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Food Preference as a Factor in Distribution and Abundance of *Phoetaliotes nebrascensis*

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Food Preference as a Factor in Distribution and Abundance of *Phoetaliotes nebrascensis*[1,2]

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Abstract
Western wheat grass, *Agropyron smithii*, was the plant most frequently ingested by *Phoetaliotes nebrascensis* (Thomas) in 4 of 5 habitats and was preferred in all. All grasses were eaten to some extent; nonpreferred plants may support populations in otherwise suitable habitats. Most forbs were unattractive but all tested species of Cichoriaceae were acceptable. Plant-finding was by random searching; selection was made only after contact through the mouthparts. While habitats in which preferred hosts were more abundant had higher grasshopper populations, annual changes in grasshopper abundance within a habitat were independent of abundance of primary food plants.

Phoetaliotes nebrascensis (Thomas) is widely distributed on the Great Plains, where it is considered an important rangeland grasshopper. On the basis of mandibular structure (Isely 1944), it would be classified as a mixed feeder. Western wheat grass, *Agropyron smithii*; bluegrass, *Poa pratensis*; and little bluestem, *Andropogon scoparius* have been reported as the most frequently ingested plants in Montana, North Dakota, and Kansas, respectively (Anderson and Wright 1952, Mulkern et al. 1964). Mulkern et al. (1962) reported ingestion of alfalfa by this species in North Dakota. The degree of selectivity is probably inherent in each grasshopper species, but the expression of selectivity is determined by the plants available in a habitat (Mulkern 1967). In an attempt to determine if food specificity influences distribution and abundance of *P. nebrascensis*, plant ingestion in 5 habitats under field conditions was compared with preferences exhibited in laboratory trials.

Methods

Frequent sweep-net collections were made during a 7-year period, 1960–66, on rangeland near North Platte, Nebraska. All instars of *P. nebrascensis* were represented in these samples. Plant ingestion was determined by using the crop-contents analysis method (Mulkern and Anderson 1959).

The study area was an 82-acre pasture on the south upland escarpment bordering the South Platte River. The 26 sample sites were grouped into 5 habitats having different soil and vegetative characteristics. Vegetative ground cover and relative plant abundance were determined by making 100 or more point counts at least twice a year in each sample site.

Habitat 1 included 9 sample sites on the higher ridges with typical short-grass vegetation. Its soil is a Colby very fine sandy loam. Blue grama grass, *Bouteloua gracilis*, and threadleaf sedge, *Carex filafolia*, together comprised 78% of the total vegetation. Habitat 2 included 3 sample sites not conveniently classified elsewhere. Two sites were on a broken phase of Colby very fine sandy loam with calcareous material deposited on the surface; the other site was an area which had been broken for cultivation but was permitted to return to native vegetation. A great variety of plants occurred in niches too small for independent sampling. Nine sample sites consisting of relatively flat but narrow swales were grouped in habitat 3. Its soil is a colluvial phase of Hall very fine sandy loam. *Agropyron smithii* was the predominant grass, making up 34% of all vegetative cover. Many other grasses and forbs were present in lesser abundance with no single species composing more than 10% of the total vegetation. Habitat 4 consisted of 3 patches of sandreed grass, *Calamovilfa longifolia*, with an understory of *Carcx filafolia*, these 2 plants constituting 88% of total vegetation. This type of plant community was common on the slopes separating habitats 1 and 3. Habitat 5 was composed of 3 sample sites, once part of habitat 2, which were used for winter feeding of cattle. Vegetation consisted mostly of annual forbs and grasses, with *Kochia scoparia* making up 65% of all vegetation.

Food preferences were determined in cage trials conducted in the laboratory in 1965. Fresh plant material was cut and placed with water in cotton-stoppered vials. Approximately equal quantities of each plant species were offered alone and in choice with *A. smithii*, the most frequently ingested plant in the field. Ten field-collected 4th-instar to adult grasshoppers were permitted to feed 24 hr. Plant consumption was evaluated on a 0–4 scale, the respective numerical ratings representing no visible feeding (0), < ¼, ¼–½, ½–¾, and > ¾ of the plant eaten. A minimum of 2 replicates was used in the case of plants which were refused even when offered alone; 4 or more replicates were used for all plants which proved acceptable to some degree.

