Published in Biotropica 15, issue 3, 207-216, 1983
which should be used for any reference to this work

The Palatability of Ferns and the Ecology of Two Tropical Forest Grasshoppers

C. H. F. Rowell, M. Rowell-Rahier

Zoologisches Institut der Universität, 4051 Basel, SWITZERLAND

H. E. Braker

Dept. of Zoology, University of California at Berkeley, California 94720, U.S.A.

G. Cooper-Driver

Dept. of Biological Sciences, Boston University, Massachusetts 02215, U.S.A.

and

L. D. Gómez P.

Museo Nacional de Costa Rica, San José, COSTA RICA

ABSTRACT

Fern-eating forest grasshoppers of two species were studied in Costa Rica. *Hylopedetes nigrithorax* lives in groups on particular ferns in light-gaps. *Homeomastax dentata* is solitary and found throughout the forest. The relative palatability of 13 species of fern was established, including species supporting *Hylopedetes* colonies, species on which *Homeomastax* was found, and controls. The palatability scores obtained with *Homeomastax* were relatively closely grouped and only the least palatable plant was significantly less preferred. The scores obtained from *Hylopedetes* were more widely spread, and the most palatable plants were significantly preferred. This suggests that *Hylopedetes* is more specialised in its feeding habits, *Homeomastax* more generalised. The rank order of palatability to the two grasshoppers was significantly positively correlated. The proximal basis of palatability differences seems to be chemical, but the content of phenols, nitrogen, tannins and fiber showed no correlation with palatability. The siting of *Hylopedetes* colonies appears to be determined by sunlight and fern palatability. Most colonies are found on the most palatable fern, but the longest lived colonies occur on a less preferred species which better survives successional change.

Acridid grasshoppers are usually thought of as generalist, but not indiscriminate feeders (*e.g.,* Williams 1954, Mulkern 1967, and Gangwere 1972). There are, however, a considerable number of species which feed on only a few or even one species of plant (Joern 1979). Such grasshoppers occur in many different environments (*e.g.,* from the temperate forests of North America, where *Dendrotettix quercus* eats oak leaves (*e.g.,* Valek 1971), or *Bocagella acutipennis* feeding on the composite *Vernonia guineensis* in the west African savanna (Duviard 1970), to *Paulinia acuminata* eating *Salvia* and *Pistia* floating on the lakes of South America (Carbonell 1964)) and may be especially characteristic of some, such as warm temperate desert (Otte and Joern 1977) or tropical rain forest (Rowell 1978). Among the latter, several genera of neotropical grasshoppers eat ferns (Rowell 1978 and unpubl. obs.), either exclusively or as an important component of their diet along with other plants (*e.g., Homeomastax,* Eumastacoidea: *Leptomerinthoprora, Hylopedetes, Micropaon,* and *Scirtopaon,* Acridoidea: many tettrigids).

Because ferns were among the oldest vascular plants, and Orthoptera among the oldest herbivorous insects (Smart and Hughes 1971), the relations of their modern descendants are of interest to plant/herbivore theory. To date, relatively little is known of interactions between ferns and their herbivores (see however Kaplanis *et al.* 1967, Cooper-Driver 1977, Gerson 1979) apart from two areas of recent research. The first of these concerns the commercially important bracken fern *Pteridium aquilinum* (Bernays 1977; Jones and Firn 1979a, b; Lawton 1982; Rigby and Lawton 1981; Schreiner 1980; Tempel 1981). Secondly, there has been some controversy as to whether ferns as a group suffer less from herbivory than do angiosperms (Clark 1973, Balick *et al.* 1978, Hendrix 1980, Auerbach and Hendrix 1980); this discussion is inhibited by the paucity of information about tropical species.

This paper reports the results of tests of the relative palatability of several ferns from a tropical montane forest to two unrelated species of grasshopper, both fern feeders from this habitat. *Homeomastax dentata* (Saussure 1903) is a representative of the Eumastacoidea, an extremely ancient group of the Orthoptera, which has had the opportunity to coevolve with the ferns probably since the Carboniferous, a period in excess of 200 million years. Many modern eumastacids feed on modern ferns, and though it would be naive to regard the current forms of either line as either ancient or primitive [*e.g.,* Harris (1973), and Lovis (1977), on the evolution of modern ferns and Descamps (1971, 1973), on the Eumastacoidea], this may well be a very ancient association (Blackith 1973, Descamps 1973). *Hylopedetes nigrithorax* Descamps and Rowell 1978 belongs to the subfamily Rhytidochrotinae (Amedegnato 1976) of the Acrididae, a relatively recent group (Carbonell 1977, Amedegnato and Descamps 1979).

In undisturbed habitats, *H. nigrithorax* is found in small isolated groups centered on individual fern fronds in forest light-gaps. These fronds belong to only a few species of fern. These groups can persist on the same plants for at least four years. Although some individuals leave to colonise other favorable sites (Braker, unpubl. obs.), in montane forest they are rarely found away from the established colonies. *Homeomastax dentata* does not show the marked site-specificity of *H. nigrithorax,* and is found on ferns in both light-gaps and closed forest. Individuals are never grouped, except for copulating pairs. Microscopic examination of the faeces of wild-caught individuals, using a modified version of the techniques of Brusven and Mulkern (1960) and Launois (1976), confirms that in this habitat both species eat almost exclusively ferns and virtually no angiosperms (Rowell, unpubl. obs.).

