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Biological Sciences

SPATIAL AND TEMPORAL INFLUENCES OF ENVIRONMENTAL CONDITIONS ON BENTHIC MACROINVERTEBRATES IN NORTHEAST LAKE JESUP, CENTRAL FLORIDA

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Abstract: *The benthic macroinvertebrate community composition and selected water and sediments physico-chemical parameters at 15 permanent sampling stations in northeast Lake Jesup, central Florida, were studied monthly from December 1996 to December 1997. Crustacea (primarily Ostracoda) were numerically dominant (mean $3,645/m^2$), followed by Oligochaeta ($898/m^2$), Gastropoda (mostly* Tryonia aequicostata $898/m^2$)*, Chironomidae larvae (predominantly* Glyptotendipes paripes $383/m^2$)*, Chaoboridae larvae ($112/m^2$) and Hirudinea ($107/m^2$). Ordination analysis (CCA and variation partitioning) showed that month of sampling and sampling station together explained 64% of benthic community variability; sampling station explained 45% and sampling month 19% of variation. Significant density differences of various taxa were noted between sampling stations, but not between months of sampling. Clustering of benthic community by using TWINSPAN revealed differences between sand and soft organic sediments. CCA indicated sediment type as the most important environmental factor. The highest biomass and species number were recorded on sand substrate, with Isopoda, Nematoda,* Polypedilum *spp. larvae and* Glyptotendipes paripes *larvae as the typical inhabitants of sand sediment, whereas Tanypodinae larvae, Chaoboridae larvae and* Tryonia aequicostata *were typical for soft muck sediment.*

Key Words: Benthic invertebrates, community, Canonical Correspondence Analysis, Detrended Correspondence Analysis, sediments, physico-chemical conditions

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THE sublittoral and littoral zones of lakes are an important transitional divide between terrestrial and aquatic environments in that they are subject to high variability of environmental influences and often support a diverse benthic community (Håkanson and Jansson, 1983). Qualitative and quantitative compositions of benthic organisms are sensitive and complex indicators of nutrient status of the lakes (Brundin, 1949; Prat, 1978; Winnel and White, 1986). However, use of benthos data as bioindicators of eutrophication is often complicated due to high spatial variability because of patchy distributions of benthic community as well as variations due to seasonality (Verneaux and Aleya, 1998; Reid et al., 1995; Kilgour et al., 2000).

Some man-made and natural lakes in central Florida produce phenomenal numbers of adult chironomid midges that can cause severe nuisance problems and substantial economical losses (Ali, 1995). Larvae of some nuisance midge species may often occur in the littoral part of the lakes (Rasmussen, 1984). Therefore, a better understanding of environmental factors affecting the spatio-temporal distribution patterns of benthic communities in shallow lakes or in littoral parts of deep lakes is needed. The aim of this study was to investigate spatio-temporal changes of benthic community in a shallow littoral area of a natural lake in central Florida and to relate this pattern to simultaneous spatial and temporal changes of selected environmental variables.

METHODS—*Study area*—The study was conducted in 350 ha northeast portion of eutrophic Lake Jesup (28°44′N, 81°14′W), Seminole County, Florida, north of Davis Point (28°45′N) to the confluence with the St. Johns River. Water depth in the study area was ca. 1 m but fluctuated due to local precipitation; water flow in either direction depended upon relative water elevation between the lake and the St. Johns River. For sampling purposes, fifteen evenly spaced stations were permanently established in the study area and a portable Global Positioning System (GPS) receiver was employed to navigate to each station in a double-hulled pontoon boat. Water, sediment and benthic samples were collected between 0800 and 1200 h on one day during the first week of each month from December 1996 to December 1997.

Sampling—Selected water physico-chemical parameters were quantified monthly at each station. Water depth was measured with a graduated pole fitted with a disk at the base to prevent sediment penetration. Secchi disk transparency was assessed with a 20 cm diameter Secchi disk. Dissolved oxygen (Model 54A meter, Yellow Springs Instruments Company, Yellow Springs, OH), specific conductance and water temperature (Model 140 Conductivity-Temperature-Salinity meter, Orion Research Company, Boston, MA) were measured at the middle of water column, and at air-water and sediment-water interfaces. Water samples were collected from the middle of the water column at each station with a 2.2 L horizontal Alpha Bottle (Wildlife Supply Company, Saginaw, MI) to determine pH, turbidity and chlorophyll (*a, b* and total). These samples were transported on ice to the laboratory, and then stored at 4°C in the dark until analyzed within 24 hours.

For sediment parameters, depth of soft sediments was measured with a graduated pole at each station monthly, while seasonal (December 1996, January, April, July and October 1997) quantitative sediment samples were collected using a sediment corer (Ali, 1984; Ali et al., 1988; Ali and Alam, 1996). Three surficial sediment samples (5 cm deep from sediment-water interface) were collected at stations 3, 6, 9, 12 and 15 and composited. Each composite sample was placed in a labeled polyethylene bag, transported to the laboratory on ice, and subsequently maintained at −10°C until processed and analyzed.

To sample benthic organisms, one 15 × 15 cm Ekman dredge sample was collected monthly at each station during the study period. Where necessary, a pole-mounted Ekman dredge was used to insure sufficient substrate penetration. Sediment physical composition (muck, sand, or detritus) was visually

determined and recorded. Ekman dredge samples were transferred to 5 gallon plastic buckets for transport to the laboratory. Samples that could not be immediately processed on return to the laboratory were stored at 4°C and processed within 48 h of collection.

Laboratory methods—The pH of water samples was measured in the laboratory at room temperature using an Orion Research Company Model 710A pH/ISE meter, and turbidity with a HF Instruments Company (Bolton, Ontario, Canada) Model DRT 1000 turbidity meter.

For chlorophyll determination, 1000 ml of each water sample was vacuum filtered through 0.45 μm, 47 mm diameter nylon filters (No. 7404-004, Whatman International Ltd., Maidstone, UK) using Buchner funnels. All chlorophyll analyses were done under green light to avoid chlorophyll photo-degradation (Inskeep and Bloom, 1985; Moran and Porath, 1980). Filters were placed in storage dishes, wrapped in aluminum foil to exclude light and stored at −10°C until analyzed within 4 weeks. Chlorophyll *a, b,* and total chlorophyll were determined using N,N-dimethylformamide (DMF) extraction and spectrophoto-metric analysis (Inskeep and Bloom, 1985; Moran and Porath, 1980). Filtered water obtained from the chlorophyll analysis was used for the remaining water analyses. Fifty ml of the filtrate was used for Soluble Reactive Phosphorus (SRP) determination using the ascorbic acid method (APHA, 1992). Twenty five ml of the filtrate was acidified with 3 drops 12N HCl and stored in scintillation vials at −10°C until transported to the University of Florida's Analytical Research Laboratory (ARL) in Gainesville, FL, for determination of Total Kjeldahl Nitrogen (TKN) and Total Phosphorus (TP).