Results

Table 1 gives the more frequently ingested plants and their relative abundance in each habitat. Had no selectivity occurred, each plant should have been ingested in proportion to its abundance; significant departures ($x^2 \leq 0.01$) from random consumption occurred in all plots. Analyses were based on the total number of grasshoppers collected in each habitat (Table 3) less the number with empty crops (15–18% of total). Disproportionate ingestion may not reflect specificity per se but can result from a nonrandom distribution of the grasshopper with the species collected in only small portions of a habitat in which certain plants occur. Nonetheless, if a grasshopper occurs in only those areas, plant consumption indicates something about the habitat which the species can occupy.

Table 1. Mean plant abundance (% total vegetation) vs. ingestion by *P. nebrascensis* in 5 habitats, North Platte, Nebraska, 1960–66

	Habitat									
	1		2		3		4		5	
Plant species	P[a]	I[b]	P	I	P	I	P	I	P	I
Agropyron smithii	1	26	12	56	34	67	T	10	6	47
Andropogon scoparius	T	0	8	5	T	T	T	3	0	0
A. gerardi	0	0	T	1	4	4	1	1	T	T
Bromus tectorum	T	3	5	4	5	3	T	1	3	3
Calamovilfa longifolia	T	1	2	1	3	2	64	40	T	0
Carex eleocharis	0	0	6	4	8	1	0	0	T	T
C. filafolia	28	19	T	1	T	0	24	26	1	0
Bouteloua gracilis	50	7	21	2	10	1	T	T	1	T
Panicum capillare	T	2	T	2	1	2	T	1	4	20
Kochia scoparia	T	2	1	1	4	2	T	0	65	22
Lactuca scariola	T	0	1	T	2	T	1	4	T	0
Stipa comata	9	9	10	6	9	4	4	9	1	T
Sporobolus cryptandrus	3	0	6	2	6	1	1	1	2	1

a. % of total vegetation; T=trace
b. % of total number of grasshoppers ingesting plant

Table 2 summarizes results of cage-feeding trials. Plants classified as "preferred" were ingested at a significantly greater rate (5% level) than *Agropyron smithii* when offered in direct comparison, "equally attractive" at a rate not different from *A. smithii*, "less attractive" at a lower rate in direct comparison but at an equal rate when offered alone, and "unattractive" at a lower rate both in comparison and alone. Plants "refused" in 2 trials were not further tested and do not differ statistically from "unattractive" plants.

Table 3 is a summary of population changes over the 7-year period. These changes are related to abundance and ingestion of the primary host plant in each habitat.

Discussion

A. smithii was ingested out of proportion to its abundance in all habitats, suggesting a definite preference of that plant. Relative preference varied inversely with abundance of the plant. In habitat 1, *P. nebrascensis* occurred in only marginal areas where this plant occurred sparsely. The grasshopper was most abundant in habitat 3 where *A. smithii* was most abundant. Annual changes in abundance of the primary host seemed to have no effect on populations in any habitat.

Table 2. Food preferences of *P. nebrascensis* as determined in cage studies

Plant species	Nonchoice[a] ingestion	Preference[b] index
	Preferred plants	
Grasses:		
Bromus tectorum	4.00	+3.25
Echinochlora crusgalli	4.00	+2.25
Elymus canadensis	3.50	+1.00
Hordeum jubatum	4.00	+1.25
Koehleria cristata	4.00	+1.25
Panicum capillare	4.00	+2.25
Panicum scribnerianum	4.00	+3.25
Forbs:		
Lygodesmia juncea	3.75	+0.92
Taraxacum officinale	3.50	+2.00
Tragopogon pratensis	4.00	+1.25
	Equally attractive plants	
Grasses:		
Agropyron smithii	2.45	0.00
Andropogon gerardi	2.75	+0.25
A. scoparius	3.00	+0.25
Bromus inermis	3.50	+0.50
Carex eleocharis	2.50	–0.25
C. filafolia	1.75	–0.02
Eragrostis cilianensis	3.00	+0.50
Panicum virgatum	2.25	+0.50
Setaria viridis	2.00	+0.50
Forbs:		
Lactuca scariola	2.75	–0.40
Tribulus terrestris	3.00	–0.33
	Less attractive but readily ingested	
Grasses:		
Bouteloua curtipendula	2.25	–0.92
B. gracilis	3.25	–1.67
Buchloe dactyloidcs	3.00	–0.62
Schedonnardus imbricatus	2.25	–1.50
Sporobolus cryptandrus	2.12	–0.92
Forbs:		
Chichorium intybus	2.00	–2.00
Euphorbia marginata	2.67	–1.00
	Unattractive—sparingly ingested when alone	
Grasses:		
Aristida oligantha	0.50	–3.25
Calamovilfa longifolia	0.50	–1.00
Muhlenbergia cuspidata	1.00	–1.75
Poa pratensis	0.50	–2.12