There are hundreds of fern species in the habitat of these two grasshoppers. We designed experiments to answer the following questions: Do the two grasshoppers discriminate markedly between different species of ferns? To what extent do they approach the "generalist" or "specialist" ends of the spectrum of host-plant specificity? To what extent is the observed association between *H. nigrithorax* and certain individual ferns a function of the greater palatability of those ferns? Assuming that the two species of grasshopper each show a rank order of preferences among ferns from their habitat, how do the two rank orders compare with each other? Are the same sorts of ferns found to be acceptable or distasteful by both insects? Are there obvious correlations between the physical and chemical characteristics of the fern leaves and their degree of palatability?

METHODS

STUDY SITE.—Field work was done at Finca Las Cruces, San Vito de Jaba, Costa Rica, a field station of the Organization for Tropical Studies, University of Costa Rica. It is situated in "Premontane Rain-Forest" in the Holdridge Life Zone classification (Tosi 1969), at about 1200 m altitude. The climate is characterised by an exceptionally low annual variation in monthly mean temperatures (1.1°C in 1963), uniformly high humidity (87–91% in 1963), heavy rainfall (mean 4031 mm/year, 1953–64), and persistent cloud cover (only 1400 h unobstructed sunlight in 1963). Less than three h sunshine per day are recorded for eight months of the year, rising to 5.6 h/day in the dry season December to March (Scott 1971). The insects and plants used were obtained from primary forest. Within this forest daytime shade temperatures are characteristically 18–20°C. This equable, cool, shady and moist habitat is very rich in ferns.

CHOICE OF FERNS.—We selected 13 ferns, falling into four operational categories. The scientific names (determined by Gómez) and code designations of these ferns are listed in Table 1. The first category (H series, $N = 5$) were plants which provided "home fronds" for known colonies of *H. nigrithorax*. "Home fronds" were defined as those fronds which usually had grasshoppers on them. Typically, the home fronds of a colony comprised one or two particular fronds of a single individual plant. One large colony used fronds of two different plants of the same species, and to a lesser extent also used a frond of a third plant of another species.

The second category of ferns (E series, $N = 4$) were species on which individual *Homeomastax dentata* were caught. Originally rather a large category, this group was then restricted to a few distinctive species which were sufficiently abundant to provide adequate material for experiments and chemical analysis.

Two control groups of ferns were selected. Neither had any association with either grasshopper, but were ferns of the same habitat, habit and leaf texture as the plants in the E and H series. The HC series ($N = 2$) were ferns adjacent to the home frond of one particular colony of *Hylopedetes,* but on which grasshoppers were never seen. The F series ($N = 2$) were selected from species growing alongside E ferns.

Of these 13 species of ferns, 11 were tested in food choice trials with both species of grasshopper. The remaining two ferns were tested only with either *Hylopedetes* or *Homeomastax*.

FEEDING TRIALS.—Fern fronds were gathered and stored individually at room temperature in moist polyethylene bags for no more than one day before use in feeding trials. Grasshoppers were caught in the field with minimum disturbance, used for tests and then liberated at the original capture site. For feeding trials, single adults of either sex were placed in a transparent plastic box (85 × 36 × 36 mm) along with some dry absorbent tissue paper and an excess, measured quantity of two different ferns. As they are small animals (female *Hylopedetes* are 14 mm long, female *Homeomastax* 18 mm, the males smaller) these containers are adequately large. Trials were set up in the afternoon and examined early the following morning, about 18 h later. Each grasshopper species was tested with all possible (66) combinations of the 12 different ferns, maximally ten times. At the end of the trial the amount eaten from each fern was noted. If the grasshopper was to be used in further trials, it was placed soon afterwards in a clean new box with the next combination of plants, which did not include either of the immediately preceding combination. If the insect had eaten little or none of either plant, care was taken to include at least one plant known to be palatable in the next combination, in order to avoid starvation. Each animal was used for 2–3 trials before liberation.

Analysis of feeding trials.—For each combination of ferns a relative score was allotted to each of the two ferns. These scores corresponded to the following categories: much more eaten, slightly more eaten, equally eaten, slightly less eaten, and much less eaten. The categories were allotted arbitrary numerical scores of +2, +1, 0, −1, and −2 respectively. For each plant ($N = 12$) the 11 scores were then summed, and the totals used to determine a rank order in palatability. The highest and lowest attainable scores would be +22 and −22. The rank order so obtained was checked against the results obtained by direct comparison of adjacent plants in the rank order. The direct comparison was also used to break ties obtained by the score method. To assess the significance of the differences between plants, a Wilcoxon rank-sign test was used. The above procedures were duplicated for each of the grasshopper species. Rank orders were then compared using Kendall's coefficient of rank correlation.

The use of relative scores, as outlined above, compensates for differences between individual insects, *e.g.*, in hunger or in size, and the number of insects used (>20) minimizes the effect of individual idiosyncracies. The most important source of error is probably the small number of replicates of each combination (never more than 10). However, when 8–10 replicates were made, little variation was seen, and it is here assumed that the results are representative. It is further assumed that males and females have the same qualitative preferences; this is supported by field observations and by direct comparison of experimental results where the number of trials is large enough to justify the assumption.

Chemical analysis.—Fresh ferns were gathered and air-dried at 20°C for 20 h. Whenever possible, the same individual plant was used as for the feeding trials. They were then packed in sealed polyethylene bags during transport to San José de Costa Rica (18 hours), air-dried for a further 12–36 h at 20°C, and finally air-dried at 60°C for eight h and packed in sealed containers. Later, the material was powdered, and for each sample total nitrogen, total phenols, condensed tannins (proanthocyanidins), relative astringency, non-extractable components, and lignin were estimated. The chemical analyses were performed on specimens identified by codes unknown to the chemists involved.

Total nitrogen was measured by a standard Kjehldahl method. The results are expressed as percent dry weight of the dryleaf powder.