Frozen sediment samples were thawed at room temperature, overlying water carefully decanted off and each was thoroughly mixed in a beaker. Sediment pH was determined with an Orion 710A pH/ISE meter. Fifteen grams of wet sediment from each sample were transferred to extraction flasks with 45 ml of distilled, deionized water and shaken for one hour. The contents of each extraction flask were vacuum filtered through a 0.2μm filter and 25 ml of the filtrate used for SRP determination using the ascorbic acid method (APHA, 1992). One gram of wet sediment was placed in a tared beaker and dried at 100°C for 24 h to determine percent dry weight. The remaining wet sediments were dried at room temperature in disposable plastic trays, ground to pass through a 350 μm mesh sieve and analyzed for Total Organic Carbon (TOC) using the method of Nelson and Sommers (1982). Samples of remaining dried sediments were sent to ARL, Gainesville, FL, for determination of TKN and TP.

Benthic macroinvertebrate samples collected with Ekman dredge were washed through a 350 μm mesh sieve in the laboratory. Each washed sample was transferred to a gridded, 30 × 40 cm white pan and examined under 2–4× of a dissecting microscope (Ali et al., 1976). Invertebrates were separated, identified and counted. The following taxonomic keys were used: Annelida to class—Pennak (1989); non-insect Arthropoda to class—Edmondson (1959) and Pennak (1989); Insecta to family—Merritt and Cummins (1996); Chironomidae to lowest practical level—Epler (1995); Mollusca to species—Thompson (1984), Heard (1979) and Pennak (1989); and other invertebrates to phylum—Edmondson (1959). For dry biomass determination, benthic invertebrates were divided into two groups: one group contained only Chironomidae and the other all other invertebrates including Mollusca with their shells in place. Each group was placed in a tared weighing dish and dried at 60°C for 24 h (Dermott and Paterson, 1974).

Data analysis—Temporal and spatial analysis of collected data was done by using the computer software Instat version 2.05a. Where necessary, log(n+1) transformations of data were used to improve homoscedasticity. During analysis of data, stations were sorted by descending muck depth and station numbers reassigned from greatest depth (station 1) to least (station 15). These reassigned station numbers were used in all analyses. TWINSPAN (Hill, 1979) was used for clustering of community data and Canoco for Windows 4.0 was used for Detrended Correspondence Analysis (DCA), Canonical Correspondence Analysis (CCA), (ter Braak and Verdonschot, 1995; ter Braak and Šmilauer, 1998) and variation partitioning (Borcard et al., 1992). Indirect ordination DCA was used to indicate approximate influence of all investigated environmental parameters, including those measured on seasonal basis (missing data were replaced by most probable values as recommended by ter Braak (1988), these values were obtained by extrapolation from known seasonally measured values). For CCA and variation partitioning, the variables with missing data points (measured on seasonal basis) were excluded.

TABLE 1. Overall mean (±SD) and maximum and minimum values of selected water and sediment physico-chemical parameters sampled at 15 permanent stations in Lake Jesup, central Florida, December 1996–December 1997.

Parameter	Mean ± SD	Maximum	
		Water	
Depth (m)	0.9 ± 0.3	1.6	0.2
Secchi Disk Transparency (cm)	44 ± 11	100	25
Temperature (°C)[1]	23.4 ± 3.8	29.4	16.3
Dissolved O_2 (ppm)[1]	7.6 ± 1.7	10.9	1.9
Conductance (µS/cm)[1]	1,035 ± 338	1,885	565
pH	8.67 ± 0.50	9.92	7.00
Turbidity (NTU)	13.2 ± 5.6	32.0	2.6
SRP (µg/l)	4.7 ± 4.2	32.0	<0.1
Total P (mg/l)	0.02 ± 0.06	0.40	<0.01
TKN (mg/l)	4.7 ± 2.3	12.8	1.0
Chlorophyll a (mg/m^3)	74.5 ± 33.8	173.6	8.4
Chlorophyll b (mg/m^3)	13.6 ± 18.3	133.8	<0.1
Total Chlorophyll (mg/m^3)	88.4 ± 40.6	288.6	16.5
		Sediment	
Muck depth (cm)	51 ± 24	120	<1
pH	6.64 ± 0.15	7.00	6.36
SRP (mg/kg)	6.2 ± 2.6	11.41	1.1
Total P (mg/g)	0.8 ± 0.4	1.1	0.2
TKN (mg/g)	12.8 ± 10.9	74.4	0.2
Dry mass (%)	23.0 ± 17.9	75.0	10.0
TOC (%)	9.6 ± 4.3	17.0	0.1

RESULTS AND DISCUSSION—Mean water depth during the study was 0.9 ± 0.3 m, and ranged between 0.2 and 1.6 m (Table 1). Water clarity was generally poor during the study as indicated by the overall mean Secchi disk transparency of 44 cm (range 25 to 100 cm). Mean turbidity value amounted to 13.2 NTU, ranged between 2.6 and 32.0 NTU. The minimum turbidity and maximum Secchi disk transparency values were recorded at station 15, closest to the confluence of the lake with the St. Johns River, largely under the influence of water exchange with water flow from the river into the lake. Overall daytime mean water temperature was 23.3°C and ranged between 16.3 and 29.4°C. Dissolved oxygen varied considerably, ranging from 1.9 to 10.9 ppm, with an overall mean of 7.6 ppm. Overall mean value of specific conductance amounted to 1,035 µS/cm, with a maximum value of 1,885 and minimum of 565. Water was alkaline, with mean pH value of 8.67. Nutrient content in the water as indicated by overall mean values of SRP (4.7 µg/l), TP (0.02 mg/l), and TKN (4.7 mg/l) was high. Chlorophyll content was generally high, with overall mean chlorophyll a amounting to 74.5 mg/m^3 (range 8.4 to 173.6 mg/m^3), and total chlorophyll 88.4 mg/m^3 (range 1.6 to 288.6 mg/m^3). The minimum chlorophyll value was recorded under the same conditions where low Secchi disk transparency and turbidity values had prevailed.

