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Plant Preference and Plant Succession

A Consideration of Evolution of Plant Preference in *Schistocerca*

Daniel Otte

Department of Zoology, University of Texas, Austin, Texas 78712

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Summary. The theory that early successional plants and annual plants will be less well defended against generalist herbivores than later successional plants and perennial plants, because they avoid herbivores by escaping in space and time, is evaluated. The theory is not supported in the ecosystem examined. The correlation between level of preference and the ability of plants to support growth and survival is examined and shown to be high.

Introduction

Cates and Orians (in press) give evidence that chemical defenses of plants are correlated with their successional status. They argue that since early successional stages grow rapidly, mature early, disperse their seeds quickly and have high rates of population turnover, their locations may be unpredictable in space and time. Generalist herbivores feeding on those plants might, as a result, be less likely to find them. Consequently, Cates and Orians predict that early successional plants will devote less energy to defenses against herbivores. If this is the case, such plants should be more edible to generalist herbivores than later successional plants which are more predictable in space and time. Carrying out preference studies on forest and weedy plants in the Pacific Northwest, with slugs as generalist herbivores, their predictions are largely supported.

In the present paper we evaluate the validity of their theory for an entirely different ecosystem and for very different organisms. I had previously carried out preference studies of Texas plants, using polyphagous grasshoppers (*Schistocerca*), without knowledge of the Cates-Orians theory. The original goal of the preference studies was to assemble a preliminary list of plant taxa and their relative edibilities to generalist herbivores. Preference data were collected from three related polyphagous grasshoppers, *Schistocerca americana*, *S. emarginata*, and *S. obscura*.

The ultimate reasons why certains plants are acceptable and other are rejected may be complex and involve the interactions of various factors, but four general kinds of factors may be principally responsible for selecting for degree of edibility. These are a) chemical defenses which may adversely affect survival or growth; b) structural inhibitors to feeding which protect otherwise edible or nutritious plants; c) nutrient content for support of growth and reproduction; or d) degree of protection offered by the plant against physical or biotic limiting factors (*e.g.*, desication, visually hunting predators). The last factor acts indirectly insofar as the herbivore evolves the ability to utilize a plant that is desirable for other reasons.

The present paper lists the preferences of three grasshopper species in relation to a large number of plants belonging to a wide variety of plant taxa and belonging to different successional stages. It also examines the relationship (or correlation) between the degree of preference of *Schistocerca americana* for a given plant and the ability of that plant to support growth and survival. For the latter test I chose from among the large series of plants, whose relative edibility was known, a series of eight species for which *S. americana* displayed quite different degrees of preference.

Methods

1. Taxonomic-Ecological Survey. Feeding trials were carried out in the summer of 1971 on plants collected around Austin, Texas. Early successional plants were collected mainly from vacant lots and along roadsides, while later successional plants were collected from along railroad lines and from relatively less disturbed hillsides west of the city. Plants were cut and transported back to the laboratory in water. From 2 to 5 plant species were used during each trial; this included one edible species which served as a standard against which feeding on other plants could be compared. Nymphs of *S. emarginata* and *S. obscura* were hatched from eggs layed the previous fall by field-caught adults. Nymphs of *S. americana* hatched from eggs of adults caught in the Spring of that same year. Trials were carried out in wire gauze cages of two sizes. Smaller cages (1′×1′×1′) each contained at least 100 individuals. Trial plants were left in cages for at least 2 days. The amount of feeding on each plant was estimated on a scale from 0 to 5. A plant left completely untouched was scored 0, and a plant largely or completely defoliated was scored 5. Some plants were used in several trials and in different combinations, others were tested only once. Plants were subsequently identified by a systematic botanist (Dr. B. L. Turner) and classified into the following broad categories:

a) native (N) or introduced (I);
b) annual (A), perennial (P), or tree-shrub-vine (TSV);
c) successional stage (1, 2, or 3).

Successional stage 1 plants include the very first species likely to enter a disturbed area; stage 3 plants are climax plants.

2. Association between Edibility and Suitability. Eight plant species differing in edibility were tested for suitability, *i.e.*, for their ability to promote growth and survival. Eight groups of 26 early instar (1st and 2nd) nymphs of *S. americana* were raised to the adult stage on each of 8 plant species differing in edibility. At 1 week intervals number of surviving individuals and number of adults were counted. All individuals in a group were weighed together and a mean weight was computed. Preference for plants was determined using a group of animals being reared separately on a mixed diet. Preferences were carried out twice, once at the beginning and once at the end of the rearing experiment. In the first test 15 late instar nymphs (4 male and 11 female) were presented with each of 8 test plants. Each individual was presented with the test plant for 2 min after a day of starvation. In the second test 25 adults (12 male and 13 female were used. Criteria used to determine preferences were a) total time spent in feeding; b) number of interruptions in feeding, and c) number of times individuals bit into a plant without chewing.

Results

(1) The high degree of polyphagy in *Schistocerca* is seen in the fact that only 23% of the naturally occurring plants tested in the vicinity of Austin were not eaten at all (33 out of 140) (Table 1). Of the plants eaten, about 28% were readily eaten (preference levels between 2.5 and 5). Preference levels of the three species for all plants tested are given in Table 1.