Total phenols were estimated by the use of the Folin-Denis reagent as described by Goldstein and Swain (1965). This reagent reacts with tannins, coumarins, phenolic acids and other phenols. Results are expressed as percent phenols per dry weight of tissue using tannic acid as a standard.

Condensed tannins were estimated in both the 50 percent methanol extract and the unextracted powder. Proanthocyanidins were determined by heating an equal aliquot of plant extract with *n*-butanol containing 5 percent (v/v)

TABLE 1. *Order of preference for different fern species shown by* Hylopedetes nigrithorax *and* Homeomastax dentata.

Fern		*Hylopedetes*		*Homeomastax*	
Name	Code	Rank order	Palatability score	Rank order	Palatability score
Hypolepis hostilis	H_2	1	+13	1	+9
Dennstaedtia obtusifolia	H_4	2	+12	8	−3
Pteris podophylla[a]	H_0	3	+6	3	+8
Diplazium expansum	H_1	4 } [c]	+4	2	+9
Diplazium aff. *herbaceum*	E_5	5 } [c]	+3	9	−6
Nephelea mexicana	E_8	6	+2	7	+2
Pteris podophylla[a]	F_6	7 } [c]	−1	5	+2
Cyathea multiflora	H_1C_2	8 } [c]	−4	10	−6
Pteris altissima	FP	9	−4	6	+2
Thelypteris subdecussata	F_9	10	−6	4	+5
Thelypteris atrovirens	H_1C_1	11	−9	11	−20
Diplazium striatastrum	H_3B	12	−15	(not tested)	
Thelypteris aff. *opulenta*	E_1	(not tested)		7.5[b]	−2

[a] Different individual plants of the same species—see text.
[b] Excluded from rank order for *Homeomastax* to allow comparability with *Hylopedetes*.
[c] Rank order reversed in direct comparisons between the two species. When calculating the correlation between the two ranks, these values were treated as ties.

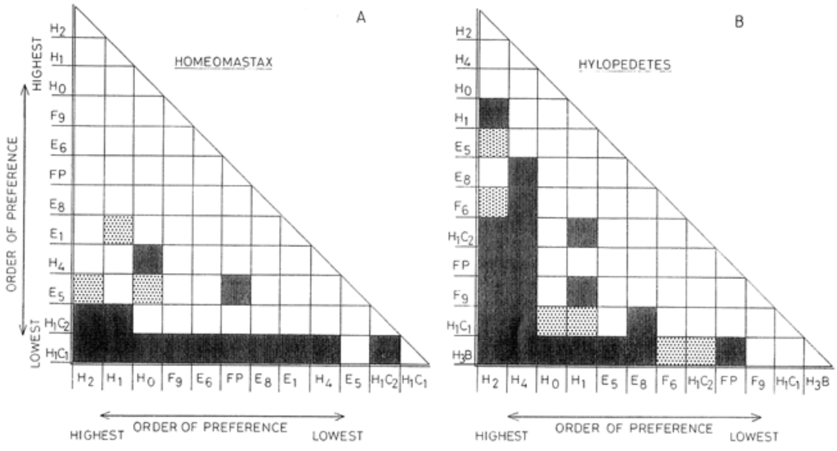

FIGURE 1. Matrix showing which combination of ferns resulted in a significant difference in the feeding behaviour of the grasshopper. Solid squares, $P \leq 0.05$; dotted squares, $0.05 < P < 0.07$; open squares, $P > 0.07$. A statistically significant difference in this context is the equivalent of a large difference (see text), and its absence does not necessarily imply that no real difference exists. 1A. *Homeomastax dentata*. Most of the large differences in palatability are associated with the least preferred plant (H_1C_1, *Thelypteris atrovirens*). 1B. *Hylopedetes nigrithorax*. Large differences in palatability are associated both with preferred plant species (H_2 and H_4, *Hypolepis hostilis* and *Dennstaedtia obtusifolia*) and disliked species (H_3B, *Diplazium striatastrum*), but principally with the former.

concentrated HCl for 2 hours at 95°C, and measuring the absorbance at 545 nm (procyanidin) and 560 nm (prodelphinidin). Proanthocyanidins in the residue were estimated similarly after the powder and a small amount of 50 percent aqueous methanol were first boiled for 4–5 minutes.

Relative astringency was estimated by the method of Bate-Smith (1973). For each sample, one ml of a 50 percent methanol extract of fern powder was mixed with one ml of diluted blood (1:50 with water). The tannin-protein precipitate was removed by centrifugation and the residual haemoglobin determined by absorbance at 578 nm. The binding ability of this extract is measured relative to a standard tannin, tannic acid. Astringency is expressed in tannic acid equivalents (TAE). TAE is equal to percent tannin if the tannin in the sample has the same properties as tannic acid. The astringency of an extracted residue was similarly estimated.

To estimate non-extractable components, fern powder was successively extracted with chloroform : ether (3:1), ether, 80 percent methanol, and then hydrolyzed with 3 percent H_2SO_4 at 100°C for 30 min. The residue was then dried and weighed. The non-extractable component ('fiber') was calculated from the formula: (dry weight of the residue/weight of the powder before extraction) × 100 = percent fiber. Fiber measured by this method probably consists of hemicellulose, cellulose and lignin.

Lignin was measured using the method of Morrison (1972). Lignins were extracted from plant tissues with 25% acetyl bromide in acetic acid for three min. These tissues had previously been extracted with water, ethanol, acetone and ether. The absorbance of the neutralized solution was measured at 280 nm. Lignin is expressed as a percent of the total plant powder before extraction, using fiber from *Spartina alterniflora* as standard.

