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Nutritional ecology of *Schistocerca piceifrons piceifrons* adults from Socorro Island, Mexico

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Abstract

Nutritional ecology of the Central American locust *Schistocerca piceifrons piceifrons* was studied using specimens from Socorro Island, Mexico. They were fed in the laboratory with common plants obtained from the island: *Ficus cotinifolia* (Moraceae), *Cordia curassavica* (Boraginaceae), *Nicotiana stocktonii* (Solanaceae), and *Psidium sartorianum* (Myrtaceae). We measured nutritional and growth rates in dry weights: intake, gain in weight, as well as some Waldbauer indices equivalents: efficiency of conversion of ingested food (*ECI*), efficiency of conversion of digested (absorbed) food (*ECD*), and approximate digestibility (*AD*). We compared nutritional indices equivalents between female and male, between gregarious and solitary phases and between diets, employing ANCOVAs. We found no differences in metabolic efficiencies between female and male locusts, no differences between gregarious and solitary locusts. We found that *F. cotinifolia* is a food plant that favors the intake, nutritional efficiencies and steady growth of the Central American locust, in comparison to other food plants.

Key words

feeding behavior, nutritional indices, metabolic constraints, Central American locust

Introduction

Socorro Island is a natural protected area within Mexico, located in the Revillagigedo Archipelago on the Pacific Ocean, at lat 18° 41' 57" N, long 110° 56' 33" W (Brattstrom, 1990). The presence of *Schistocerca piceifrons piceifrons* (Walker, F., 1870) has been noted in this area since 1995-1996. This species, commonly known as the "Central American locust" (Jiménez 1973), has a wide distribution and a great importance in Mexico and the rest of Central America, since it is able to aggregate into dense moving masses of individuals which devastate any vegetation they encounter. Although the species has been well studied at the level of population ecology, its nutritional ecology is poorly understood.

The main goal of nutritional ecology is to determine how an organism interacts with its host plants and other foods, behaviorally and physiologically. A quantitative approach measures the food consumed, digested, assimilated, excreted, metabolized, and so converted into biomass (Waldbauer 1968, Woodring *et al.* 1979). These rates are related to the growth of the organism during its feeding period, in order to assess how food properties affect the performance and adaptation of the insect (Scriber & Slansky 1981). Some commonly used measurements are weight gain (*G*), intake (*C*), approximate digestibility (*AD*), efficiency of conversion of digested food to biomass (*ECD*), and efficiency of conversion of ingested food to biomass (*ECI*).

Methods

In order to study the nutritional ecology of *S. piceifrons piceifrons*, we fed *Cordia curassavica* Roem. & Schult. (Boraginaceae), *Nicotiana stocktonii* Brandege (Solanaceae), *Ficus cotinifolia* H.B. & K. (Moraceae) and *Psidium sartorianum* Nied. (Myrtaceae) to solitary (*S*) and gregarious (*G*) females and males between February and May 2004. The four plant species are abundant on the island and attractive to the locusts (Cano-Santana *et al.* 2005).

The insects were collected by net on the island as adults. We obtained gregarious locusts from swarms and caught solitary locusts dispersed in the field. Numbers in the experiment were 17 gregarious males, 21 gregarious females, 22 solitary males and 21 solitary females. The insects were kept individually in cylindrical transparent plastic containers measuring 10 cm in diameter, 7 cm in height. Each locust was given 1g of fresh leaves every day for four days from one of the four different food-plant species. As a control, every day we placed three replicates of fresh leaves, one from each of the four plant species, under the same conditions as the experimental leaves — but without a locust (48 control sets total).

We concluded the experiment after four days. We obtained the dry weights (*dw*) of the sets of control leaves and whatever food material was left in the insect cages, together with grasshopper feces. Dry weights of feces and uneaten experimental leaves were obtained by drying the material in an oven (at a constant 80°C) until obtaining a stable measure with an analytic scale (accuracy 0.001 g). We measured each locust's final fresh weight and then sacrificed and dried each specimen (individually) to its (minimum) dry-weight value. We undertook a regression analysis (independent variable final fresh weight *vs* dependent variable final dry weight) to predict the daily dry weights of the locusts.

Effects of gregariousness (solitary *vs* gregarious locusts), gender and diet (plant species) as independent variables, upon nutritional indices equivalents for *S. piceifrons piceifrons* were determined following Raubenheimer and Simpson (1992), using an analysis of covariance. For intake, ingested food was the dependent variable and as its covariable, initial weight; for growth, final weight was the dependent variable, and as its covariable initial weight; for the *ECI* equivalent we used growth as a dependent variable, and as its covariable intake; for the *ECD* equivalent we used growth as the dependent variable, and as its covariable intake minus the fecal dry weight; and finally for the *AD* equivalent we used feces as dependent variable, intake as covariable (Simpson pers. com.). Calculations were made with the program Statistica version 6.0 (StatSoft, 2004).