(2) Table 2 compares preferences for native annuals (NA) native perennials (NP) and native trees, shrubs and vines (NTSV). NA plants are relatively less

Table 1. Plants tested and preference levels displayed by three polyphagous grasshopper species, *Schistocerca emarginata* (S.e.), *S. obscura* (S.o.), and *S. americana* (S.a.). A = annual plant; P = perennial plant; T = tree; S = shrub; V = vine; 1, 2, and 3 (under status) = successional stage

No.	Species	Family	Status	Preference level in			Mean	Family mean
				S.e.	S.o.	S.a.		
3.	*Medicago hispida*	Poaceae	A I 1	2.16	1.6		1.88	2.68
1.	*Bromus catharticus*	,,	A I 1	3	3		3.00	
9.	*Bromus* sp.	,,	A I 1	3.33	3		3.16	
18.	*Distichlis spicata*	,,	P N 3	2.5			2.50	
20.	*Stenotarphrum gramineum*	,,	P I 1	3			3.00	
116.	*Bothriochloa saccharoides*	,,	P N 2	2			2.00	
117.	*Paspalum dilatatum*	,,	P N 1	2			2.00	
202.	*Paspalum* sp.	,,	P N 1		2		2.00	
19.	*Sorghum halepense*	,,	P I 1	5	5	5	5	
145.	*Elymus canadensis*	,,	A N 2	5			5.00	
162.	*Phragmites* sp.	,,	P I —	0			0.00	
190.	*Leptochloa* sp.	,,	P N 2	3	3		3.00	
142.	*Sorghum*	,,	P I —	4.5	4.4	5	4.66	
6.	*Sonchus oleraceus*	Asteraceae	A I —	0.94	1.00	3.3	2	0.90
14.	*Conyza canadensis*	,,	A N 1	0.5	1.0		1	
32.	*Ambrosia trifida*	,,	A N 1	1.0	1.6	2.0	2	
34.	*Parthenium hysterophorus*	,,	A N 1	1.5			1.5	
36.	*Ratibida columnaris*	,,	A N 1	1.0	0.75		1.0	
38.	*Achillea millefolium*	,,	P N 1		0		0	
43.	*Aster subulatus*	,,	A N 1	0			0	
44.	*Hymenopappus scabiosaeus*	,,	B N 2	0	1	0.33 (3)	1	
58.	*Gaillardia pulchella*	,,	A N 1	0 (2)	0		0	
59.	*Coreopsis tinctoria*	,,	A N 1	0.2	1		1	
56.	*Engelmania pinnatifida*	,,	P N 2		1	2	1.5	
61.	*Lindheimera texana*	,,	A N 2			1	1	
71.	*Heterotheca psammophila*	,,	A N 1	1	0.5		1	
76.	*Rudbeckia* sp.	,,	A N 1	2 (3)	1	1	1.3	
81.	*Ambrosia psilostachya*	,,	P N 1	1	0 (2)		0.5	
82.	*Helianthus* sp.	,,	A N 1	0	0		0	
84.	*Aphanostephus ramosissimus*	,,	A N 1	0	0		0	
96.	*Liatris* sp.	,,	P N 2	0			0	
97.	*Centaurea americana*	,,	A N 1	0.5 (2)	1	1	0.8	
105.	*Aster* sp.	,,	P N 2	0 (2)	0		0	
108.	*Senecio* sp.	,,	A N 1	4 (2)	5		4.5	
118.	*Helianthus annus*	,,	A N 1	0	0	1	1	
120.	*Vernonia* sp.	,,	P N 2	0			0	
122.	*Lactuca* sp.	,,	A I 1	0.5 (2)			0.5	
134.	*Aster* sp.	,,	P N 2	0	1		0.5	
188.	*Heterotheca latifolia*	,,	P N 1	2.5 (4)	5	4	3.8	
192.	*Aster* sp.	,,	P N 2			0	0	
196.	*Conyza canadensis*	,,	A N 1	0		0	0	
197.	*Vernonia* sp.	,,	P N 2			0	0	
211.	*Vernonia lindheimeri*	,,	P N 3	1	0		0.5	
216.	*Zexmenia hispida*	,,	P N 3			2.5 (2)	2.5	
220.	*Gutierezia* sp.	,,	A N 1			0	0	

Table 1 (continued)