RESULTS

Rank order of plants in palatability.—Table 1 shows the order of preference in which ferns were eaten by the two grasshopper species. Instances in which this rank order conflicted with that obtained by direct comparison between the two plants in question are indicated. No conflicts were found in the case of *Homeomastax*, and the two instances found in *Hylopedetes* were simple reversals of order which would not otherwise alter the overall ranking. The rank orders derived from the two grasshoppers are similar (probability of chance occurrence = 0.038, by Kendall's coefficient of rank correlation (τ = 0.49, n = 11, N = 50). The most acceptable and the least acceptable ferns are the same for both insects. There are only two major exceptions: *Dennstaedtia obtusifolia* is well received by *Hylopedetes* and accepted only with reluctance by *Homeomastax*, whereas the reverse is true of *Thelypteris subdecussata*. The most acceptable ferns to both grasshoppers are those of the H series, that is, the ferns with which *Hylopedetes* is associated in the wild; the next most acceptable are the E series, those known to be eaten in the wild by *Homeomastax*.

DISTRIBUTION OF SIGNIFICANT DIFFERENCES BETWEEN PLANTS.—The distribution of significant differences in palatability, calculated as described in the Methods, is indicated in Figures 1A and B. It should be noted that the criteria of significance derive ultimately from the magnitude of the individual differential score (which is a function of the feeding behaviour of the grasshopper) and from the number of plants with which the two species under consideration are compared (a function of the experimental design). Thus the data in Figure 1 merely indicate the distribution of large differences in palatability. It can safely be assumed that all combinations would be found significantly different if a large enough number of test species were used, unless the two plants were precisely identical in palatability.

Trials with *Homeomastax* produced a significant difference in palatability ($P < 5\%$) in only 14 out of 66 combinations. Further, 10 of these 14 involve one plant (*Thelypteris atrovirens*) which was very distasteful (palatability score of −20 out a possible −22). Palatable plants did not have very high relative scores (+8, +9 and +9 out of a possible +22). The plants were closely grouped in palatability (over a range of 16 units out of a possible 44) to *Homeomastax,* except for one very unpalatable species; no plants are clearly preferred to all the rest.

Trials with *Hylopedetes* produced a different result. There were more significantly different combinations of plants ($P < 5\%$ in 21/66 combinations) than in trials with *Homeomastax*. The palatability scores are more widely distributed, over a range of 29 out of a possible 44 units, and the most palatable plants are more highly preferred (scores of +13 and +12). Significantly different comparisons are associated with palatable plants more often than with unpalatable ones, unlike the situation in *Homeomastax*. The comparison between the two grasshopper species can be refined by excluding the two species of fern *Thelypteris* sp. aff. *opulenta* and *Diplazium striatastrum* which were not tested with both grasshoppers. Then the "unpalatable" category is involved in 9 of 13 significant differences for *Homeomastax* but only 3 of 14 for *Hylopedetes*. For *Hylopedetes,* responses indicated both very palatable and unpalatable species, and there is a wider range of palatability than for *Homeomastax* (Fig. 2).

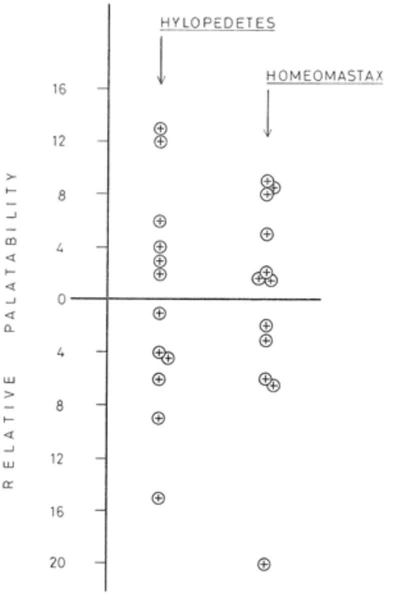

FIGURE 2. The relative palatability of the different ferns (from data in Table 1), plotted on a vertical scale for each of the two grasshopper species. *Homeomastax* perceives the ferns as relatively closely grouped in palatability, with the exception of one very distasteful species. *Hylopedetes* perceives the ferns spread out over a wider perceptual range, with some more highly preferred species.

CHEMICAL ANALYSIS AND RELATION TO PREFERENCE.—The results of the chemical analyses are shown in Table 2, which also shows the order of preference of both grasshoppers for the various ferns. No obvious correlation exists between the palatability of the ferns and any of the variables measured. A multiple linear regression indicated a weak positive relation between palatability and total nitrogen and a weak negative relation between palatability and total phenols in *Hylopedetes*; in *Homeomastax* both relationships were weak and negative. Examination of the variance (Snedecor and Cochran 1962) showed that in neither insect were the two slopes significantly different from each other or from zero, and that the regression on

