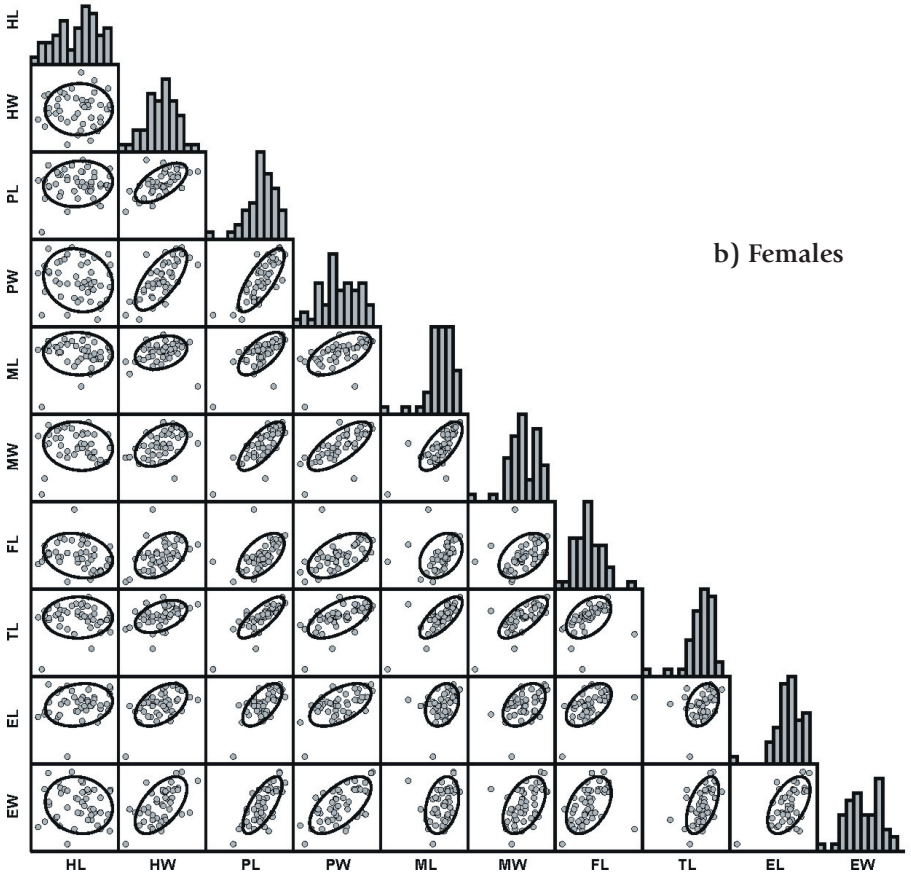

Fig. 1. Histograms and scatterplots, Pearson correlation matrix for the nonsize-adjusted **a**) male and **b**) female, morphological traits. See Methods section for explanation of variables.

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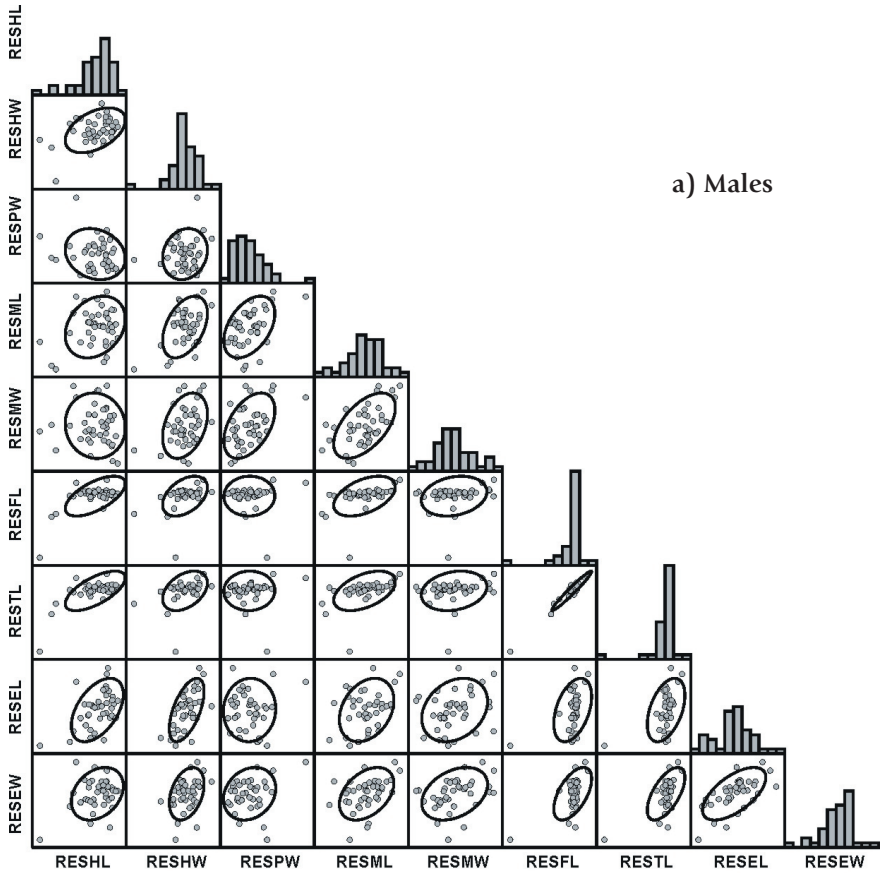