No.	Species	Family	Status	Preference level in			Mean	Family mean
				S.e.	S.o.	S.a.		
4.	*Lamium amplexicaule*	Lamiaceae	A I 1	2 (6)			2	0.64
57.	*Monarda citriodora*	,,	A N 1	0.5 (2)	2 (3)		1.25	
143.	*Salvia farinacea*	,,	P N 2	0.5 (2)			0.25	
163.	*Salvia coccinea*	,,	P N 1	0			0	
172.	*Monarda pectinatus*	,,	A N 1	0	0		0	
209.	*Hedeoma drummondii*	,,	A N 2	0		0	0	
137.	*Salviastrum texanum*	,,	P N 3	1			1	
7.	*Oenothera speciosa*	Onagraceae	A N 1	2.8 (7)	1 (3)		1.9	1.37
8.	*Oenothera serrulata*	,,	P N 2	3.1 (11)	2.3 (3)		2.7	
24.	*Gaura parviflora*	,,	A N 1	0.5 (4)	2		1.25	
56a.	*Oenothera laciniata*	,,	A N 1		0.5 (2)	1.5	1	
146.	*Gaura coccinea*	,,	P N 1	0 (4)	0 (2)		0	
10.	*Torilus arvensis*	Apiaceae	A I 1	4.3 (39)	4 (15)	4.6	4.3	2.81
45.	*Daucus pusillus*	,,	A N 1	0 (2)	0		0	
62.	*Oxypolis rigidior*	,,	P N 2	5 (2)	4	0	3	
119.	*Polytaenia nuttallii*	,,	P N 2	2.5 (4)	3.3 (3)	1	2.26	
63.	*Chaerophyllum* sp.	,,	A N 1	5	4		4.5	
11.	*Oxalis dillenii*	Oxalidaceae	A N 1	2 (5)	3 (2)	1	2	2.0
13.	*Melilotus indicus*	Fabaceae	A I 1	3 (2)	0.75 (4)	1 (2)	1.58	1.47
23.	*Lupinus texensis*	,,	B N 1	1.66 (3)			1.66	
79.	*Amorpha fruticosa*	,,	S N 2	1.75 (4)	3 (3)		2.37	
114a.	*Psoralea* sp.	,,	P N 2	0.5 (4)	1		0.75	
	Locoweed	,,	A N 1			1	1	
28.	*Commelinatia pringlei*	Commelinaceae	P N 2	1 (3)			1	1.0
30.	*Lepidium virginicum*	Brassicaceae	A N 1	2.75 (4)	4.2 (5)	1	2.65	2.65
33.	*Geranium texanum*	Geraniaceae	A N 1	5			5	5.00
89.	*Sapium sebiferum*	Euphorbiaceae	T I 1	1	0.5 (2)		0.75	2.34
136.	*Croton* sp.	,,	A N 1	3.2 (6)	3 (2)	1	2.4	
152.	*Poinsettia dentata*	,,	A N 1	0 (2)	2 (3)		1	
159.	*Croton* sp.	,,	P N 2	3.5 (6)	3.5 (4)		3.5	
173.	*Croton* sp.	,,	P N 1	4.6 (5)	3.6 (3)	3	3.73	
212.	*Stillingia texana*	,,	P N 3	3	1 (2)	4	2.66	
37.	*Amaranthus* sp.	Amaranthaceae	A N 1		2	1	1.5	0.5
164.	*Amaranthus* sp.	,,	A N 1	0 (2)	0.5 (2)		0.25	
194.	*Amaranthus* sp.	,,	A N 1	0	0.5 (2)		0.25	
221.	*Amaranthus* sp.	,,	A N 1		0		0	
46.	*Verbena bipinnatifida*	Verbenaceae	A N 2	0 (2)	0		0	0.5

Table 1 (continued)

No.	Species	Family	Status			Preference level in			Mean	Family mean
						S.e.	S.o.	S.a.		
74.	*Vitex* sp.	Verbenaceae	T	—	1	2.5 (2)	1		1.75	
115.	*Lantana horrida*		S	N	1	0	0		0	
171.	*Vitex* sp.	”	S	—	1	1 (2)	0.5 (2)		0.75	
200.	*Lantana camara*	”	S	—	2	0	0 (2)	0	0	
50.	*Valerianella amarella*	Valerianaceae	A	N	1	2	1.5 (2)		1.75	1.75
73.	*Melia azedarach*	Meliaceae	T	—	1	0.2 (5)	0 (3)	0	0	0
94.	*Abutilon incanum*	Malvaceae	P	N	2	2.43 (7)	3.6 (3)	2	2.67	3.53
135.	*Sida* sp.	”	P	N	1	2 (2)	4 (2)	3	3	
156.	*Sida rhombifolia*	”	P	N	1	5 (10)	5 (8)		5	
244.	*Sida physocalyx*	”	P	N	2			5	5	
204.	*Malviscus drummondii*	”	S	N	2	2			2	
	Bumelia lanuginosa	Sapotaceae	T	N	2	1.5 (3)	2 (3)	3 (2)	2.16	2.16
65.	*Ulmus crassifolia*	Ulmaceae	T	N	2	3 (2)	2.3 (3)		2.65	3.45
88.	*Celtis laevigata*	”	T	N	2	3 (27)	5 (52)	3	3.66	
	Ulmus americana	”	T	N	3	4.5 (2)	3.6 (3)		4.05	
66.	*Prosopis juliflora*	Mimosaceae	T	N	2	1 (2)	1		1	1.1
98.	*Acacia angustissima*	”	T	N	2	1	0.6 (3)	0	0.8	
	Mimosa	”	T	—	—	3	0		1.5	
72.	*Quercus* sp.	Fagaceae	T	N	3	4 (7)	1.6 (3)		2.8	2.93
102.	*Quercus virginiana*	”	T	N	3	3	4 (2)		3.5	
	Quercus stellata	”	T	N	3	4	1		2.5	
	Platanus occidentalis		T	N	2	2.6 (3)	1.5 (2)	3 (2)	2.36	2.36
75.	*Chenopodium album*	Chenopodiaceae	A	—	1	2.5 (3)	4		3.25	3.25
78.	*Houstonia nigricans*	Rubiaceae	P	N	2		0.6 (3)		0.6	1.37
99.	*Rubus* sp.	”	P	N	1	3.3 (3)	1		2.15	
80.	*Ilex* sp. ?	Aquifoliaceae	S	N	2	1	0		0.5	0.75
205.	*Ilex decidua*	”	S	N	2	1 (3)	1		1	
83.	*Solanum eleagneafolium*	Solanaceae	P	N	1	2 (2)	4	2 (2)	2.66	1.05
138.	*Solanum dimidiatum*	”	P	N	2	0.5 (2)			0.5	
86.	*Physalis* sp.	”	P	N	1	0	0		0	
87.	*Jasminum* sp.	Oleaceae	S	—	1	1 (2)	1		1	1.5
109.	*Ligustrum* sp.	”	S	—	1	2 (3)	2 (4)		2	
90.	*Hicoria pecan*	Juglandaceae	T	N	3	4.5 (2)	3 (2)	4.5 (5)	4	4.0
91.	*Salix nigra*	Salicaceae	T	N	1	4 (4)	2	2	2.66	2.66

