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BODY-SIZE AND WING-LENGTH VARIATION AMONG SELECTED GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE) FROM NEBRASKA'S SANDHILLS GRASSLANDS

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Morphological variation in six grasshopper species is examined. Statistics describing collections (adult males and females) made during July 1986 and July and August 1987 are given. Five of the species are characterized by long wings, and the sixth is wing-length dimorphic. Additional collections at several western Nebraska grassland sites were used to examine relationships between nymph population density and wing-length frequencies in adults. Coefficients of variation were also calculated to facilitate designs of future experiments.

† † †

INTRODUCTION

The presence of phenotypic variation in natural populations can be a cue indicating interesting biological phenomena. This cue is often used in research efforts investigating tradeoffs in life history traits, evidence for differential survival or reproduction, phenotypic plasticity and genetic polymorphism among others (Falconer, 1981). Additionally, variation can be an important factor affecting the design of experimental treatments and sample sizes in manipulative research, which in turn influence interpretations of results (Federer, 1955). Parametric statistical procedures inevitably require *à priori* knowledge of probability distributions for observations. Finally, descriptive data bases are intrinsically valuable by themselves. Not only do they provide a mechanism for spatial and temporal comparisons among populations, but they can also be used to evaluate the potential importance of such variation in population dynamics (Joern and Gaines, 1990).

Clearly, it would be difficult to characterize all forms of variation in any given population. Instead, I focused on external morphological characters which are used as indicators of dispersal capability and reproductive output. Specifically, dispersal theory is based on two hypotheses: 1) migration and reproduction both require significant allocations of resources and so cannot occur simultaneously and 2) wing-length variation is indicative of variation in dispersal capabilities (Johnson, 1969).

Many insects exhibit dispersal polymorphisms (Harrison, 1980; Dingle, 1985). Grasshoppers are no exception, the most notable case being gregarious and solitary locusts in sub-Saharan Africa (Uvarov, 1966, 1977). Even though North American grasshopper species are not known to swarm and migrate, intraspecific wing-length variation is frequently observed (Otte, 1979,1981,1984; Vickery and Kevan, 1983). Descriptive definitions of wing-length polymorphism employ discrete categories: wingless, brachypterous, macropterous, etc., with two or more of the categories present within populations. Other species are categorized as monomorphic. "Monomorphism" can be a somewhat misleading category since there may be considerable variation among individuals within and between populations of monomorphic species.

I examined the degree of variation in six grasshopper species from a Sandhills grassland, Arapaho Prairie, in Arthur County, NE. My goal was to determine the degree of variation in important morphological characters associated with dispersal and reproduction (Gaines, 1989). It was assumed that increasing wing lengths and body sizes are indicative of increasing dispersal and reproductive capabilities respectively.

Table I. Morphological traits and measurements (mm) for wild-caught (1986) grasshoppers. Mean, standard deviation (in parentheses), and coefficient of variation X 100% (in italics) are given for each trait.

Trait Measured (N)	*Ageneotettix deorum* (47)	*Amphitornus coloradus* (117)	*Melanoplus sanguinipes* (21)	*Mermiria bivitatta* (26)	*Phoetaliotes nebrascensis* (20)
Wing Length*	12.79	16.87	19.04	22.17	8.24
	(1.26)	(1.68)	(1.12)	(3.62)	(3.88)
	10.6	*10.0*	*5.9*	*16.3*	*47.1*
Hind Femur Length	11.76	12.38	12.43	17.61	13.08
	(1.04)	(1.18)	(0.56)	(2.92)	(1.28)
	8.8	*9.5*	*4.5*	*16.6*	*9.8*
Hind Femur Width	3.27	2.70	3.29	2.54	3.13
	(0.31)	(0.27)	(0.20)	(0.36)	(0.13)
	9.5	*10.0*	*6.1*	*14.2*	*9.9*
Hind Tibia Length	9.26	10.14	10.00	16.27	10.60
	(0.80)	(0.98)	(0.54)	(2.74)	(1.12)
	8.6	*9.7*	*5.4*	*16.8*	*7.0*
Middle Femur Length	4.02	4.07	4.55	5.08	4.43
	(0.41)	(0.41)	(0.37)	(0.75)	(0.31)
	10.2	*10.1*	*8.1*	*14.8*	*7.0*
Fore Femur Length	3.39	3.30	3.73	4.67	3.86
	(0.33)	(0.29)	(0.33)	(0.60)	(0.27)
	9.7	*9.9*	*6.3*	*15.5*	*11.5*
Head Length	3.40	3.75	3.17	4.84	3.56
	(0.24)	(0.37)	(0.20)	(0.75)	(0.41)
	7.1	*9.9*	*6.3*	*15.5*	*11.5*
Head Width	4.20	3.82	4.16	3.94	4.28
	(0.41)	(0.44)	(0.24)	(0.81)	(0.49)
	9.8	*11.5*	*5.8*	*20.6*	*11.4*
Pronotum Length	3.55	3.94	4.96	4.94	5.26
	(0.35)	(0.40)	(0.30)	(0.83)	(0.45)
	9.9	*10.1*	*6.0*	*16.8*	*8.6*
Pronotum Width	3.87	3.62	3.76	3.81	4.07
	(0.35)	(0.41)	(0.17)	(0.77)	(0.45)
	9.0	*11.3*	*4.5*	*20.2*	*11.1*
Pronotum Height	3.93	3.72	4.07	3.81	4.31
	(0.36)	(0.48)	(0.22)	(0.73)	(0.53)
	9.2	*12.9*	*5.4*	*19.2*	*12.3*