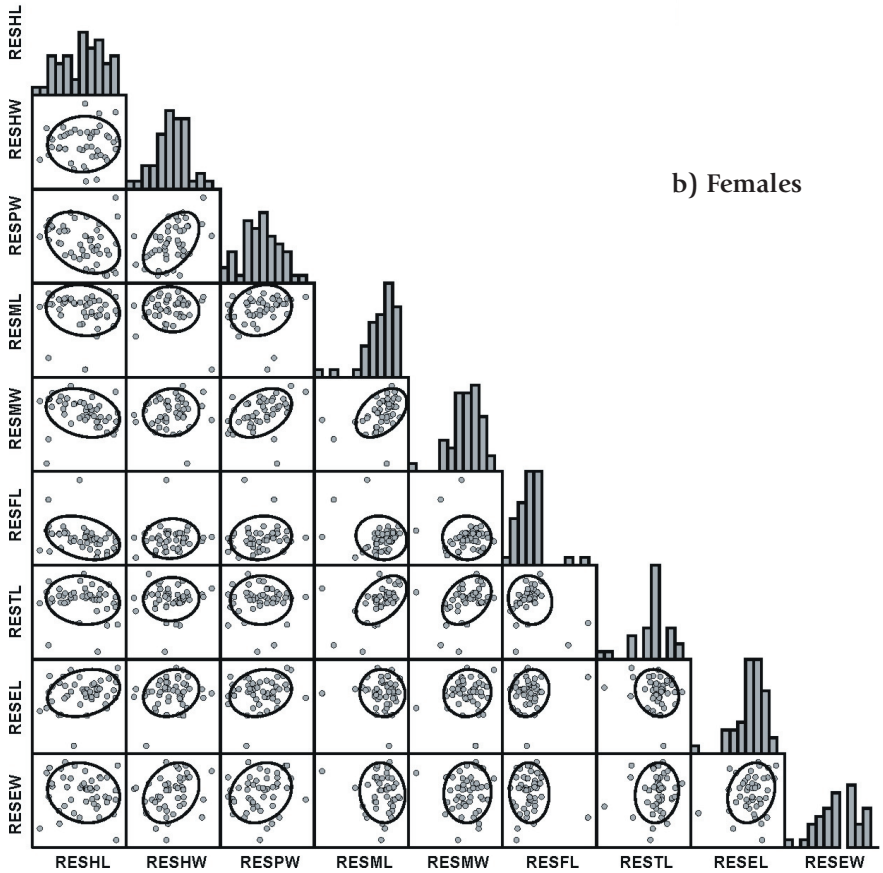

Fig. 2. Histograms and scatterplots, Pearson correlation matrix for size-adjusted **a**) male and **b**) female, morphological traits. See Methods section for explanation of variables.

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first conspicuously displaying their hind legs above their head, and then vigorously kicking at rival males. In our study population in Southeastern Louisiana, adult male lubbers set up territories around gravid females (resource defense polygyny) and then defended access by vigorously kicking at intruding males (Vincent & Lailvaux unpub.). Hence we predicted in the introduction to this paper that males should exhibit stronger patterns of hind-limb integration compared to females and the phenotypic integration analysis clearly supports this prediction: males showed a near perfect correlation between the tibia and femur in both the nonsize and size-adjusted matrices, whereas the hind limb elements were uncorrelated with one another in both matrices for females (Tables 3, 4). Further work is thus needed to directly test if hind-limb length provides a significant kicking performance advantage in lubbers and whether it influences the outcome of male contests.