TABLE 2. Mean[1] (±SD) depth of soft sediment, mean number of invertebrate taxa, cumulative number of species and mean biomass at 15 permanent sampling stations in northeast Lake Jesup, central Florida, December 1996–December 1997.

Sampling station	Muck depth (cm)	Mean number of taxa/station	Cumulative number of taxa	Biomass (g/m^2)
1	86 ± 17 g	5.5 ± 1.1 bc	12	27.9 ± 61.6 ab
2	72 ± 10 fg	5.5 ± 1.4 bc	14	22.4 ± 52.3 ab
3	67 ± 14 efg	5.0 ± 1.5 bc	12	79.3 ± 131.4 ab
4	62 ± 14 def	4.6 ± 1.3 c	12	1.0 ± 2.1 a
5	58 ± 9 cdef	4.5 ± 1. c	12	19.3 ± 50.9 a
6	53 ± 23 cdef	6.6 ± 1.4 b	13	239.6 ± 303.5 b
7	53 ± 19 cdef	5.2 ± 1.3 bc	12	60.9 ± 93.8 ab
8	52 ± 13 bcdef	5.1 ± 1.0 bc	12	47.5 ± 71.2 ab
9	51 ± 23 bcde	5.7 ± 1.7 bc	14	118.0 ± 226.8 ab
10	50 ± 10 bcde	5.0 ± 1.5 bc	12	1.1 ± 2.4 a
11	48 ± 10 bcde	4.2 ± 1.0 c	11	52.4 ± 126.0 ab
12	43 ± 14 bcd	5.0 ± 1.8 bc	13	24.0 ± 57.6 ab
13	40 ± 23 bc	5.6 ± 1.7 bc	15	96.3 ± 144.6 ab
14	32 ± 17 b	4.3 ± 1.4 c	14	125.6 ± 273.3 ab
15	1 ± 3 a	8.5 ± 2.3 a	17	517.6 ± 299.2 c

[1] Means in each column with the same letter were not significantly ($P > 0.05$) different by repeated measures ANOVA and Tukey-Kramer multiple comparisons post test.

Mean depth of muck sediments in the study area was 51 cm, ranging between <1 and 120 cm (Table 1). The lowest value existed at the sand bottom station 15 closest to the St. Johns River. Sediments were slightly acidic, with overall mean pH value of 6.64, ranging between 6.36 and 7.00. Nutrient concentrations in the sediments were high, with mean SRP 6.2 mg/kg, TP 0.8 mg/g, and TKN 12.8 mg/g. These nutrients were at the lowest concentrations at station 15. Mean total organic carbon content value was 9.6% with a range of 0.1% (station 15) to 17.0% (station 1). Sediments in the study area had a high water content, with overall mean of 23.0% dry mass, and ranging from 10% (station 9) to 75% in predominantly sand bottomed station 15 (Table 1).

The largest number of invertebrate taxa (overall mean 8.3 taxa/station and cumulative of 17 total taxa collected) and highest macroinvertebrate biomass (overall mean 519.1 g/m^2) were recorded at station 15 with sand bottom (Table 2). Among the invertebrate fauna, Crustacea predominated by Ostracoda (3,645/m^2) were numerically the most abundant, followed by Oligochaeta (898/m^2), the gastropod *Tryonia aequicostata* (584/m^2), Chironomidae larvae (predominantly *Glyptotendipes paripes*, 382/m^2), Chaoboridae larvae (112/m^2) and Hirudinea (107/m^2) (Table 3). Ostracods had the highest frequency of occurrence (93.8% of benthic samples), followed by Oligochaeta (91.0%), larvae of the chironomid subfamily Tanypodinae (75.9%), Chaoboridae larvae (54.8%), Hirudinea (42.5%), and the mollusks *Viviparous georgianus* (37.9%), and *T. aquicostata* (30.3%). Other taxa shown in Table 3 occurred in ca. 20% of samples or less. The gastropod *V. georgianus*, though relatively few in numbers, apparently made the largest contribution to total invertebrate biomass due to their large size ranging up to 2 cm in

TABLE 3. Overall mean (±SD) density, maximum density (No./m²), and occurrence frequency (%) of benthic fauna at 15 sampling stations in northeast Lake Jesup, central Florida, December 1996–December 1997.

	Taxa	Mean density	Maximum density	Occurence frequency (%)
Nematoda		65 ± 318	3,655	14.3
Annelida	Oligochaeta	898 ± 3442	39,345	91.0
	Hirudinea	107 ± 510	6,751	42.5
Mollusca	*Viviparous georgianus*	79 ± 172	1,161	37.9
	Tryonia aequicostata	584 ± 2055	12,900	30.3
	Physella heterostropha	0.2 ± 3.1	43	0.5
	Elliptio buckleyi	0.2 ± 3.1	43	0.5
Crustacea	Amphipoda	111 ± 492	12,212	19.4
	Copepoda	17 ± 53	473	16.9
	Decapoda	6 ± 23	215	8.7
	Isopoda	3 ± 19	172	4.6
	Ostracoda	3,645 ± 20,119	271,760	93.8
Insecta	Hemiptera	2 ± 13	129	4.1
	Chironomus crassicaudatus	8 ± 51	645	9.2
	Glyptotendipes paripes	382 ± 2,259	18,361	21.3
	Polypedilum spp.	0.7 ± 6.8	86	1.0
	Tanytarsini	2 ± 9	172	4.1
	Tanypodinae	88 ± 115	903	75.9
	other Chironomidae	0.7 ± 7.0	86	1.5
	Chaoboridae	112 ± 176	1,032	54.8
Hydracarina		1 ± 7	43	0.5

diameter, measurements made with shells in place. This contribution is reflected in total dry biomass station values being the lowest (stations 4 and 10) where *V. georgianus* densities were the lowest compared to the other stations (Tables 2, 4). The finding that highest diversity and biomass was associated with sand substrates is in agreement with other lake benthos studies conducted in Florida (Cowell and Vodopich, 1981; Schramm and Jirka, 1989) and elsewhere in South Africa (Cyrus and Martin, 1988).