Table 1 (continued)

No.	Species	Family	Status			Preference level in			Mean	Family mean
						S.e.	S.o.	S.a.		
92.	*Ampelopsis arborea*	Vitaceae	V	N	1	0.6 (2)	1		0.8	0.8
93.	*Ipomaea* sp.	Convolvulaceae	V	N	1	0			0	0
100.	*Rumex* sp.	Polygonaceae	P	N	1	0.5 (2)	1	0	0.75	2.87
131.	*Rumex crispus*	,,	P	N	2	5 (2)	5		5	
101.	*Sapindus drummondii*	Sapindaceae	T	N	2	0	0 (2)		0	0
104.	*Lithospermum* sp.	Boraginaceae	P	N	2	0			0	0
238.	*Heliotropium convolvulaceum*	,,	P	N	2			0	0	
107.	*Toxicodendrom radicans*	Anacardiaceae	V	N	2	0	1		0.5	1.8
157.	*Rhus aromatica*	,,	S	N	2		2		2	
210.	*Rhus virens*	,,	S	N	1	4 (3)	0	5	3	
110.	*Aesculus pavia*	Hippocastenaceae	S	N	2	0	0		0	0
112.	*Nerium oleander*	Apocynaceae	S	—	1	0	0	0	0	0
115b.	*Phacelia congesta*	Hydrophyllaceae	A	N	1	0	0		0	0
121.	*Juniperus ashei*	Cupressaceae	S	N	2	0 (2)	0 (2)		0	0
208.	*Cassia lindheimiana*	Caesalpiniaceae	P	N	2		2 (2)	1	1.5	1.5
214.	*Asclepias* sp.	Asclepiadaceae	P	N	3	5	3		4	4
144.	*Ruellia* sp.	Acanthaceae	P	N	2	1 (2)	5		3	3
158.	*Ptelea trifoliata*	Rutaceae	S	N	2	5 (5)	0.75 (4)		2.87	2.87
176b.	*Leucophyllum frutescens*	Scrophulareaceae	S	N	2	1	0		0.5	0.5
	Tribulus terrestris	Zygophyllaceae	A	N	1	0 (2)	0	4	1.33	1.33
184.	*Mentgelia* sp.	Loasaceae	A	N	1	2.5 (2)	0		1.25	1.25
183.	*Berberis trifoliata*	Berberidaceae	S	N	2	4	2		3	3

Table 1 (continued)

No.	Species	Family	Status	Preference level in S.e.	S.o.	S.a.	Mean	Family mean
185.	*Polanisia dodecandra*	Coppand-aceae	A N 1	1	0		0.5	0.5
207.	*Acer* sp.	Aceraceae	T N 1	0			0	0
Cultivated plants								
170.	*Lonicera* sp.				1		1	
176.	*Morus* sp.	Moraceae	T — —	0.5 (3)	0.5 (2)		0.5	
165.	*Pittosporum* sp.		S — —	0 (3)			0	
203.	*Punica* sp.		T — —	4	5		4.5	
	Rosa sp.		S — —	5			5	
	Mulberry		T — —		1	5	3	

Table 2. Edibility of native annual (NA) and native perennial herbs (NP) and native trees, shrubs and vines (NTSV). Numbers in parentheses indicate percent of plant species in each category. S.e. = *Schistocerca emarginata*; S.o. = *S. obscura*; S.a. = *S. americana* (low: 0–2.5; high: 2.5–5)

Preference level	Number of plant species tested in: S.e.	S.o.	S.a.	all 3 species (mean)
		Native annuals		
low	31 (79)	31 (86)	14 (93)	44 (90)
high	8 (21)	5 (14)	1 (6)	5 (10)
		Native perennials		
low	23 (66)	18 (58)	11 (65)	29 (64)
high	12 (48)	13 (42)	6 (35)	16 (36)
		Native trees, shrubs, and vines		
low	17 (59)	21 (80)	2 (33)	21 (68)
high	12 (41)	5 (20)	4 (66)	10 (32)

edible than NP or NTSV plants, and there is no significant difference in preference for NP and NTSV plants. Also, the preferences of the three grasshopper species are not significantly different.

(3) Preferences for native plants in successional stages 1 and 2 were not different, but both stages appear to have a lower proportion of preferred species than stage 3 plants, most of which were trees. Preferences of the three grasshopper species are again not different.

(4) A comparison between NA plants of different successional stages is not possible because few NA2 plants were found. Among NP species, no difference was found between stage 1 and stage 2 plants. Among stage 1 plants, NA species have a higher proportion of relatively inedible species than NP and NTSV species.