Stipa comata	0.50	–2.75
Forbs:		
Apocynum sibiricum	0.25	–2.50
Asclepias pumila	0.50	–3.00
A. speciosa	0.50	–2.75
Amaranthus retroflexus	0.50	–2.75
Amorpha canescens	0.50	–3.50
Chcnopodium album	0.75	–0.75
Euphorbia geyeri	0.67	–3.17
Ipomoea leptophylla	0.50	–3.00
Kochia scoparia	1.00	–2.08
Kuhnia eupatoroides	0.12	–2.00
Medicago sativa	0.50	–2.50
Melilotus alba	0.50	–2.25
M. officinale	0.75	–2.00
Oenothera serrulata	0.50	–1.50
Parosela aurea	0.50	–3.25
Petalostemon purpureum	0.75	–2.75
Polygonum pennsylvanicum	0.50	–2.75
P. erectum	0.75	–3.50
Psoralea esculenta	0.50	–2.75
Sphaeralcea coccinea	0.25	–2.25
Symphoricarpos occidentalis	0.50	–2.50
	Refused	
Forbs:		
Allionia linearis	0.00	–3.25
Ambrosia psilostachya	0.00	–2.75
Artemesia ludoviciana	0.00	–2.75
Asclepias incarnatus	0.00	–2.75
Croton texensis	0.00	–2.75
Dalea enneanara	0.00	–2.50
Glycyrrhiza lepidota	0.00	–3.25
Gutierrezia sarothrae	0.00	–3.25
Helianthus annuus	0.00	–0.75
Petalostemon candidum	0.00	–3.50
Physalis heterophylla	0.00	–3.50
Psoralea argophylla	0.00	–3.00
Ratibida columnifera	0.00	–3.00
Thelesperma trifidum	0.00	–3.50
Verbena stricta	0.00	–1.75

a. Rated 0–4; 0 = no ingestion, 4 = plant > ¾ consumed

b. Mean difference in ingestion in choice with *A. smithii*

Table 3. Populations of *P. nebrascensis*, 1960–66, in relation to primary food plant in each of 5 habitats

	1960	1961	1962	1963	1964	1965	1966
Habitat 1							
No. grasshoppers examined	33	11	22	39	14	27	4
No./100 sweeps	1	T	1	1	T	1	T
% vegetative cover		71	74	60	67	68	68
% *A. smithii*	T	T	1	T	1	T	1
% feeding on *A. smithii*	36	17	17	25	8	13	25
Habitat 2							
No. grasshoppers examined	168	92	105	451	46	91	28
No./100 sweeps	8	4	7	34	4	10	6
% vegetative cover		75	75	69	73	76	73
% *A. smithii*	10	10	16	17	15	11	11
% feeding on *A. smithii*	58	54	53	56	59	38	81
Habitat 3							
No. grasshoppers examined	1,878	768	585	2,511	313	394	209
No./100 sweeps	28	11	14	62	9	14	15
% vegetative cover		88	90	80	86	88	83
% *A. smithii*	51	49	33	35	27	20	22
% feeding on *A. smithii*	73	68	72	64	53	50	59
Habitat 4							
No. grasshoppers examined	219	119	93	290	43	49	47
No./100 sweeps	10	5	7	21	4	5	12
% vegetative cover		91	92	81	76	83	77
% *C. longifolia*	70	66	65	65	52	65	65
% feeding on *C. longifolia*	48	41	21	42	23	54	53
Habitat 5							
No. grasshoppers examined	54	57	41	239	77	15	15
No./100 sweeps	2	2	4	21	4	5	12
% vegetative cover		81	92	67	89	94	85
% *A. smithii*	2	3	4	7	11	4	9
% feeding on *A. smithii*	11	39	29	60	43	50	62