Repeated measures ANOVA with Tukey-Kramer post-tests indicated significant differences ($P < 0.05$) of distribution between stations for many invertebrate taxa, especially station 15 supported significantly more *G. paripes*, *V. georgianus*, Oligochaeta, Nematoda, Decapoda, Isopoda and total benthic dry biomass (Tables 2, 4). The majority of taxa collected displayed either significantly higher density in sand substrates and/or were correlated with some sediment properties characteristic for sand substrate, such as decreasing TOC or muck sediment depth or increased sediment dry weight (Table 5). For some of these taxa, such as *G. paripes,* such habitat preferences have been documented (Provost, 1956; Cowell et al., 1975; McLachlan, 1976; Milleson, 1978; Rasmussen, 1984). Taxa that formed the bulk of the community on muck substrates usually did not display any significant preference for this substrate. The only exceptions were *T. aequicostata* and Hirudinea, which were significantly ($P < 0.05$) more abundant in muck sediments than sand. Stations

TABLE 4. Distribution (mean[1] no. ± SD per m^2) of selected invertebrate taxa collected from 15 permanent sampling stations in northeast Lake Jesup, central Florida, December 1996 to December 1997.

Sampling station	Nematoda	Oligochaeta	Hirudinea	Tryonia aequicostata	Viviparous georgianus	Decapoda	Isopoda	Glyptotendipes paripes
1	0 ± 0 a	370 ± 413 a	60 ± 166 a	7 ± 16 a	30 ± 51 a	10 ± 26 a	0 ± 0 a	10 ± 26 a
2	3 ± 12 a	593 ± 607 a	34 ± 23 a	23 ± 52 a	25 ± 41 a	3 ± 13 a	0 ± 0 a	23 ± 62 a
3	13 ± 32 a	361 ± 304 a	50 ± 94 a	40 ± 64 a	56 ± 117 ab	0 ± 0 a	0 ± 0 a	0 ± 0 a
4	0 ± 0 a	363 ± 280 a	20 ± 42 a	20 ± 42 a	3 ± 12 ab	13 ± 27 a	0 ± 0 a	7 ± 16 a
5	3 ± 12 a	328 ± 327 a	8 ± 6 a	10 ± 36 a	10 ± 26 a	3 ± 12 a	0 ± 0 a	0 ± 0 a
6	12 ± 24 a	110 ± 108 a	828 ± 1,814 b	2,968 ± 4,045 b	234 ± 335 b	7 ± 16 a	3 ± 12 a	1,293 ± 4,572 ab
7	7 ± 16 a	718 ± 516 a	79 ± 199 a	3 ± 12 a	53 ± 96 a	3 ± 12 a	0 ± 0 a	13 ± 27 a
8	0 ± 0 a	565 ± 311 a	17 ± 48 a	7 ± 16 a	31 ± 41 ab	0 ± 0 a	0 ± 0 a	18 ± 33 a
9	0 ± 0 a	120 ± 131 a	56 ± 59 a	5,323 ± 4,160 c	72 ± 142 ab	0 ± 0 ab	0 ± 0 a	30 ± 95 a
10	0 ± 0 a	458 ± 318 a	24 ± 41 a	39 ± 83 a	3 ± 12 a	0 ± 0 a	0 ± 0 a	10 ± 19 a
11	0 ± 0 a	490 ± 351 a	36 ± 55 a	7 ± 24 a	46 ± 102 a	0 ± 0 a	0 ± 0 a	26 ± 83 a
12	3 ± 12 a	593 ± 513 a	18 ± 33 a	158 ± 385 a	13 ± 37 a	0 ± 0 a	0 ± 0 a	10 ± 26 a
13	30 ± 71 a	388 ± 340 a	34 ± 53 a	147 ± 245 a	79 ± 126 ab	7 ± 16 a	0 ± 0 a	17 ± 48 a
14	3 ± 12 a	219 ± 312 a	195 ± 361 ab	4 ± 12 a	63 ± 142 ab	0 ± 0 a	0 ± 0 a	1,412 ± 5,092 ab
15	899 ± 877 b	7,790 ± 1,157 b	151 ± 206 a	0 ± 0 a	471 ± 212 c	37 ± 72 b	49 ± 55 a	3,479 ± 5,142 b

[1] Means in each column with the same letter were not significantly ($P > 0.05$) different by repeated measures ANOVA and Tukey-Kramer multiple comparisons post test.

TABLE 5. Matrix of significant ($P < 0.05$) correlation coefficient values (r) between selected sediment physico-chemical parameters and benthic macroinvertebrates sampled at 15 permanent stations in northeast Lake Jesup, central Florida, December 1996 to December 1997.

Taxon	Muck depth $n = 195$	Total organic carbon $n = 45$	% Dry weight $n = 45$
Chironomus crassicaudatus larvae	—	—	0.40
Glyptotendipes paripes larvae	—	−0.63	0.77
Polypedilum spp. larvae	—	−0.33	0.41
Tanytarsini larvae	—	—	—
Total Chironomidae larvae	—	−0.69	0.86
Isopoda	−0.37	−0.55	0.69
Viviparous georgianus	−0.44	−0.72	0.87
Oligochaeta	—	−0.59	0.72
Hirudinea	—	—	—
Nematoda	−0.472	−0.602	0.787
Total dry biomass (mg/m³)	−0.33	−0.55	0.66

6 and 9 supported significantly more *T. aequicostata* than the other stations, while station 6 supported a significantly higher population of Hirudinea than all other stations except 14. Apparently, the sand bottom meets ecological requirements of a larger pool of benthic species recorded in our study than soft, organic substrates, thus higher benthos diversity was recorded in sand substrates. Despite apparent wide temporal differences in monthly mean densities of invertebrates sampled, no significant differences ($P > 0.05$) by ANOVA were detected. This was due to large values of variances occurring between aggregated distributions of the invertebrates sampled.

Faunal differences between sand and soft organic sediments were also apparent at the community level. TWINSPAN clearly separated sand sediment station 15 from the other stations (Fig. 1), some muck sites were also ordinated into this cluster. No clear trend was noted between benthic invertebrate densities collected from muck sites. Some trend can be observed temporally; invertebrate samples from sites that contained Amphipoda as characteristic taxa contained summer invertebrate samples more often than other groups (Fig. 1).

Figure 2 shows ordination diagrams of community data and environmental variables. Detrended Correspondence Analysis (Fig. 2a) interprets the pattern of all community data variability which is then correlated with environmental variables (indirect analysis). Selection of environmental variables does not affect species position in ordination diagram. In Figure 2a, all environmental variables, including those measured seasonally, were used. Two main gradients can be distinguished; the first (sediment condition gradient) follows the horizontal axis and represented a shift from sand to muck sediment (type of sediment, sediment dry mass, TOC and depth of soft sediment closely correlated with horizontal axis). The second (temporal gradient), was represented by water parameters which were highly variable during the year.