Table 3. Significance of comparisons shown in Table 2

Comparison	d.f.	χ^2	P^a
NA—NP	1	7.3	0.01
NA—NTSV	1	4.7	0.05
NP—NTSV	1	0.002	n.s.
S.e.—S.o. (NA)	1	0.2	n.s.
S.e.—S.o. (NP)	1	0.15	n.s.
S.e.—S.o. (NTSV)	1	2.19	n.s.

[a] χ^2 test for two independent variables.

Table 4. Edibility of native plants in successional Stages 1, 2, and 3 (N1, N2, and N3) (low: 0–2.5; high: 2.5–5)

Preference level	Number of plants tested in:			
	S.e.	S.o.	S.a.	all three species
		Native Stage 1 plants		
low	43 (78)	40 (80)	17 (77)	52 (81)
high	12 (22)	10 (10)	5 (23)	12 (19)
		Native Stage 2 plants		
low	28 (70)	25 (74)	12 (75)	37 (76)
high	12 (30)	9 (26)	4 (25)	12 (24)
		Native Stage 3 plants		
low	2 (20)	4 (50)	0 (0)	4 (36)
high	8 (80)	4 (50)	3 (100)	7 (64)

A large share of NA plants belong to the generally less edible Asteraceae. Therefore, the difference between annual and perennial species shown in Table 6 has a strong taxonomic bias. Preferences shown by the three grasshopper species are not significantly different.

(5) Comparisons among various classes of introduced species is difficult because of the small number tested, but no significant difference between introduced annuals (IA) and introduced perennials plus trees, shrubs, and vines (IP + ITSV) is evident (Fisher Exact Probability Test).

(6) Average edibility of introduced annuals (Table 8) is higher than the average edibility of native annuals (Table 2); but this is merely a trend since not enough introduced annuals were tested.

(7) The associations between preference, growth rate, and mortality are given in Figs. 1–3 and Tables 9 and 10. Some changes in preference are obvious between the beginning and the end of the experiment, *i.e.*, between the first and second test. Late instar nymphs were used during the first test and adults were used in the 2nd test. Thus, changes in preference could be due to the developmental changes in the grasshoppers or to phenological changes in the plants or both.

Table 5. Significance of comparisons shown in Table 4

Comparison	d.f.	χ^2	P_1
N1—N2	1	0.26	n.s.
N1—N3	1	8.45	0.01
N2—N3	1	4.68	0.05
S.e.—S.o. (N1)	1		n.s.
S.e.—S.a. (N1)	1		n.s.
S.e.—S.a. (N2)	1		n.s.

Table 6. Edibility of native annuals, native perennials, and native trees, shrubs and vines in successional Stages 1, 2 and 3

Preference level	S.e.	S.o.	S.a.	All species (mean)
		NA1		
low	29 (80)	29 (85)	13 (93)	40 (91)
high	7 (20)	5 (15)	1 (7)	4 (9)
		NA2		
low	3 (75)	2 (100)	2 (100)	3 (75)
high	1 (25)	0 (0)	0 (0)	1 (25)
		NP1		
low	8 (66)	7 (58)	2 (40)	9 (64)
high	4 (33)	5 (42)	3 (60)	5 (36)
		NP2		
low	12 (66)	9 (56)	9 (90)	16 (70)
high	6 (33)	7 (44)	1 (10)	7 (30)
		NP3		
low	2 (40)	3 (75)	0 (0)	3 (50)
high	3 (60)	1 (25)	2 (100)	3 (50)
		NTSV1		
low	5 (71)	5 (100)	1 (50)	5 (71)
high	2 (29)	0 (0)	1 (50)	2 (29)
		NTSV2		
low	13 (72)	16 (89)	1 (25)	14 (78)
high	5 (28)	2 (11)	3 (75)	4 (22)
		NTSV 3		
low	0 (0)	2 (40)	0 (0)	1 (20)
high	5 (100)	3 (60)	1 (100)	4 (80)

Table 7. Significance of comparisons shown in Table 6

Comparison	d.f.	χ^2	P
NA1—NA2	test not possible		
NA1—NP1	1	3.89	<0.05
NP1—NP2	1	0.001	n.s.
NP2—NTSV2	1	0.05	n.s.
NP1+NTSV1 —NP2+NTSV2	1		n.s.
NP2/NTSV2 —NP3+NTSV3	1	3.69	<0.1 >0.05

Table 8. Edibility of introduced plants. Differences between annuals and perennials and perennials plus trees, shrubs and vines is not significant (Fisher Exact Probability Test)

Preference level	S.e.	S.o.	S.a.	All three species
		Introduced annuals		
low	6 (60)	3 (43)	2 (40)	6 (60)
high	4 (40)	4 (57)	3 (60)	4 (40)
	Introduced perennials, trees, shrubs, and vines			
low	9 (64)	10 (83)	2 (50)	10 (71)
high	5 (36)	2 (17)	2 (50)	4 (29)

By and large the correspondence between the two tests is rather close, suggesting that whatever changes were occurring in either the insect or the plants were relatively minor. The number of individuals remaining alive after each interval is given in Fig. 1, and the number of individuals reaching the adult stage during successive intervals is shown in Fig. 2. Growth rates are compared in Fig. 3. Clearly, the plants which the insects preferred are in general the best at supporting growth and survival.

(8) Table 9 illustrates several interesting features. Feeding time is closely correlated with the number of times the insects bit into a leaf but failed to chew on it, and only poorly correlated with the number of interruptions in feeding. The latter behavioral feature is therefore probably a poor indicator of plant preference.