More generally, the nature of variance-covariance relationships within complexes of sexually selected traits such as armaments has, to our knowledge, received little attention in any animal species (but see Blows *et al*. 2004). The present study strongly suggests that sexually selected traits could potentially shed significant light on how phenotypic integration evolves in general, and how exaggerated male morphologies evolve in particular.

In conclusion, our findings suggest that phenotypic integration does not constrain the evolution of sexual size dimorphism in the grasshopper *R. microptera*. Furthermore, morphology in general appears to be more integrated in males compared with females. These results, coupled with significant sex differences in feeding morphology and diet (Vincent 2006), suggest that selection has been important in the evolution of the **P** matrix in males and females in this species.

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References

Andersson S, 1992. Female preference for long tails in lekking Jackson's widowbirds: experimental evidence. Animal Behaviour 43: 379-388.

Arnold S.J. 1992. Constraints on phenotypic evolution. American Naturalist Supplement 140: S85-S107.

Bennet-Clark H.C. 1990. Jumping in Orthoptera, pp. 173-203. In: Chapman R.F., Joern A. (Eds) Biology of Grasshoppers. John Wiley, New York.

Berg R.L. 1960. The ecological significance of correlational pleiades. Evolution 14: 171-180.

Blanckenhorn W.U. 2005. Behavioral causes and consequences of sexual size dimorphism. Ethology 111: 977-1016.

Blows M., Chenoweth S.F., Hine E. 2004. Orientation of the genetic variance-covariance matrix and the fitness surface for multiple male sexually selected traits. American Naturalist 163: 329-340.

Burrows M., Morris O. 2002. Jumping in a winged stick insect. Journal of Experimental Biology 205: 2399-2412.

Burrows M., Morris O. 2003. Jumping and kicking in bush crickets. Journal of Experimental Biology 206: 1035-1049.

Butler M.A., Sawyer S.A., Losos J.B. 2007. Sexual dimorphism and adaptive radiation in *Anolis* lizards. Nature 447: 202-205.

Cheverud J.A. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. Evolution 39: 1335-1351.

Cheverud J.A. 1988. A comparison of genetic and phenotypic correlations. Evolution 42: 958-968.

Coltman D.W., Pilkington J., Kruuk L.E.B, Wilson K., Pemberton J.M. 2001. Positive genetic correlation between parasite resistance and body size in a free-living ungulate population. Evolution 55: 2116-2125.

Delph L.F. 2005. Processes that constrain and facilitate the evolution of sexual size dimorphism. American Naturalist 166: S1-S4.

Falconer D.S. 1989. Introduction to Quantitative Genetics. Longman, New York.

Fedorka K.M., Winterhalter W.E., Mousseau T.A. 2007. The evolutionary genetics of sexual size dimorphism in the cricket *Allonemobius socius*. Heredity 99: 218-223.

Foerster K., Coulson T., Sheldon B.C., Pemberton J.M., Clutton-Brock T.H., Kruk L.E.B. 2007. Sexually antagonistic genetic variation for fitness in red deer. Nature 447: 1107-1110.

Guntrip J., Sibley R.M., Holloway G.J. 1997. The effect of novel environment and sex on the additive genetic variation and covariation in and between emergence body weight and development period in the cowpea weevil, *Callosobruchus maculatus*. Heredity 78: 158-165.

Hatle J.D., Faragher S.G. 1998. Slow movement increases the survivorship of a chemically defended grasshopper in predatory encounters. Oecologia 115: 260-267.

Hatle J.D., Borst D.W., Juliano S.A. 2003. Plasticity and canalization in the control of reproduction in the lubber grasshopper. Integrative and Comparative Biology 43: 635-345.

Jensen H., Saether B.E., Ringsby T.H., Tufto J., Griffith S.C., Ellegren H. 2003. Sexual variation in heritability and genetic correlations of morphological traits in house sparrows (*Passer domesticus*). Journal of Evolutionary Biology 16: 1296-1307.