To partition between temporal and spatial aspects of variability, two approaches were used. The first used CCA and variation partitioning (Fig 2b–d); the second

G. paripes larvae
V. georgianus
Nematoda
Amphipoda

Chaoboridae larvae
Tanypodinae larvae

0   Hirundinea   1
Chaoboridae larvae   Amphipoda
Copepoda   T. aequicostata   Isopoda   Amphipoda

00 |(N=111)

1-Dec 96, Jan-Jun, Sep-Dec 97
2-Dec 69, Jan-Jul, Sep-Dec 97
3-Nov, Dec 97
4-Dec 96, Jan-Apr, Jun-Sep, Nov, Dec 97
5-Dec 96, Jan-Apr, Jul-Dec 97
6-Dec 96, Feb, Apr, Oct-Dec 97
7-Dec 96-Feb 97, Apr,Sep-Dec 97
8-Dec 96, Jan-Apr, Aug-Oct, Dec 97
9-Dec 96, Feb, Oct 97
10-Jan-Mar, May, Sep-Dec 97
11-Dec 96, Jan-Mar, May, Sep-Dec 97
12-Dec 96-May 9, Jul, Sep-Dec 97
13-Jul, Aug, Nov, Dec 97
14-May, Sep-Dec 97

01 |(N=54)

1-Jul, Aug 97
2-Aug 97
3-Dec 96-Apr 97, Jul-Sep 97
4-May, Oct 97
5-May, Jun 97
6-Jan, May-Sep 97
7-May-Aug 97
8-May-Jul, Nov 97
9-Jan, Mar, Apr-Aug 97
10-Dec 96, Apr, Jul, Aug 97
11-Jun-Aug 97
12-Jun, Aug 97
13-Dec 96-Mar 97, Sep, Oct 97
14-Dec96, Feb, Apr, Jun-Aug 97

10 |(N=12)

1-Oct 97
7-Jan 97
13-Jun 97
15-Dec96-Mar 97, Jul-Dec 97

11 |(N=13)

3-May, Jul, Oct 97
3-Jun 97
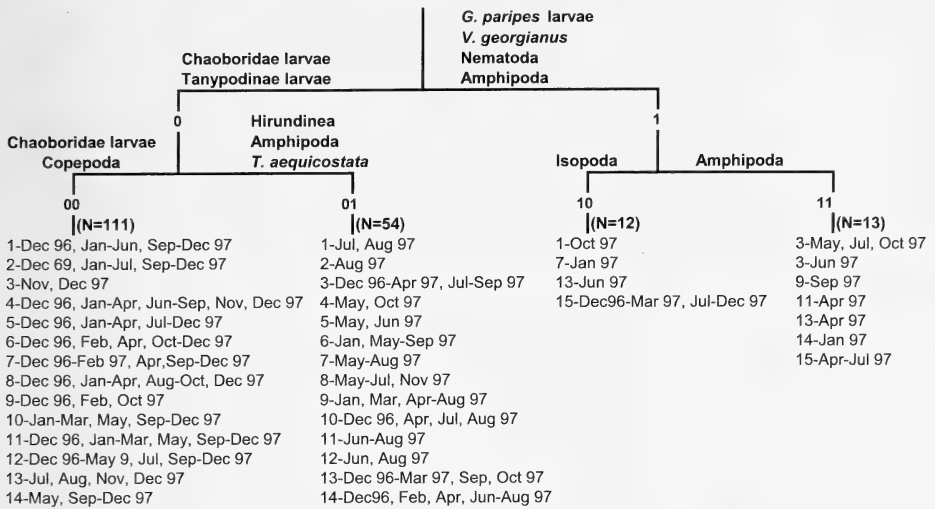9-Sep 97
11-Apr 97
13-Apr 97
14-Jan 97
15-Apr-Jul 97

FIG. 1. Cladogram of benthic communities (TWINSPAN) recorded monthly from 15 sampling stations in northeast Lake Jesup, central Florida, December 1996 to December 1997; (0, 2, 5, 20, and 100 were used cut levels). The numbers in each column under each group (group 00–11) are sampling station numbers that are followed by month(s) of sampling.

compared correlations between species and environmental variables based either on month or station means (Table 6). To partition overall spatial and temporal effects, the month and site of sampling were used as the only explanatory variables in CCA (ordination diagram not shown). Month and sample station combined explained 64% of benthic community variability, station variation explained 45% and monthly (temporal) variation 19%. This is in agreement with Verneaux and Aleya (1998) who reported influence of spatial and temporal factors on benthic community organization, with spatial environmental variability being prominent.

In Figure 2b, only significant ($P < 0.05$) monthly measured variables determined by forward selection were included in CCA. The general pattern is similar to Figure 2a, where the most important horizontal gradient is represented by presence or absence of sand, with the water parameters representing a vertical, temporal gradient. When effect of time was removed (months used as covariables), the presence or absence of sand sediment became the most important environmental variable (Fig 2c).