(9) Preference criteria, as well as the ability of plants to support growth and survival are ranked in Table 10. The following features are noteworthy: a) Edibility ratings of plants between first and second tests are close, with the exception of *Sorghum* which ranked low in the second test, even though fresh young leaves were used in both tests. b) The correlation between growth rate and mortality is high and both correlate well with the first two preference criteria, *i.e.*, feeding time and number of bites without chewing.

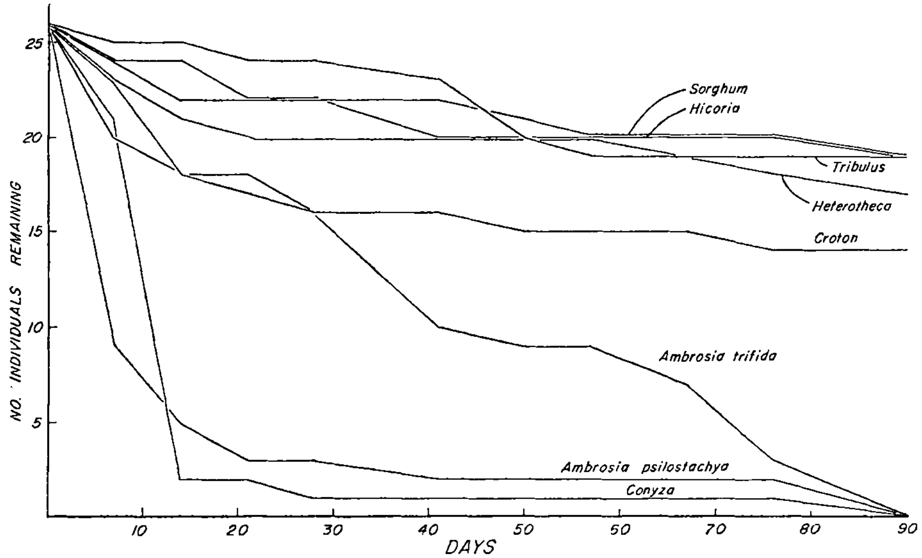

Fig. 1. Number of individuals remaining alive after successive intervals. Mortality rates are highest for low preference plant species (see Table 10)

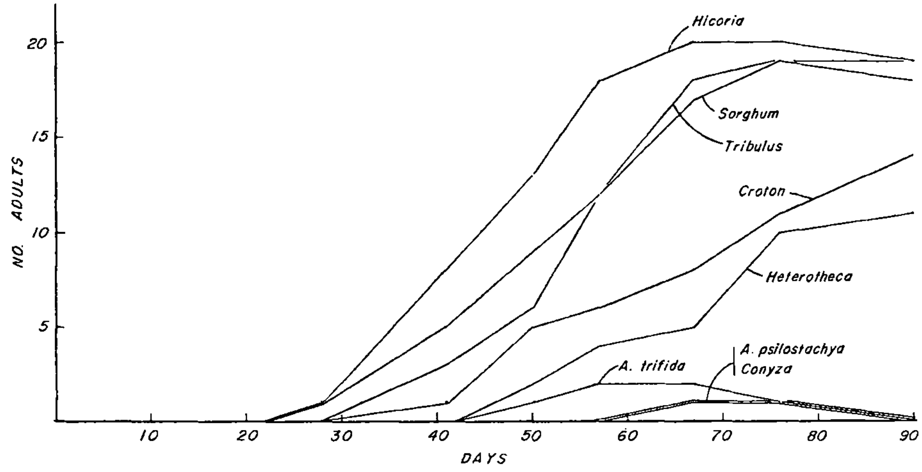

Fig. 2. Number of individuals reaching the adult stage during successive intervals

(10) Grasshoppers have a characteristic method of eating leaves which involves a series of chewing motions as the head is repeatedly moved from a forward position backwards. The number of times the mouthparts open and close during each such sweep depends partly on leaf shape. With large leaves the head may make long sweeps a centimeter or more in length, but when leaves are small the entire leaf can be consumed in one chewing series. Leaf hardness and leaf thickness may also determine the number of movements per sweep. However, there appears