TABLE 2. *Chemical analysis of the ferns used in foodplant trials.*

Plant	Palatability score (*Homeomastax*)	% N_2	% phenols	PA powder	PA extract	TAE powder	TAE extract	% fiber	% lignin
			A. Arranged in the preference order of *Homeomastax*						
H_2 *Hypolepis hostilis*	+9	2.98	2.05	1.6	1.0	2.1	2.4	61.8	9.7
H_1 *Diplazium expansum*	+9	3.08	1.90	0.4	0.0	2.3	2.4	60.2	4.0
H_0 *Pteris podophylla*	+8	3.43	0.35	0.3	0.0	1.6	1.0	58.8	4.4
F_9 *Thelypteris subdecussata*	+5	2.82	2.60	9.5	3.4	2.6	6.4	64.4	5.9
FP *Pteris altissima*	+2	3.21	0.80	0.5	0.0	2.1	2.6	66.8	5.6
E_8 *Nephelea mexicana*	+2	3.21	3.90	3.0	5.5	2.7	3.9	59.6	5.0
H_4 *Dennstaedtia obtusifolia*	−3	4.26	0.90	1.2	0.5	1.3	1.5	59.0	5.6
E_5 *Diplazium* aff. *herbaceum*	−6	4.33	1.70	0.9	0.0	1.4	0.9	59.0	2.9
H_1C_2 *Cyathea multiflora*	−6	2.38	3.15	1.7	1.3	2.5	4.5	47.4	2.6
H_1C_1 *Thelypteris atrovirens*	−20	2.45	2.9	1.9	1.0	2.5	4.4	47.0	2.8
			B. Arranged in the preference order of *Hylopedetes*						
H_2 *Hypolepis hostilis*	+13	2.98	2.05	1.6	1.0	2.1	2.4	61.8	9.7
H_4 *Dennstaedtia obtusifolia*	+12	4.26	0.90	1.2	0.5	1.3	1.5	59.0	5.6
H_0 *Pteris podophylla*	+6	3.43	0.35	0.3	0.0	1.6	1.0	58.8	4.4
H_1 *Diplazium expansum*	+4	3.08	1.90	0.4	0.0	2.3	2.4	60.2	4.0
E_5 *Diplazium* aff. *herbaceum*	+3	4.33	1.70	0.9	0.0	1.4	0.9	59.0	2.9
E_8 *Nephelea mexicana*	+2	3.21	3.90	3.0	5.5	2.7	3.9	59.6	5.0
H_1C_2 *Cyathea multiflora*	−4	2.38	3.15	1.7	1.3	2.5	4.5	47.4	2.6
FP *Pteris altissima*	−4	3.21	0.80	0.5	0.0	2.1	2.6	66.8	5.6
F_9 *Thelypteris subdecussata*	−6	2.82	2.60	9.5	3.4	2.6	6.4	64.4	5.9
H_1C_1 *Thelypteris atrovirens*	−9	2.45	2.90	1.9	1.0	2.5	4.4	47.0	2.8
H_5B *Diplazium striatastrum*	−15	2.82	2.70	0.9	0.6	1.4	1.5	60.0	8.3

the two variables accounted for only 5–10 percent of the total variance.

DISCUSSION

GENERALIST VERSUS SPECIALIST RESPONSES TO FEEDING TRIALS.—Laboratory feeding trials tend to produce more positive responses than is representative of the wild animal. This is because the animal is deprived of its normal search behaviour (the experimenter may confront the animal with a plant which it normally would never encounter) and furthermore it has a restricted choice (if confined with two unpalatable plants, hunger may compel it to eat something which it would normally reject). Consequently the number of plants accepted in an experiment such as this may not reflect feeding specialization of wild insects. The relevant data are the differences in apparent palatability between the plants tested. A specialist feeder would be expected to discriminate strongly between the plants it preferred and the majority of other plants; the latter may still show differences in palatability. A more generalist feeder should discriminate less strongly in favour of any particular species, but would still be expected to discriminate strongly against very unpalatable species. These two schemata seem to represent these results and the natural history of *Hylopedetes* and *Homeomastax*. *Hylopedetes* is associated with certain individuals and species of fern in the wild, whereas *Homeomastax* is encountered on a wide range of ferns in various forest habitats.

While *Hylopedetes* is a more restricted feeder than *Homeomastax*, it is not monophagous. Some insects, including some forest grasshoppers (*e.g.*, various species of the genera *Ampelophilus*, *Lithoscirtus* and *Drymophilacris*, which eat only a few species of Solanaceae and of Compositae (Rowell 1978 and unpubl. obs.)) will refuse all but the preferred food(s) and starve to death if deprived of it (them). In these experiments, *Hylopedetes* accepted fern species on which it has not been found in the wild. Whatever its longterm fitness on these might be, its behavioural food selection process is clearly not as extreme as in some insects. This is of interest in view of the need of *Hylopedetes* and other flightless grasshoppers which live in the transient light-gap habitat to colonise new sites. In the course of dispersal they must traverse closed forest where their normal foodplants are rare or absent. The ability to subsist temporarily on other plants must be of advantage.

DIFFERENCES IN PALATABILITY RELATED TO INDIVIDUAL FERNS AND TO THEIR SYSTEMATIC POSITION.—Table 1 indicates no obvious relation between the systematic position of the fern and its palatability. Where different species of the same fern genus are compared, they are often quite different—thus *Diplazium expansum*, *D.* sp. nr. *herbaceum*, and *D. hians* receive palatability scores of +4, +3 and −12 from *Hylopedetes*, and *D. expansum* and *D.* sp. aff. *herbaceum* obtain ratings of +9 and −6 from *Homeomastax*. Similarly, the two tree ferns tested (*Cyathea multiflora* and *Nephelea mexicanum*) are neither conspicuously more nor less palatable than the true ferns. These findings are perhaps no surprise, but it might have been expected that the somewhat more specialist *Hylopedetes* would have had some preferred genera. Within our sample this is not obviously so.