Considering the sediment condition gradient (Figs. 2b, c), Isopoda, Nematoda, *Polypedilum* larvae and *G. paripes* larvae were characteristic for sand substrates, whereas Tanypodinae larvae and Chaoboridae larvae were typical for soft muck sediment. However, the latter two taxa did not display significant correlations with sediment conditions associated with muck sediments (Table 5). Thus, these taxa were probably tolerant of soft organic sediment (and associated conditions such as low dissolved oxygen in the sediments) rather than having a preference for these sediments. Predator avoidance could also be a factor influencing these organisms.
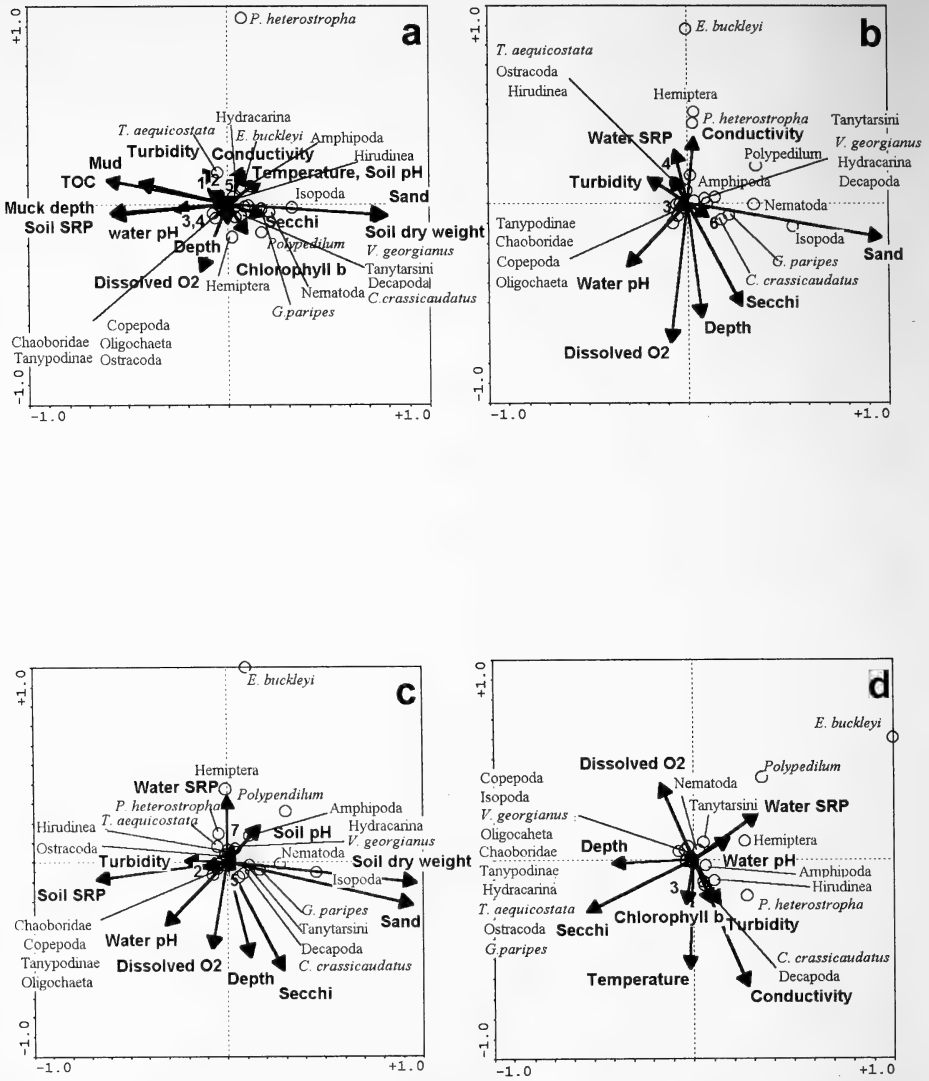
FIG. 2. Ordination diagrams of benthic communities and environmental variables recorded monthly from 15 permanent sampling stations in northeast Lake Jesup, central Florida, December 1996–December 1997. a—DCA, b—CCA of significant ($P < 0.05$) variables selected by forward selection, c—pCCA of spatial variability (months of sampling used as a covariables), significant ($P < 0.05$) variables selected by forward selection, d—pCCA of temporal variability (sampling station used as covariables) significant ($P < 0.05$) variables selected by forward selection. For all presented CCA and pCCA analyses, the first ordination axes were significant ($P < 0.005$). Footnote: **1**—Water SRP, **2**—Chlorophyll *a*, **3**—Total chlorophyll, **4**—Water N, **5**—Water P, **6**—Chlorophyll *b*, **7**—Temperature.

When the effect of sampling station was removed, water temperature and depth were the most important environmental variables (Fig. 2d). The high importance of temperature for seasonal variation in invertebrate community is in agreement with findings of Thorp and Chesser (1983). The effect of depth is likely to be indirect given by correlation of seasonal changes of water level in the lake with most of other water parameters. Important also were temporal changes in water depth and phytoplankton abundance (measured by chlorophyll *b* and total chlorophyll concentration). These parameters may also affect some water properties such as Secchi disk transparency, turbidity and pH (Fig 2d).

Ordination analysis indicated that the sediment parameters had more influence on spatial variability whereas water parameters were associated with temporal variability; however, many water parameters showed spatial correlations (Fig 2c, Tables 6, 7). The spatial and temporal effect of individual water variables on individual taxa was often not consistent (Tables 6, 7). In only three cases did temporal and spatial correlations significantly follow the same trend, such as the positive correlation between Chaoboridae larvae and dissolved oxygen concentration. This may imply that Chaoboridae larvae reflect oxygen concentration directly and that they are sufficient migrants to follow this gradient. Most often, the response of a taxon to a factor was significant only spatially or temporally (Tables 6, 7). For example, Chaoboridae larval density was significantly correlated (negative correlation) with monthly mean water temperature, but not with spatial variation of temperature. This preference for cooler conditions may be a temporal adaptation by the insect to exploit resources with less interspecific competition or to avoid predators. The lack of spatial correlation of chaoborid larvae with water temperature is not surprising because spatial variability of temperature was negligible at any given time but was substantial temporally. In some cases, opposing spatial and temporal responses to a given factor (sign of correlation coefficients differed) were noted, such as between Amphipoda and specific conductance. There could be several reasons for inconsistent spatial and temporal responses or taxa to individual factors. One may be the difference in temporal and spatial variability as described above for temperature. Another, that correlation was affected by co-linearity with other factors. For some correlations, especially those with low correlation coefficients, the significance may be a chance occurrence or a statistical artifact. An additional aspect that can complicate evaluation of spatio-temporal patterns is that spatial distribution is strongly affected by previous history. Many benthic organisms are slow migrants or sessile during most of their life cycle and spatial distribution may be affected by not only actual conditions but also conditions when a generation was established. Finally, organisms may be influenced by environmental parameters in different ways during their life cycle.

The present study also provides baseline data to elucidate changes and possible effects on benthic invertebrate communities and water and sediment conditions in northeastern Lake Jesup resulting from a proposed restoration of historic water flow between the St. Johns River and the lake (Ali et al., 1998). The proposed restoration could result in greater water flows within the northeastern section of the lake, causing scouring of soft, organic sediments and leaving sand substrates in a greater

TABLE 6. Matrix of significant ($P < 0.01$) temporal (monthly means) ($n = 13$) correlation coefficient values (r) between selected water physico-chemical parameters and benthic macroinvertebrates sampled at 15 stations in northeast Lake Jesup, central Florida, December 1996 to December 1997. Correlation coefficients in same direction as spatial correlation coefficient are underlined, in opposite direction are italics.