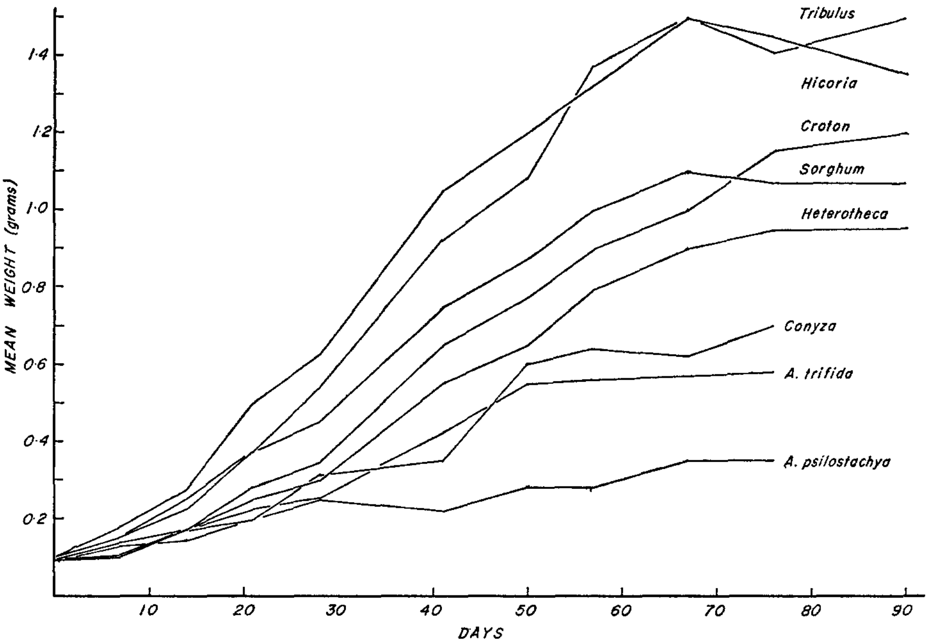

Fig. 3. Mean weight of individuals remaining alive after each interval

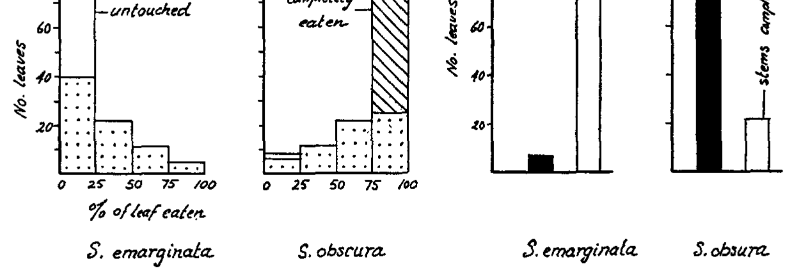

Fig. 4. Edibilities of three plant species, *Celtis laevigata, Torilus arvensis,* and *Solanum eleagneafolium* (the last not shown) to *S. emarginata* and *S. obscura*. Edibility of the last plant was equal in the two species. The three plants were presented to each species simultaneously. In other tests *S. emarginata* showed a high preference for *Celtis* and *S. obscura* showed a high preference for *Torilus*. The data show that the particular combination of plants presented may be a confusing factor in preference determination

Table 9. Responses of 15 last instar *S. americana* nymphs (4 male and 11 female) to each of 8 different plant species. Individuals had been starved for 24 hrs prior to testing. Each individual was presented with the test plant for 2 min. B = biting into a leaf but not chewing on it

Plant species	Total feeding time (min) $N = 15$	Mean feeding time	No. interruptions in feeding	No. B	Range, mean biting motions/series
Sorghum halepense	25.4	1.69	0	0	3–16 (8.1)
Hicoria pecan	23.8	1.59	1	0	2–14 (5.6)
Heterotheca latifolia	22.3	1.48	11	1	4–15 (9.2)
Tribulus terrestris	11.2	0.75	20	13	1–14 (5.0)
Ambrosia trifida	7.1	0.47	8	4	
Conyza canadensis	6.1	0.41	13	24	
Ambro. psilostachya	4.8	0.32	11	35	5–12 (6.7)
Croton. sp.	4.6	0.30	6	30	3–11 (6.1)

Table 10. Ranking of 8 test plant species in terms of the time grasshoppers fed on them (in a 2-min trial period), number of biting without chewing motions (B), number of interruptions in feeding, and growth and mortality of grasshoppers feeding on each plant. Low rank numbers indicate longer feeding times, fewer biting without chewing motions, higher growth rates and lower mortalities

Plant species	1st test			2nd test Feeding time	Growth rate	Mortality rate
	Feeding time	No. B	No. interruptions			
Sorghum halepense	1	1	1	8	3	1
Hicoria pecan	2	1	2	1	1	1
Heterotheca latifolia	3	3	4	2	5	4
Tribulus terrestris	4	5	8	4	1	3
Ambrosia trifida	5	4	6	3	7	6
Conyza canadensis	6	6	7	5	6	8
Ambrosia psilostachya	7	7	4	7	8	7
Croton sp.	8	8	3	6	4	5

to be little correlation between number of chewing motions per series and preference for the plant. The amount of leaf material removed during each bite has not been examined.

(11) Although the overall preference of the three *Schistocerca* species for a large variety of plants are remarkably similar and did not differ significantly in respect to the comparisons made above, the preferences displayed for certain plants are strikingly different. Two such differences are shown in Fig. 4. Nymphs of *S. emarginata* and *S. obscura* were given a choice of three plants: a tree, *Celtis laevigata* (hackberry), a perennial forb, *Solanum eleagneafolium* (Solanaceae) and an annual forb, *Torilus arvensis* (Apiaceae). *S. emarginata* showed a striking preference for *Celtis* over *Torilus*, while *S. obscura* showed a marked preference of *Torilus* over *Celtis*. Preference levels for *Solanum* were roughly equal. Another strong preference difference was shown in tests with the plant *Ptelea trifoliata*

(Rutaceae); the plant was highly edible to *S. emarginata* and scarcely touched by *S. obscura*. *S. obscura* and *S. emarginata* showed a strong preference, and *S. americana* showed a low preference, for *Oxypolis rigidior* (Apiaceae).

(12) Table 1 suggests that the following families have high average edibilities: Poaceae, Apiaceae, Brassicaceae, Geraniaceae, Euphorbiaceae, Malvaceae, Ulmaceae, Fagaceae, Chenopodiaceae, Juglandaceae, Salicaceae, Polygonaceae, Rutaceae, and Berberidaceae. But in some families only one species was tested. Note that four of the families comprise trees—*i.e.*, late successional plants.