*Measurements for both fore- and hind wings require destruction of specimens but have shown a strong correlation (R^2 = 0.94). Hind-wing lengths were used for all analyses to ensure that vouchers remain intact.

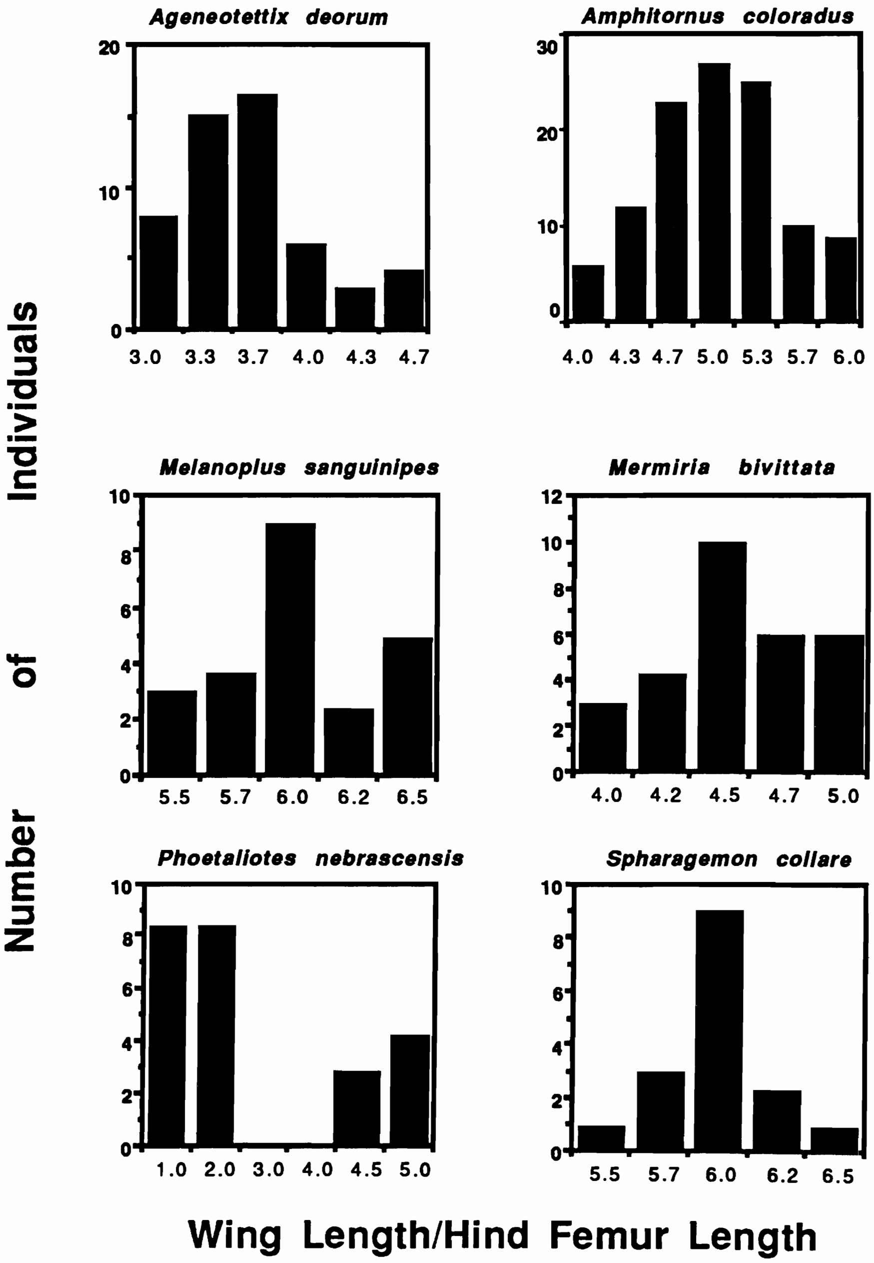

Figure 1. Frequency distributions for 5 long-winged grassland grasshopper species showing continuous wing-length variation and one dimorphic species. Wing-length/hind-femur length ratios are used to standardize size among large and small grasshopper species as well as those showing strong sexual dimorphism.

MATERIALS AND METHODS

Collections

I collected adult individuals of five grasshopper species in July 1986 and measured eleven morphological traits (wing length, hind-femur length and width, hind-tibia length, middle-femur length, fore-femur length, head length and width, and pronotum length, width, and height). In 1987, I collected samples of three grasshopper species in July (early season) and August (late season). Comparisons of three morphological traits (wing length, hind-femur length and head length) between two collection dates allowed me to determine whether any changes in distributions occurred through time. Finally, for the only wing-length dimorphic species included in this study, *Phoetaliotes nebrascensis*, I collected samples from several grassland sites in western Nebraska during July, August and September 1987 to examine the prediction that increasing nymph-densities are related to increasing frequencies of long-winged adults.

All collections were made on sunny days with little wind (<10 mph). At Arapaho Prairie, sampling was executed in three 30 min periods. After fifty consecutive sweeps were taken while I walked along a randomly selected compass heading, I emptied my net completely into a collecting bag, fifty more sweeps were taken, emptied, etc., until 30 minutes had passed. Each 30-min sample was collected on a different, randomly selected, compass heading. At all other grassland sites, I sampled by sweeping along two 50 m transects within the site. Specimens were sorted and individuals of the target species were pinned, labelled and air dried for measurements to be taken at a later date. All measurements were made using an ocular micrometer.

Statistics

Means, standard deviations, coefficients of variation, and wing-length frequency distributions were calculated for all Arapaho Prairie collections. Distribution means and variances were compared using t-tests and Bartlett's test for homogeneity of variance. Principal components analysis (PCA) was used to examine relationships among morphological characters for 1986 collections (11 morphological variables). SAS Version 5.16 (SAS Institute, 1985) was used for all statistical analyses.