Taxon	Water Depth	Secchi Disk Transparency	Water Temperature	Dissolved Oxygen	Specific Conductance	Water pH	Soluble Reactive Phosphorus	Chlorophyll a	Chlorophyll b	Total Phosphorus	Total Kjeldahl Nitrogen
Nematoda	-0.639					0.532			0.603		
Oligochaeta						0.638				0.635	
Hirudinea					*0.539*						
Viviparous georgianus	0.666		0.606	-0.698							
Tryonia aequicostata											
Amphipoda					*0.768*		0.538				
Copepoda					-0.551						
Isopoda	0.729						0.595				
Ostracoda		0.629							0.905		
Polypedilum spp. larvae			-0.568	0.597							
Tanypodinae larvae	0.545							-0.536			
Chaoboridae larvae			-0.831	0.639	-0.569			-0.601			-0.576

TABLE 7. Matrix of significant (*P* < 0.01) spatial (station means) (*n* = 15) correlation coefficient values (*r*) between selected water physico-chemical parameters and benthic macroinvertebrates sampled at 15 stations in northeast Lake Jesup, central Florida, December 1996 to December 1997. Correlation coefficients in same direction as temporal correlation coefficient are underlined, in opposite direction are italics.

Taxon	Water Depth	Secchi Disk Transparency	Water Temperature	Dissolved Oxygen	Specific Conductance	Water pH	Turbidity	Soluble Reactive Phosphorus	Chlorophyll *a*	Total Phosphorus
Nematoda		0.626					−0.536		−0.507	
Oligochaeta		0.613	0.517				−0.544			
Hirudinea					*−0.608*					
Viviparous georgianus		0.534								
Tryonia aequicostata			*−0.610*		*−0.619*					
Amphipoda					*−0.686*					
Decapoda		0.561								
Isopoda		0.606								
Ostracoda		0.522				−0.620		0.527	−0.594	
Hemiptera		0.505				−0.727	−0.510			
Chironomus crassicaudatus larvae				*−0.703*						
Glyptotendipes paripes larvae		0.587	*0.531*				−0.591			
Polypedilum spp. larvae		0.690				−0.542	−0.526		−0.581	
Tanypodinae larvae	−0.692	0.833	*0.589*			−0.607	−0.736		−0.727	
Chaoboridae larvae				0.594		0.683				0.623

area of the lake bottom. With the greater abundance and diversity of benthic macroinvertebrates recorded at sand bottom station 15, this could result in greater overall abundance and diversity of macrobenthos in this section of Lake Jesup.

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NUTRIENT COMPOSITION OF SOME INSECTS AND ARACHNIDS

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Abstract: *Although many aspects concerning the nutrient requirements of insectivores are poorly understood, it is important to ascertain the nutrient composition of a wide range of invertebrate prey species so that more informed decisions can be made with respect to the feeding regimes used to maintain insectivores in captivity. In addition, this information is essential for a more comprehensive understanding of the diet composition and optimal foraging decisions of insectivores under natural conditions. In this study I report on the nutrient composition (water content, ash, crude fat, total nitrogen, minerals and trace elements, and fat-soluble vitamins) of 16 species of arachnids comprising 4 orders and 20 species of insects comprising 9 orders. Water content ranged from 58–71%. Crude fat content (as % dry matter, DM) ranged from 11–72%, with typically higher values observed for larval stages of insects as compared to adults. Total nitrogen, neutral detergent fiber, and ash ranged from 3–10% DM, 10–19%, and 2–9%, respectively. The insects and arachnids sampled in this study met the dietary requirements of insectivores with respect to minerals and trace elements including Mg, P, Ca, Cu, Fe, Mn and Zn. Concentrations of vitamins E and A were quite variable among the taxa. In spiders, vitamin E content ranged from 43.2–201.2 IU/kg; vitamin A levels ranged from 144.5–426.3 IU/kg. Scorpions and whipscorpions had significantly lower levels of vitamin E. In insects, vitamin E levels ranged from 17.7–512.5 IU/kg; vitamin A levels ranged from 11.4–803.2 IU/kg. The values recorded for these fat-soluble vitamins fell below the daily requirements that are known for some insectivores.*

Key Words: arachnids, insects, nutrient composition

Insects and spiders comprise a major portion of the diets of numerous insectivores, including those species maintained in zoos and research laboratories. The ability to keep animals healthy and to breed them under captive conditions depends on diets containing essential nutrient requirements. Although there is a large body of information available on various behavioral aspects of feeding in insectivores (Curio, 1976; Price, 1997; Punzo, 1998a, 2000a), little information is available on the actual nutrient composition of arthropods (Scriber and Slansky, 1981; Simpson and Raubenheimer, 1995; Barker et al., 1998).

Most of the research on the nutrient composition of arthropods has focused on the mineral content of commercially-raised insects (McFarlane, 1991; Studier and Sevick, 1992; Finke, 2002) with less attention given to other nutritional components such as fat-soluble vitamins, crude fat, and total nitrogen (Barker et al., 1998). In addition, few data are available on the nutrient composition of arachnids (Nentwig, 1987; Foelix, 1996).

The purpose of this study is to provide more comprehensive data on the nutrient

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composition of naturally-occurring insects and arachnids from a variety of mesic and xeric habitats that can be used primarily by individuals involved in field studies on the energy budgets of insectivores in areas where these invertebrates occur. In addition, the data may also be useful for scientists involved in the mass rearing of arthropods, as well as in animal husbandry where the evaluation of the diets of insectivores maintained in laboratories or zoological parks is of paramount importance.

MATERIALS AND METHODS—*Species and locality information*—Table 1 lists the species of insects and arachnids used in this study, their capture sites, and mean body masses and lengths. Some of the species analyzed (*Drosophila melanogaster, Acheta domesticus, Tenebrio molitor*) were obtained from laboratory stock cultures maintained in my laboratory for 5–6 years. The other species were collected from areas of the Sonoran (Cochise Co., Arizona) and Chihuahuan (Brewster, Presidio, and Terrell Counties) deserts in Texas, and from various locations in Florida during early summer months (June and July). These months were chosen because they represent periods where arachnids and insects, as well as their animal and plant foods, are in greatest abundance (Punzo, 2000a, 2000b, 2001). Insects and arachnids were collected from trees, shrubs, grasses, rock faces, and ground surfaces using sweep nets, pitfall traps, adhesive boards (type 2874 Stiky Strips, BioQuip, Gardena, CA), Burlese funnels (Model 3464, Carolina Biological Supply, Burlington, NC) ultraviolet (Model 2836) and New Jersey (Model 2856) light traps (BioQuip), and a portable insect vacuum pump (BioQuip, Model 2820A).