Jones C.G., Whitman D.W., Compton S.J., Silk P.J., Blum M.S. 1989. Reduction in diet breadth results in sequestration of plant chemicals and increases efficacy of chemical defense in a generalist grasshopper. Journal of Chemical Ecology 15: 1811-1822.

Juliano S.A., Olson J.R., Murrell E.G., Hatle J.D. 2004. Plasticity and canalization of insect reproduction: testing alternative models of life-history transitions. Ecology 85: 2986-2996.

Kachigan S.K. 1991. Multivariate Statistical Analysis: a Conceptual Introduction. Radius Press, New York.

Lamb M.A., Otto D.J., Whitman D.W. 1999. Parasitism of eastern lubber grasshopper by *Anisia serotina* (Diptera: Tachinidae) in Florida. Florida Entomologist 82: 366-371.

Lande R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain-body size allometry. Evolution 33: 402-416.

Lande R., Arnold S.J. 1983. The measurement of selection on correlated characters. Evolution 37: 1210-1226.

Manly B.F.J. 1991. Randomization and Monte Carlo Methods in Biology. Chapman & Hall, New York.

Parker T.H., Garant D. 2004. Quantitative genetics of sexually dimorphic traits and capture of genetic variance by a sexually selected condition-dependent ornament in red junglefowl (*Gallus gallus*). Journal of Evolutionary Biology 17: 1277-1285.

Pigliucci, M. 2003. Phenotypic integration: studying the ecology and evolution of complex phenotypes. Ecology Letters 6: 265-272.

Resusch T., Blanckenhorn W.U. 1998. Quantitative genetics of the dung fly *Sepsis cynipsea*: Cheverud's conjecture revisited. Heredity 81: 111-119.

Revell L., Harmon L.J., Langerhans R.B., Kolbe J.J. 2007. A phylogenetic approach to considering the importance of constraint on phenotypic evolution in the neotropical lizard *Anolis cristatellus*. Evolutionary Ecology Research 9: 261-282.

Roff D.A. 1995. The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture. Heredity 74: 481-490.

Roff D.A. 1996. The evolution of genetic correlations: an analysis of patterns. Evolution 50: 1392-1403.

Roff D.A. 2000. The evolution of the G matrix: selection or drift? Heredity 84: 135-142.

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Roff D.A., Mousseau T. 2005. The evolution of the phenotypic covariance matrix: evidence for selection and drift in *Melanoplus*. Journal of Evolutionary Biology 18: 1104-1118.

Schluter D. 1996. Adaptive radiation over genetic lines of least resistance. Evolution 50: 1766-1774.

Schluter D. 2000. The Ecology of Adaptive Radiation. Oxford University Press, Oxford.

Shine R. 1989. Ecological causes for the evolution of sexual size dimorphism: a review of the evidence. Quarterly Review of Biology 64: 419-461.

Simpson G.G. 1953. The Major Features of Evolution. Columbia University Press, New York.

Slatkin M. 1984. Ecological causes of sexual dimorphism. Evolution 38: 622-630.

Sokal R.R., Rohlf F.J. 1981. Biometry. W.H. Freeman, San Francisco.

Steppan S.J., Phillips P.C., Houle D. 2002. Comparative quantitative genetics: evolution of the G matrix. Trends in Ecology and Evolution 17: 320-327.

Vincent S.E. 2006. Sex-based divergence in head shape and diet in the Eastern lubber grasshopper (*Romalea microptera*). Zoology 109: 331-338.

Vincent S.E., Dang P.D., Kley N.J., Herrel A. 2006. Morphological integration and adaptation in the snake feeding system. A comparative phylogenetic study. Journal of Evolutionary Biology 19: 1545-1554.

Vincent S.E., Herrel A. 2007. Functional and ecological correlates of ecologically-based dimorphisms in squamate reptiles. Integrative and Comparative Biology 47: 172-188.

Wagner G.P. 1988. The influence of variation and of developmental constraints on the rate of multivariate phenotypic evolution. Journal of Theoretical Biology 1: 45-66.

Wagner G.P., Schwenk K. 2000. Evolutionarily stable configurations: functional integration and the evolution of phenotypic stability. Evolutionary Biology 31: 155-217.

Yosef R., Whitman D.W. 1992. Predator exaptations and defensive adaptations in evolutionary balance – no defense is perfect. Evolutionary Ecology 6: 527-536.

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