In habitat 4, more grasshoppers ate *C. longifolia* than any other plant; nevertheless, it was significantly nonpreferred when plant abundance is considered, an observation which supports results obtained in cage trials. Needle-and-thread, *Stipa comata*, was nonpreferred in habitat 3 where *A. smithii* was abundant but was preferred in habitat 4 where a preferred host was scarce. Additional tests, comparing only *S. comata* and *C. longifolia* confirmed that the former was relatively more attractive.

Carex eleocharis and *C. filafolia* were as attractive as *A. smithii* in the laboratory but non-preferred in the field. Only in habitat 4, where *C. filafolia* was uniformly distributed throughout the habitat, was this plant ingested in proportion to its abundance. In other plots, populations of the grasshopper were notably lower where either *C. filafolia* or *C. eleocharis* was abundant. This observation suggests either that the grasshopper cannot subsist on these plants alone or that the plants occur most abundantly in habitats otherwise unsuitable for the insect.

While the environmental requirements of *P. nebrascensis* are unknown, it is almost always found in areas of taller vegetation and spends most of its time on plants. The grasshopper feeds to a large extent on glumes of grasses (excluded in this summary since the glumes usually could not be identified to plant species in crop analyses) and rests at night on the taller vegetation. No plant selectivity for resting was noted other than that determined by plant height. The relatively short sedges are not favored for resting; plants of *C. filafolia* cannot support the weight of the grasshopper, which fact may explain why that plant is ingested only when intermingled with taller vegetation.

Most grasses which were preferred over *A. smithii* in the laboratory were too scarce in the study area to permit a comparison with field ingestion. Downy bromegrass, *Bromus tectorum*, and witchgrass, *Panicum capillare*, were both frequently ingested in the field, the latter significantly preferred in habitat 5, where it was relatively abundant and other preferred hosts were scarce. Both of these plants are of short seasonal occurrence, *B. tectorum* being succulent and available only to early instars, and *P. capillare* emerging in time to provide food for only later instars and adults. Thus neither could support a population of the grasshopper if occurring in homogenous stands. Except for plants of short seasonal occurrence, no differences in food preferences by grasshoppers of different ages were discovered, and all instars are combined in the summary tables.

Of the plants rated equal to *A. smithii* in acceptability, 3—big bluestem, *Andropogon gerardi*; little bluestem, *A. scoparius*; and bromegrass, *Bromus inermis*—have been observed to support populations of the grasshopper in other habitats where they form a larger portion of the vegetation. *B. inermis* commonly occurs in abundance only under cultivation, and harvesting of this grass may preclude occupation of those habitats.

All available grasses were acceptable to some extent ; even unattractive grasses in comparative feeding trials may support field populations. *Poa pratensis* is listed as the most frequently ingested plant in a North Dakota habitat, though when considered in relation to its abundance, it was nonpreferred. The same was true of *C. longifolia* in habitat 4 in this study.

Few forbs are ingested in the field. *Kochia scoparia*, though unattractive, was frequently ingested in habitat 5. But *P. nebrascensis* does not occur in habitats where *Kochia* is the only available plant. Prickly lettuce, *Lactuca scariola*, was rated as preferred in habitat 4. Because of its late emergence, it could be an important part of the diet only in habitats having other acceptable plants early in the season. The acceptability of snow-on-the-mountain, *Euphorbia marginata*, was somewhat surprising as this plant was never observed to be eaten in the field. Puncture vine, *Tribulus terrestris*, does not ordinarily occur on rangeland in the type of habitat occupied by the grasshopper. Of the 7 forbs readily ingested in cage trials, it seems notable that 5 belong to that group of Compositae having a milky sap (Cichoriaceae); this observation suggests the possible presence of a phagostimulant.