On the other hand, on the one occasion when two individual plants of the same species were tested, they were treated differently by both insects. H_0 is a plant of *Pteris podophylla* which supported a colony of *Hylopedetes* for years, until shaded by the growth of a nearby tree. It received high palatability ratings from both species of grasshopper. Fern F_6 is another individual of the same species, growing 53 metres away. It is shaded and has not supported a *Hylopedetes* colony during the last six years. This individual plant received appreciably lower ratings from both species, and for *Hylopedetes* the difference between H_0 and F_6 was nearly statistically significant. This finding shows that there is appreciable variation between individual fern plants of a species in their palatability, and that the potential resource of suitable host plants may be smaller in fact than it appears to an outside observer. Similar cases of differences between individual plants and the consequences for herbivores have been previously described (*e.g.*, Edmunds and Alstad 1978). In some angiosperms it has been demonstrated that the plant responds to herbivore attack with an increased production of secondary compounds, resulting in lowered palatability and/or nutritive value for subsequent herbivores (*e.g.*, Green and Ryan 1972, Haukioja and Niemela 1977, Carrol and Hoffman 1980). No information is available on this aspect for ferns. If the phenomenon occurs, the low density and additionally the nomadic existence of *Homeomastax* or the territorial defense of the occupied pinnule by *Hylopedetes* males would tend to reduce its impact on these grasshoppers.

THE CHEMICAL BASIS OF PALATABILITY.—The distinction has been made (Feeny 1976) between 'quantitative' and 'qualitative' chemical defenses against herbivores. Tannins are considered a classical example of the former, based largely on the work of Feeny (1970) on oak leaves. Tannins are notoriously difficult to assess in a biologically meaningful way, especially when working from dried material (Swain 1979), as in our case. If taken at face value, the results reported here suggest that neither tannin content nor total phenolic content determines the palatability of these ferns to two relatively specialised fern herbivores. Fox and Macauley (1977) observed a similar lack of correlation between leaf tannins and acceptability to a specialist Chrysomelid beetle feeding on *Eucalyptus* species. Similarly, total nitrogen is but a crude measure of the potential of the foodplant to supply the nitrogen needs of the consumer, but shows here no obvious correlation with order of preference by the grasshoppers, although in other instances it has been shown to be an important factor (*e.g.*, Slansky and Feeny 1977, McNeill and Southwood 1978, Scriber and Slansky 1981). Fibre content varies little between the ferns tested, and they do not obviously differ in other physical defenses such as hairs or glands. We assume by exclusion that the proximate bases of discrimination are probably undetermined secondary chemicals acting as attractants or repellents, as is frequently the case with herbivorous insects eating angiosperms. The ultimate reasons for the preferences shown by the grasshoppers (*e.g.*, toxicity or nutritive value) are unknown. Experience with angiosperms and their herbivores has shown that palatability and relative risk to attack are the products of highly complex situations; it is not too surprising that our shot-gun analysis techniques failed to isolate the critical chemical stimuli for the insects in question.

THE ECOLOGY OF *HYLOPEDETES NIGRITHORAX* IN RELATION TO ITS FEEDING PREFERENCES.—*Hylopedetes nigrithorax* is found in groups of individuals which are associated with specific areas and with specific fern fronds within those areas; the ferns chosen are a small fraction of those available. In this choice at least two factors, sunlight and palatability, appear to be critically important.

The habitat is cool and with remarkably little direct sunlight. In such a habitat there would seem to be a significant advantage to a poikilotherm to use what sunlight it can to raise its body temperature. The "home fronds" of *Hylopedetes* are always located where they can intercept available sunlight.

Although *Hylopedetes* groups damage their fronds appreciably by feeding, their populations are small enough (<20 adult individuals per colony) to avoid destroying them. Most colony shifts which have occurred in the study site over the past six years have been clearly associated with successional change. The apparent need for sunlight of *Hylopedetes* confines them to ferns growing in light-gaps. As other plants grow, especially trees, the former light-gap becomes shaded out. In one case the only two sunlit fronds of a large and otherwise suitable fern plant were smashed to the ground by a falling tree, and the colony which had lived there for at least four years vanished; another colony appeared simultaneously on a new, previously unoccupied, plant 20 m away, and probably represents the same group. If growing in a large treefall clearing, where competition is intense, the fern may become completely smothered by other vegetation. Colonies which persist the longest are those in which the host fern is not only long-lived (as most are) but also succeeds in remaining in the sun. This happens when the fern is an erect and vigorous species which can resist rapid overgrowth, or grows at the edge of paths kept open by man or other animals.

Homeomastax is much less strongly associated with sunlit environments than *Hylopedetes*. It also breeds throughout the year, whereas *Hylopedetes* and other acridids of this habitat breed principally in the relatively dry period January–March. These observations suggest that *Homeomastax* may have a greater tolerance for low body temperatures, but no direct data are available.

The most obvious fact from Table 1 is that the four ferns most preferred by *Hylopedetes* are all "H-series" ferns (ferns which *Hylopedetes* uses as "home fronds"). Clearly, site selection by the colony is partly based on palatability. At first it appears anomalous that the only remaining "H-series" fern (H_3B, *Diplazium striatastrum*) is the most unpalatable of all ferns tested. This plant, however, is only a "subsidiary home frond" to a colony whose "home frond" is the palatable *Pteris podophylla*; the *Diplazium striatastrum* frond was sunlit, and apparently used only for basking (as are also various well-placed angiosperms around the home frond).