Discussion

(1) The results presented here suggest that the Cates-Orians succession-palatability theory is not valid for all communities. In the central Texas region successional stages 1 and 2 are not significantly different in edibility and both are *less* edible than late successional stages. This result is in strong contrast to the results obtained by Cates and Orians who worked with slugs in the forested Pacific Northwest. Furthermore, annual plants were significantly *less* edible than perennial forbs and woody plants. The lower average edibility of annuals may be partly due to the fact that the generally less edible Asteraceae are heavily represented among them. However, even when the Asteraceae are excluded, annuals have a lower average edibility. Does this mean that annual plants in Texas have been subject to greater predation pressure, rather than less, as predicted by Cates and Orians?

(2) *Schistocerca* are among the largest and most mobile acridoids. When disturbed they may easily fly 100 m or more before settling. Some species in the genus are also strongly migratory and may fly for hundreds of miles (*S. gregaria*, *S. cancellata*, and probably also *S. vaga*). Evidently all *Schistocerca* have very broad diets. Such a high degree of mobility suggests that individual insects normally encounter numerous plant species in their life-times (at least in the adult stage). Consequently the environment is to them fine-grained, a situation calling for a generalist or polyphagous diet. If plants differ in their suitability as food sources, then preferences should evolve and be adjusted optimally to the level of suitability, with highly suitable plants selecting for high preference and vice versa (but see 8 below). The relationship between edibility and ability of plants to support growth and survival is therefore not surprising. The correlation is in our tests not perfect (Table 10), perhaps in part because several of the plants used (*Sorghum*, *Ambrosia trifida*, and *Tribulus terrestris*) were introduced into Texas by man recently enough that *S. americana* has had insufficient time to evolve preferences in relation to the plants' relative suitabilities.

(3) We have no information on what deterrents the tested plants actually employ against insects. One can surmise that the deterrents are in some cases chemical in nature and are not fully perceived until grasshoppers bite into the plant. The hairy covering of *Tribulus terrestris* leaves may also act as a deterrent to feeding. Although this plant ranked fourth in preference in both tests and last in number of interruptions, it ranked highest in promoting growth and third highest in promoting survival. But since *T. terrestris* is introduced and furthermore is not common in native habitats which I studied, the insect may not

yet have had time to evolve preferences commensurate with the suitability of the plant as a resource, or it may not be under sufficiently strong selection to evolve a strong preference for it.

(4) Although growth and survival are important components of fitness, the ability of plants to support reproduction is also important and it does not necessarily follow that suitability in respect to one component implies suitability in respect to another. The reproductive component of fitness has not been considered in the present work, but it is highly probably that preference evolves in relation to it.

(5) Mixed diets have been shown to be better than single plant diets in several polyphagous grasshopper species (Kaufmann, 1965; Uvarov, 1966 and refs.; Mulkern, 1967 and refs.). Consequently, preferences for a given plant may change strikingly in relation to how much of that plant has already been consumed (see also Freeland and Janzen, 1974, for an explanation of diet mixing). Our results show that the edibility of *Torilus* and *Celtis* change dramatically in different combinations and may be quite different in different species (Fig. 4).

(7) If grasshoppers evolve a degree of preference which is directly related to plant suitability as food, then one should expect to find a closer correlation between preference and plant suitability in native plants than in introduced plants, because the insects would have had time to adjust to the former. No such test has been carried out, but should be quite feasible. One might also predict that the correlation between suitability and preference will be poor for those plants that grow and flower during seasons when grasshoppers are diapausing. Thus, Fall *Schistocerca* might be less able to assess the suitability of Spring annuals than they are able to assess suitability of Fall annuals. Furthermore, one might expect a two generation grasshopper such as *S. americana* to be better able to assess the suitability of Spring plants than one generation species such as *S. obscura* and *S. emarginata.*

(8) There has been much debate among entomologists, ecologists, and physiologists on what factors are most important in determining the edibility of a plant to an insect herbivore (Dethier, 1954, and refs.; Brower, 1958, and refs.). The debate has focussed on the relative importance of nutritional value of the plant (*i.e.*, whether it contains the requisites for growth, survival, and reproduction in sufficient and assimilable quantities) and on the importance of secondary plant compounds which act either as repellents or attractants. Dethier (1954) and Cates and Orians, in press, consider also the availability in space and time and Brower (1958) considered the role of plants as places of refuge for cryptically colored insects. One view of the evolution of preferences which takes various considerations into account is the following: Insects should evolve a high preference for plants that not only have high nutritional value, but that are available to the insects at the time they are needed and such that the insects can assimilate the plant material without difficulty. When pressure from herbivory is slight, defensive measures by plants may also be minor, but when predation pressure is high, plants are selected that adequately defend themselves against predation. Structural and chemical defenses may then be sufficiently strong that plant nutrients become much less available and insects may evolve a lower preference for the plants. If now an insect species is able to overcome the defenses set up by

evolving detoxification mechanisms or specialized feeding mechanisms and becomes a specialist on the plant, what originally evolved as defenses may become attractants, since they identify the plant as belonging to a certain species on which the specialist herbivore depends. Thus, repellents become attractants when they no longer deter insects and can be used by insects to locate their host plants. The underlying basis for evolution of preference in such a case is the nutritional value of the plant and the predictability of the plant in space and time.

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Dr. Daniel Otte
Department of Zoology
University of Texas
Austin, Texas 78712, USA