RESULTS

Descriptive statistics for five species and eleven morphological variables are given in Table I. All species show some sexual dimorphism in body size; *Mermiria bivitatta* is the most dimorphic and shows the largest coefficients of variation. Also, *Phoetaliotes nebrascensis* is wing-length dimorphic (short vs. long wings) and has an extremely large coefficient of variation associated with wing length measurements. Frequency distributions for relative wing lengths (corrected for body size to remove sexual dimorphic effects) are shown in Figure 1. In no case are species characterized as "monomorphic" though none of the long-winged species exhibits the same magnitude of variation as the dimorphic species.

The first principal component generated by the PCA described 79% of the variation in morphological characters and had positive loadings for all variables with wing length, hind-femur length and head length heavily weighting PCA scores. I interpret this result as a combination of dispersal capability and size; individuals with long wings relative to their body size and larger individuals (longer hind-femur and head lengths) had slightly larger scores. I did not use any of the other ten principal components as none described more than 8% of the variation by itself.

Collections of early- and late-season individuals from the same populations did not suggest that frequency distributions changed during the course of this season (Fig. 2). Population sizes did decrease; however, sample sizes were much smaller in the late season collections even though the same methodology was used each time.

Nymph and adult sample-sizes and frequencies of long-winged adults from *Phoetaliotes nebrascensis* collections at eight grassland sites are given in Table II. Long-wing frequencies were low at all sites and so did not provide supporting information for relationships between increasing density and increasing dispersal tendencies.

DISCUSSION

In general, samples of grasshoppers from Arapaho Prairie show between 8 and 11% variation in mean morphological measurements. This value is fairly consistent both across different variables and across different species. Certain obvious traits add to observed variation but can be accounted for by simple sorting techniques. For example, pooling samples of sexually-dimorphic species can increase coefficient of variations to 15–20% of the mean; separate analyses of males and females would reduce

Table II. Summary of geographical analysis of wing-length frequencies in selected populations in western Nebraska. Mean number of individuals is given for two 50-m transects at each site.