Interaction of sunlight and palatability determine the most suitable food plant species. Observations over 6 years have shown that all the long-lived colonies to date have been on *Pteris podophylla*. The only colony known on *Diplazium expansum* is recently established and its longevity not yet known. Only one individual male *Hylopedetes* was ever found on *Dennstaedtia obtusifolia*. Though extremely palatable, this species appears to be restricted to shady places, and is thus unsuitable for a permanent colony. It is also rather low-growing and would be rapidly overshadowed in a competitive situation. The situation with *Hypolepis hostilis* is particularly interesting. This is the most palatable of all ferns tested, both for *Hylopedetes* and *Homeomastax*; it is also thorny, which suggests physical defense against large herbivores, and thus may have reduced its chemical defenses. The largest number of *Hylopedetes* colonies have been found on this species. None, however, have persisted for more than three years (the life-cycle of the grasshopper is not known with precision, but the maximum is 12 months). The reason for short associations is the poor long-term competitive ability of *Hypolepis*. *Hypolepis* is a prompt coloniser of light-gaps; its long prostrate thorny fronds grow rapidly and often succeed in becoming scandent, scrambling over the regenerating vegetation. Within a relatively short time, however, it loses its "place in the sun" to more erect species, and though it may persist in the shade, it is then unsuitable for *Hylopedetes*. *Pteris podophylla* is noticeably less palatable to *Hylopedetes* than either of the preceding species, but nonetheless provides the most persistent and largest colonies. This fern is a massive erect species; the fronds have a "stalk" up to three m high, on top of which the pinnules form a horizontal palm-like "leaf" which effectively shades competitors. These ferns persist as suitable habitats until shaded out by substantial trees, which take some years to develop; their fronds are perhaps *the* typical habitat of *H. nigrithorax*.

The fitness of *Hylopedetes* on these different ferns is not known, but is probably higher in stable colonies (*i.e.*, on *Pteris podophylla*) than in transient ones. Although it is not known when dispersal to other light-gaps takes place, nor at what stage larval mortality is highest, one would imagine that more offspring will survive if some can replace their parents on a stable and suitable food-plant than if all have to disperse into the forest to find new sites. If this expectation is justified the most palatable and frequently selected host-plant (*Hypolepis*) may confer a lower fitness than a less preferred alternative species (*Pteris podophylla*). It is of course possible that *Hypolepis* has other qualities, *e.g.*, high nutritive value or shelter from predation, which compensate *Hylopedetes* for this seeming disadvantage. For example, Coley (1980) reports more herbivory on trees of the secondary succession than on shade-tolerant trees of the same Central American forests. It might be expected that *Hypolepis*, as another fast-growing member of the secondary succession, would devote less of its energies to chemical protection (even though our analysis for phenolics does not support this) or provide the herbivore with more usable assimilate than many other ferns.

ACKNOWLEDGMENTS

This study was supported in part by NSF Grant DEB-7823399 to C.H.F.R. We thank the Organization for Tropical Studies for the use of the Las Cruces Field Station, D. B. McKey for criticism of the manuscript, and M. Descamps for taxonomic help.

LITERATURE CITED

Amedegnato, C. 1976. Structure et évolution des genitalia chez les Acrididae et familles apparentées. Acrida 5: 1–16.
———, and M. Descamps. 1979. History and phylogeny of the neotropical acridid fauna. Metaleptea 2: 1–10.

Auerbach, M. J., and S. D. Hendrix. 1980. Insect-fern interactions: macrolepidopteran utilization and species-area association. Ecol. Entomol. 5: 99–104.

Balick, M. J., D. G. Furth, and G. Cooper-Driver. 1978. Biochemical and evolutionary aspects of arthropod predation on ferns. Oecologia (Berl.) 35: 55–89.

Bate-Smith, E. C. 1973. Haemanalysis of tannins: the concept of relative astringency. Phytochemistry 12: 907–912.

Bernays, E. A. 1977. Cyanogenic glycosides in plants and their relevance in protection from insect attack. Bull. SROP. 1977 (3): 123–128.

Blackith, R. E. 1973. Clues to the Mesozoic evolution of the Eumastacidae. Acrida 2: V–XV.

Brusven, M. A., and G. B. Mulkern. 1960. The use of epidermal characteristics for the identification of plants recovered in fragmentary condition from the crops of grasshoppers. N. Dakota Agr. Exp. Sta. Res. Rept. 3. 11 pp.

Carbonell, C. S. 1964. Habitat, etología y ontogenía de *Paulinia acuminata* en el Uruguay. Revta. Soc. Urug. Ent. 6: 39–48.

———. 1977. Origin, evolution and distribution of the neotropical acridomorph fauna (Orthoptera); a preliminary hypothesis. Rev. Soc. Entomol. Argentina 36: 153–175.

Carrol, C. R., and C. A. Hoffman. 1980. Chemical feeding deterrent mobilized in response to insect herbivory and counter-adaptation by *Epilachna tridecimnotata*. Science 209: 414–416.

Clark, A. 1973. Course-book 73-1, Organization for Tropical Studies, Universidad de Costa Rica, p. 310.

Coley, P. D. 1980. Effects of leaf age and plant life history patterns on herbivory. Nature 284: 545–546.

Cooper-Driver, G. 1977. Chemical evidence for separating the Psilotaceae from the Filicales. Science, 198: 1260–1262.

Descamps, M. 1971. Les Eumastacidae de Colombie. Revision des Paramastacinae et Eumastacinae (Acridomorpha Eumastacoidea). Caldasia XI, no. 51: 99–192.

———. 1973. Comment on Blackith, R. E. Acrida 2: XV–XVIII.

Duviard, D. 1970. Recherches ecologiques dans la savanne de Lamto (Cote d'Ivoire): l'entomocoenose de *Vernonia guineensis* Benth. (Composees). La Terre et La Vie 1: 62–79.

Edmunds, G. F., and D. N. Alstad. 1978. Coevolution in insect herbivores and conifers. Science 199: 941–945.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter-moth caterpillars. Ecology 51: 565–581.

———. 1976. Plant apparency and chemical defence. *In* J. W. Wallace and R. L. Mansell (Eds.). Biochemical interactions between plants and insects, recent advances in phytochemistry, 10. Plenum Press, New York and London.