Table 1. ANCOVA of the effect of gregariousness (gregarious/solitary) on nutritional and growth rates of Central American locusts fed on *Cordia curassavica* and *Nicotiana stocktonii*.

			SS	df	MS	F	p
intake	dependent variable	ingested food					
	independent variable	gregariousness	2.019	1	2.019	10.119	0.002
	covariable	initial weight	2.405	1	2.405	12.050	0.001
		intercept	0.272	1	0.272	1.363	0.247
		error	13.968	70	0.200		
growth	dependent variable	final weight					
	independent variable	gregariousness	< 0.001	1	< 0.001	0.379	0.540
	covariable	initial weight	0.041	1	0.041	37.787	< 0.001
		intercept	0.002	1	0.002	1.486	0.227
		error	0.076	70	0.001		
ECI	dependent variable	growth					
	independent variable	gregariousness	< 0.001	1	< 0.001	0.154	0.696
	covariable	intake	< 0.001	1	< 0.001	0.126	0.724
		intercept	0.001	1	0.001	0.525	0.471
		error	0.175	70	0.003		
ECD	dependent variable	growth					
	independent variable	gregariousness	< 0.001	1	< 0.001	0.154	0.696
	covariable	intake-feces	< 0.001	1	< 0.001	0.125	0.724
		intercept	0.001	1	0.001	0.526	0.471
		error	0.175	70	0.003		
AD	dependent variable	feces					
	independent variable	gregariousness	< 0.001	1	< 0.001	0.289	0.592
	covariable	intake	< 0.001	1	< 0.001	3.246	0.076
		intercept	< 0.001	1	< 0.001	0.887	0.350
		error	0.004	70	< 0.001		

Table 2. ANCOVA of the effect of gender (male/female) on nutritional and growth rates of the Central American locust.

			SS	df	MS	F	p
intake	dependent variable	ingested food					
	independent variable	gender	0.164	1	0.164	0.767	0.383
	covariable	initial weight	1.476	1	1.476	6.900	0.010
		intercept	1.825	1	1.825	8.533	0.004
		error	23.096	108	0.214		
growth	dependent variable	final weight					
	independent variable	gender	< 0.001	1	< 0.001	0.053	0.818
	covariable	initial weight	0.080	1	0.080	54.693	< 0.001
		intercept	0.001	1	0.001	0.413	0.522
		error	0.158	108	0.001		
ECI	dependent variable	growth					
	independent variable	gender	0.001	1	0.001	0.218	0.642
	covariable	intake	0.013	1	0.013	3.451	0.066
		intercept	0.016	1	0.016	4.352	0.039
		error	0.397	108	0.004		
ECD	dependent variable	growth					
	independent variable	gender	0.001	1	0.001	0.218	0.642
	covariable	intake-feces	0.013	1	0.013	3.427	0.067
		intercept	0.016	1	0.016	4.328	0.040
		error	0.397	108	0.004		
AD	dependent variable	feces					
	independent variable	gender	0.001	1	0.001	0.457	0.500
	covariable	intake	0.024	1	0.024	16.579	< 0.001
		intercept	0.006	1	0.006	3.921	0.050
		error	0.157	108	0.001		

Table 3. ANCOVA of the effect of diets — *Cordia curassavica*, *Nicotiana stocktonii*, *Ficus cotinifolia* and *Psidium sartorianum* — upon nutritional and growth rates of the Central American locust.

			SS	df	MS	F	p
intake	dependent variable	ingested food					
	independent variable	diet	2.893	3	0.964	5.019	0.003
	covariable	initial weight	1.202	1	1.202	6.254	0.014
		intercept	2.789	1	2.789	14.517	< 0.001
		error	20.367	106	0.192		
growth	dependent variable	final weight					
	independent variable	diet	0.030	3	0.010	8.157	< 0.001
	covariable	initial weight	0.094	1	0.094	77.536	< 0.001
		intercept	0.001	1	0.001	0.473	0.493
		error	0.128	106	0.001		
ECI	dependent variable	growth					
	independent variable	diet	0.072	3	0.024	7.816	< 0.001
	covariable	intake	0.002	1	0.002	0.689	0.408
		intercept	0.004	1	0.004	1.154	0.285
		error	0.325	106	0.003		
ECD	dependent variable	growth					
	independent variable	diet	0.072	3	0.024	7.825	< 0.001
	covariable	intake-faeces	0.002	1	0.002	0.687	0.409
		intercept	0.004	1	0.004	1.153	0.285
		error	0.325	106	0.003		
AD	dependent variable	feces					
	independent variable	diet	0.127	3	0.042	145.50	< 0.001
	covariable	intake	0.002	1	0.002	7.514	0.007
		intercept	0.002	1	0.002	6.072	0.015
		error	0.031	106	0.000		

Results

Comparing gregarious and solitary forms of *S. piceifrons piceifrons* fed on *Cordia curassavica* and *Nicotiana stocktonii*, we found no effect on intake, growth, *ECI*, *ECD*, and *AD* equivalents (Table 1). We did observe an effect of the covariable 'initial weight' on intake and growth (for intake: $p = 0.001$, $F = 12.05$, $df = 1$; for growth: $p < 0.001$, $F = 37.79$; $df = 1$). An ANOVA with a Tukey's *posthoc* test found that gregarious locusts were heavier than solitary from the beginning of the assay ($p < 0.001$, $F = 14.60$, $d.f. = 1$; gregarious $dw 0.571 \pm 0.02$ g, $n = 38$; solitary $dw 0.476 \pm 0.014$ g; $n = 35$).