Site	Date	Nymphs	Adults	% Long
Crescent Lake #1	7/13/88	251	-	-
(North Garden County)	8/26/88	67.5	112.5	0.9
	9/18/88	7	100	0.4
Crescent Lake #2	7/13/88	180.5	-	-
(North Garden County)	8/26/88	15.5	68	2.1
	9/18/88	1.5	39	0.0
Enders Reservoir #1	7/28/88	299.5	2	0
(Chase County)	8/30/88	32	94.5	0.6
	9/20/88	14.5	34.5	0
Enders Reservoir #2	7/28/88	322.5	1	0
(Chase County)	8/30/88	38.5	79	0.6
	9/20/88	10.5	27.5	0
Oshkosh	7/12/88	160.5	-	-
(South Garden County)	8/26/88	16	39	0
	9/18/88	0	40.5	0
Swanson Reservoir	7/28/88	131.5	8.5	0
(Hitchcock County)	8/30/88	15.5	43.5	1.0
	9/20/88	4.5	17.5	0
Wilson Ranch #1	7/13/88	83.5	-	-
(Arthur County)	8/26/88	10.5	48	2.0
	9/18/88	2	31	1.8
Wilson Ranch #2	7/13/88	312.5	-	-
(Arthur County)	8/26/88	32	103.5	0
	9/18/88	12	30.5	0

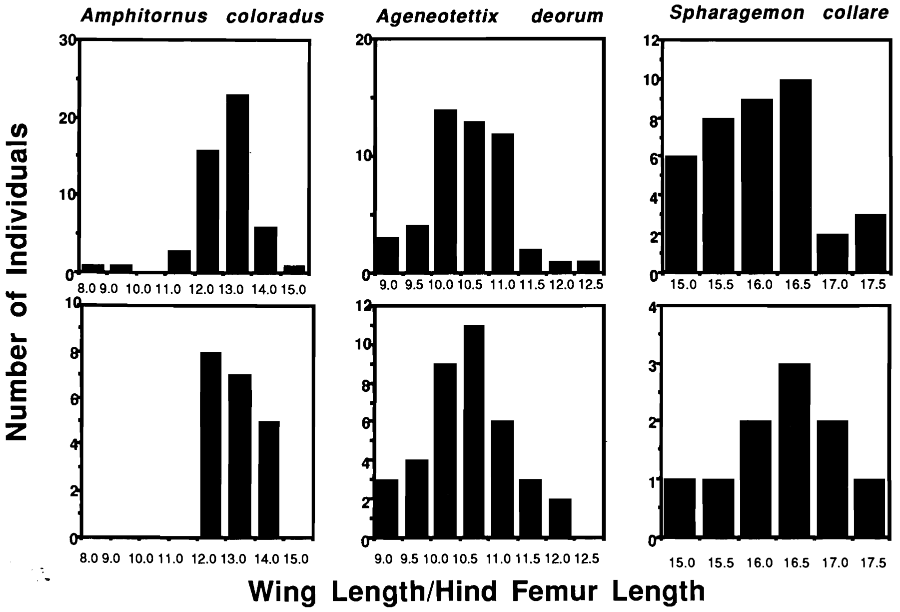

Figure 2. Wing-length/hind-femur length frequency distributions for early- (upper) and late- (lower) season collections of three species. Smaller sample sizes in late-season collections resulted from smaller populations. *A. coloradus*: t-test $p > 0.15$;: Bartlett's $p > 0.15$. *A. deorum*: t-test $p >> 0.20$; Bartlett's $p >> 0.20$. *S. collare*: t-test $p >> 0.20$; Bartlett's $p >> 0.20$.

this variation significantly. Wing-length dimorphism also produces an extremely large coefficient of variation for wing length; sorting long- and short-winged individuals would again alleviate much of this variation.

Wing-length distributions remained unchanged throughout the adult lifetimes of three species. The similarity in range and shape of early and late season distributions indicates that longer-winged individuals were not removed from the population, as would be predicted if longer-winged individuals dispersed.

Few long-winged *Phoetaliotes nebrascensis* adults were collected from a variety of grassland sites which had large nymph populations. Although it is possible that long-winged individuals were produced but dispersed between collection dates, it seems unlikely given the consistently low frequencies at all sites and all dates when adults were observed. Sample sizes did decrease throughout the season. Without further information, however, it is not possible to separate dispersal, as a potential explanation, from numerous other biotic and abiotic factors known to influence grasshopper population dynamics (Joern and Gaines, 1990).

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