Olfactory guidance does not appear important in host selection by *P. nebrascensis*. In cage studies, grasshoppers indiscriminately explored both plant species, and selection was made only after contact by the mouthparts. As a result, many forbs, observed to be nibbled on in the cage studies, may have passed undetected in crop analyses, where they would constitute only a small portion of the crop contents. Pfadt (1949) found that the migratory grasshopper, *Melanoplus sanguinipes* (F.), behaved in a similar manner, initiating feeding on any plant.

Following contact with mouthparts, feeding either commenced immediately or the plant was temporarily abandoned. A distinctive type of negative response in which the grasshopper backed away from the plant was sometimes noted. When preferred plants were periodically abandoned, the grasshopper either walked or jumped from the plant. When only an unattractive plant was available, a negative response might be repeated several times, with the grasshopper conducting random searching between feeding attempts; after several failures, the grasshopper would sometimes rest on the plant without further attempts at feeding.

Restlessness varied with relative attractiveness of the plant; considerable feeding occurred on some of the less attractive plants, but feeding was not so continuous as on attractive plants. These behavioral responses suggest that repellents, phagostimulants, and arrestants may play an important role in plant ingestion. Because of the increased exploration occurring in habitats in which preferred plants are scarce, the grasshopper could locate and ingest the few preferred hosts far out of proportion to their abundance. But since location of suitable food appears dependent upon random searching, some minimum density of acceptable food would seem essential.

Conclusions

A plant may be preferred, yet not support a grasshopper population because its seasonal occurrence does not coincide with the development of the insect, because it occurs in a habitat not suitable for the grasshopper, or possibly because it does not fulfill the nutritional needs of the insect. Since food preferences commonly coincide with dietary requirements (Mulkern 1967), the latter factor would not be limiting in most cases, especially in mixed grass habitats.

On the other hand, *P. nebrascensis* may feed on comparatively unattractive plants in habitats otherwise meeting its requirements. Since *P. nebrascensis* is able to utilize a great variety of grasses, requirements other than food are of major importance in determining its distribution. Within a favorable habitat, annual population fluctuations seem independent of abundance of preferred hosts. But realization of biotic potential may be limited by host plants, since populations of *P. nebrascensis* were consistently higher in those habitats with a higher proportion of preferred plants.

Notes

1. Orthoptera: Acrididae.
2. Published with the approval of the Director as Paper no. 2337, Journal Series, Nebraska Agricultural Experiment Station, and Contribution no. 302 of the Department of Entomology, University of Nebraska, Lincoln, 68503. Contributory to North Central Regional Project no. 52, "Factors influencing the distribution and abundance of grasshoppers."

References Cited

Anderson, N. L., and J. C Wright. 1952. Grasshopper investigations on Montana range lands. Mont. Agr. Exp. Sta. Bull. 486. 46 p.

Isely, F. B. 1944. Correlation between mandibular morphology and food specificity in grasshoppers. Ann. Entomol. Soc. Amer. 37: 47–67.

Mulkern, G. B. 1967. Food selection by grasshoppers. Annu. Rev. Entomol. 12: 59–78.

Mulkern, G. B., and J. F. Anderson. 1959. A technique for studying the food habits and preferences of grasshoppers. J. Econ. Entomol. 52: 342.

Mulkern, G. B., J. F. Anderson, and M. A. Brusven. 1962. Biology and ecology of North Dakota grasshoppers. I. Food habits and preferences of grass hoppers associated with alfalfa fields. N. Dak. Agr. Exp. Sta. Res. Rep. 7. 26 p.

Mulkern, G. B., D. R. Toczek, and M. A. Brusven. 1964. Biology and ecology of North Dakota grasshoppers. II. Food habits and preferences of grasshoppers associated with sand hill prairie. Ibid. 11. 59 p.

Pfadt, R. E. 1949. Food plants as factors in the ecology of the lesser migratory grasshopper (*Melanoplus mcxicanus*). Wyo. Agr. Exp. Sta. Bull. 290. 48 p.