On the other hand, we compared the nutritional and growth rates between female and male locusts fed on the four plant species using an ANCOVA for each one of these dependent variables. We found no effect of sex on any feeding variable and no effect of sex on growth (Table 2). But we did find an effect of the covariable 'initial weight' on the intake ($p = 0.01$, $F = 6.9$, $df = 1$) as well as on growth ($p < 0.001$, $F = 54.69$, $df = 1$), and an effect of the covariable 'intake' on the approximate digestibility equivalent ($p < 0.001$, $F = 16.58$, $df = 1$). The female locusts had a higher initial weight than the male locusts, according to ANOVA and Tukey's *posthoc* test ($p < 0.001$, $F = 33.37$, $d.f. = 1$; female $dw 0.617 \pm 0.017$ g, $n = 53$; male $dw 0.497 \pm 0.012$ g; $n = 58$). We also observed an effect of the covariable "intake" over *AD* (Table 2).

Finally we compared intake, growth, *ECI*, *ECD*, and *AD* equivalents for the Central American locust fed on the different food plants: *Cordia curassavica*, *Nicotiana stocktonii*, *Ficus cotinifolia* and *Psidium sartorianum*. Here we found an effect of diet on the nutritional and growth rates (Table 3). We ran a Tukey's *posthoc* test and found that when fed on *F. cotinifolia*, the locusts had a greater intake, growth, *ECI*, *ECD* and *AD* — than when fed on the other plant species. And

once more we found an effect of the covariable 'initial weight' on consumption ($p = 0.014$, $F = 6.25$, $df = 1$) and growth ($p < 0.001$, $F = 77.54$, $df = 1$) and an effect of the covariable 'intake' on the *AD* equivalent ($p = 0.007$, $F = 7.51$, $df = 1$). Table 4 shows the crude values of growth, intake and feces obtained from locusts fed on the different plant species.

Discussion

We found no differences in the nutritional and growth rates of gregarious *vs* solitary locusts. Previous studies have discovered some locust phase-difference effects on feeding behavior: crowded young males of *Schistocerca gregaria* ate and excreted more than males kept in isolation (Norris 1961). Despland & Simpson (2000) demonstrated that locust nymphs of this same species showed a large degree of gregarization where the food was of low nutritional quality, even more than on concentrated diets.

We found, however, that the gregarious locusts had a greater weight before the beginning of the assay than solitary locusts. This can be due to differences in adult age between gregarious and solitary locusts, given that late adults lose weight (Cheu 1952)

Table 4. Crude values of growth, intake and faeces obtained from locusts fed on *C. curassavica*, *N. stocktonii*, *F. cotinifolia* and *P. sartorianum*.

plant species	growth (mg)	$\pm s \bar{x}$	intake (mg)	$\pm s \bar{x}$	faeces (mg)	$\pm s \bar{x}$
<i>C. curassavica</i>	-0.006	0.015	45.401	5.578	0.026	0.003
<i>N. stocktonii</i>	-0.020	0.012	45.306	3.849	0.008	0.002
<i>F. cotinifolia</i>	0.105	0.013	84.595	9.142	0.277	0.028
<i>P. sartorianum</i>	-0.091	0.040	50.963	11.083	0.277	0.002

or because of previous intense feeding by gregarious locusts. We found no metabolic differences between female and male locusts. In general, sexual differences in food utilization efficiencies are small, but it has sometimes been determined that females eat more, faster, or have a greater efficiency of conversion of ingested food than males (Scriber & Slansky 1981).

We also observed that the initial dry weight of female locusts was greater than that of males. Female insects are commonly bigger and heavier than males (Scriber & Slansky 1981) as in other Orthoptera species (Chlodny 1969; Muthukrishnan & Delvi 1974). Locust growth in dry weight was in general, only around $-0.005 \pm e.e. 0.0005 \text{ mg g}^{-1} \text{ day}^{-1}$ ($N = 81$) — meaning that the adult locusts did not grow; on the contrary, their weight slightly declined.

Interestingly, only when fed with *Ficus cotinifolia* was the locusts' weight clearly increased, and they exhibited greater nutritional rates than when fed on the other plants. These results thus suggest that *F. cotinifolia* is a valuable food plant for this species, as shown in a previous feeding assay (Cano-Santana *et al.* 2005). Regarding food utilization efficiencies, we found no sexual differences and no gregariousness differences.

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