Fox, L. R., and B. J. Macauley. 1977. Insect grazing on *Eucalyptus* in response to variation in leaf tannins and nitrogen. Oecologia (Berl.) 29: 145–162.

Gangwere, S. K. 1972. Host finding and feeding behaviour in the Orthopteroidea, especially as modified by food availability: a review. Revista de la Universidad de Madrid. 21: 1–158.

Gerson, U. 1979. The associations between pteridophytes and arthropods. Fern Gazette 2: 29–45.

Goldstein, J. L., and T. Swain. 1965. The inhibition of enzymes by tannins. Phytochemistry 4: 185–192.

Green, T. R., and C. A. Ryan. 1972. Wound-induced proteinase inhibition in plant leaves—possible defence mechanism against insects. Science 175: 776–777.

Harris, T. M. 1973. What use are fossil ferns? *In* A. C. Jermy, J. A. Crabbe, and B. A. Thomas (Eds.). The phylogeny and classification of ferns. Bot. J. Linn. Soc. Suppl. 1, 67: 41–44.

Haukioja, E., and P. Niemela. 1977. Retarded growth of a geometrid larva after mechanical damage to leaves of its host tree. Ann. Zool. Fenn. 14: 48–52.

Hendrix, S. D. 1980. An evolutionary and ecological perspective of the insect fauna of ferns. Am. Nat. 115: 171–195.

Joern, A. 1979. Feeding patterns in grasshoppers (Orthoptera: Acrididae): factors influencing diet specialization. Oecologia 38: 325–347.

Jones, G. G., and R. D. Firn. 1979a. Resistance of *Pteridium aquilinum* to attack by non-adapted phytophagous insects. Biochem. System. Ecol. 7: 95–101.

———, and ———. 1979b. Some allelochemicals of *Pteridium aquilinum* and their involvement in resistance to *Pieris brassicae*. Biochem. System. Ecol. 7: 187–192.

Kaplanis, J. N., M. J. Thompson, W. E. Robbins, and B. M. Bryce. 1967. Insect hormones: alpha ecdysone and 20-hydroxyecdysone in bracken fern. Science 157: 1436–1437.

Launois, M. H. 1976. Methode d'étude dans la nature du regime alimentaire du criquet migrateur *Locusta migratoria capito* (Sauss.). Annls. Zool. Ecol. Anim. 8: 25–32.

Lawton, J. H. 1982. Non-competitive populations, non-convergent communities and vacant niches: the herbivores of bracken. *In* D. R. Strong, D. Simberloff and L. G. Abele (Eds.). Ecological communities: conceptual issues and the evidence, Princeton University Press.

Lovis, J. D. 1977. Evolutionary patterns and process in ferns. Adv. Bot. Res. 4: 229–415.

McNeill, S., and T. R. E. Southwood. 1978. The role of nitrogen in the development of insect/plant relationships. *In* J. B. Harborne (Ed.). Biochemical aspects of plant and animal coevolution, Academic Press, New York and London.

Morrison, I. M. 1972. A semimicro method for the determination of lignin and its use in predicting the digestibility of forage crops. J. Sci. Food Agric. 23: 455–463.

Mulkern, G. B. 1967. Food selection of grasshoppers. Ann. Rev. Entomol. 12: 59–79.

Otte, D., and A. Joern. 1977. On feeding patterns in desert grasshoppers and the evolution of specialized diets. Proc. Acad. Nat. Sci. Philadelphia 128: 89–126.

Rigby, C., and J. H. Lawton. 1981. Species-area relations of arthropods on host-plants: herbivores on bracken. J. Biogeogr. 8: 125–133.

Rowell, C. H. F. 1978. Foodplant specificity in neotropical rain-forest acridids. Ent. Exp. Appl. 24: 651–662.

Schreiner, I. H. 1980. Cyanogenesis and the herbivorous insects of bracken fern *Pteridium aquilinum*. Ph. D. Thesis, Cornell University.

SCRIBER, J. M., AND F. SLANSKY. 1981. The nutritional ecology of immature insects. Ann. Rev. Entomol. 183–211.

SCOTT, N. J. 1971. Ecologically important aspects of the climate of Costa Rica. *In* C. E. Schnell (Ed.). Data, keys, tables, figures and miscellanea, Organization for Tropical Studies, Univ. Costa Rica.

SLANSKY, F., AND P. FEENY. 1977. Stabilisation of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated foodplants. Ecological Monographs 47: 209–228.

SMART, J., AND N. F. HUGHES. 1971. The insect and the plant: progressive palaeoecological integration. *In* H. F. van Emden (Ed.). Insect-plant relationships, Blackwell Scientific Publ., Oxford.

SNEDECOR, G. W., AND W. G. COCHRAN. 1962. *Statistical Methods.* University of Iowa Press, Iowa City.

SWAIN, T. 1979. Tannins and lignins. *In* G. A. Rosenthal and D. H. Janzen (Eds.). Herbivores: their interaction with secondary plant metabolites. Academic Press, New York.

TEMPEL, A. S. 1981. Field studies on the relationship between herbivore damage and tannin concentration in bracken (*Pteridium aquilinum*). Oecologia 51: 97–106.

TOSI, J. A. 1969. *Mapa Ecológico de Costa Rica, 1:750,000.* Tropical Science Center, San José de Costa Rica.

VALEK, D. A. 1971. The bionomics of the oak-defoliating grasshopper *Dendrotettix quercus* Packard, in Wisconsin (Orthoptera: Acrididae). Diss. Abstr. Int. B, 32, 1938.

WILLIAMS, L. H. 1954. The feeding habits and food preferences of Acrididae and the factors which determine them. Trans. R. Ent. Soc. Lond. 105: 423–454.