Laboratory stock cultures of the adult fruitfly *Drosophila melanogaster* were reared on Instant *Drosophila* medium (Carolina Biological Supply). Yellow mealworms (*Tenebrio molitor*, 200–300 mm length) were reared on a diet of wheat bran, oatmeal, and apple and potato slices. House crickets (*Acheta domesticus*) were fed on a diet consisting of commercial dog chow (Ralston Purina, St. Louis, MO) in combination with oatmeal, spinach leaves, potato slices, and ground bone meal. Insects and arachnids collected in the field were placed on ice, frozen at $-20°C$ within 8 hr of capture, and stored for subsequent nutrient analyses.

The body length of all insects and spiders were measured using a Vernier caliper or a Unitron Model 44W dissecting microscope fitted with an ocular micrometer. All body masses were recorded to the nearest 0.1 g using a Sartorius Model 501 electronic analytical balance.

Nutrient composition analyses—Duplicate samples were tested for all nutrient analyses. To determine the percentage composition of moisture and total ash content samples were thawed at room temperature and whole specimens were homogenized using a tissue homogenizer (Model RG-70-1936, Carolina Biological Supply, Burlington, NC). Samples (0.5 g) were weighed to the nearest 0.1 g, then dried, and the percent moisture determined as described by Ellis (1984). Samples were then incinerated in a muffle furnace for 14 hr for determination of total ash content.

Crude fats were extracted and analyzed according to the AOAC method (1996). Tissue samples were dried and placed in ethyl alcohol to denature the proteins to prevent them from being washed out with the fats during the extraction period. This was followed by extraction with petroleum ether. Chitin was analyzed using neutral detergent fiber (NDF) as described by Stelmock and co-workers (1985).

Vitamins A and E were determined using the fluorometric method described by Taylor and co-workers (1976). Tissue samples were homogenized in a solution consisting of 1.0 ml of 25% sodium ascorbate and 5.0 ml of 2 mM EDTA. Samples were then mixed with 5.0 ml of 95% ethanol and 1.0 ml of 50% KOH, and saponified by incubating in a water bath (70°C) for 20 min, then cooled using an ice bath. Fat-soluble vitamins were extracted with 1.0 ml of hexane. A 1.0 ml aliquot of the hexane layer was evaporated under nitrogen, and subsequent saponification, extraction and evaporation procedures were performed under yellow light. Samples were then reconstituted with 0.30 ml of ethanol. A Beckman Model 760C liquid chromatograph with a 10-cm reversed-phase column was used to measure tocopherols and retinol as indices of vitamins E and A, respectively. The mobile phase consisted of 90:10 methanol:water for retinol, and 95:5 methanol:water for tocopherols. The flow rate was 2.5 ml/min. Concentrations of tocopherols were determined with a Beckman fluorescence spectrophotometer (ex-

TABLE 1. Species of insects and arachnids used in nutrient composition analyses and the sites at which they were collected. Data on mass (g) and body length (mm) are also included; values expressed as means ± S.D. (N = 20 specimens for each species/life cycle stage)

Species	Collection site	Mass (g)	Length (mm)
ARACHNIDA[a]			
Araneae (spiders)			
Araneidae (orbweaving spiders)			
Argiope aurantia	Hillsborough Co., FL	0.62 ± 0.18	19.3 ± 3.1
Micrathena sagittata	Polk Co., FL	0.45 ± 0.09	8.1 ± 1.1
Ctenidae			
Ctenus captiosus	Hillsborough Co., FL	0.38 ± 0.06	10.8 ± 0.9
Deinopidae (ogrefaced spiders)			
Deinopis spinosa	Hillsborough Co., FL	0.23 ± 0.04	22.7 ± 2.5
Filistatidae (crevice spiders)			
Kukulcania hibernalis	Hillsborough Co., FL	0.54 ± 0.11	10.6 ± 1.7
Lycosidae (wolf spiders)			
Hogna carolinensis	Pinellas Co., FL	3.01 ± 0.81	18.7 ± 2.8
Trochosa parthenus	Hillsborough Co., FL	0.44 ± 0.03	7.7 ± 0.6
Oxyopidae (lynx spiders)			
Oxyopes salticus	Hillsborough Co., FL	0.29 ± 0.02	4.8 ± 1.1
Theraphosidae (tarantulas)			
Aphonopelma hentzi	Presidio Co., TX	7.63 ± 1.05	32.1 ± 2.7
Theridiidae (cobweb weavers)			
Latrodectans mactans	Pinellas Co., FL	0.23 ± 0.01	9.6 ± 1.3
Theridion pictipes	Hillsborough Co., FL	0.25 ± 0.03	3.5 ± 0.8
Thomisidae (crab spiders)			
Misumenoides formosipes	Presidio Co., TX	0.33 ± 0.04	7.4 ± 0.8
Scorpionida (scorpions)			
Buthidae			
Centruroides hentzi	Highlands Co., FL	2.36 ± 0.71	38.8 ± 2.6
Vaejovidae			
Paruroctonus gracilior	Brewster Co., TX	1.89 ± 0.43	29.4 ± 1.9
Solifugae (wind scorpions)			
Ammotrechellidae			
Ammotrechella stimpsoni	Highlands Co., FL	1.17 ± 0.33	17.7 ± 2.1
Uropygi (whip scorpions)			
Thelyphonidae			
Mastigoproctus giganteus	Cochise Co., AZ	5.81 ± 0.71	41.1 ± 2.9
	Brewster Co., TX	5.37 ± 0.41	44.3 ± 1.8
INSECTA[b]			
Coleoptera (beetles)			
Carabidae (ground beetles)			
Calasoma scrutator (adults)	Brewster Co., TX	0.34 ± 0.06	9.2 ± 1.5
Omophron obliteratum (larvae)	Presidio Co., TX	0.21 ± 0.11	2.9 ± 0.4
(adults)	Presidio Co., TX	0.31 ± 0.02	8.8 ± 0.7
Cerambycidae (longhorn beetles)			
Coenopaeus palmeri (adults)	Presidio Co., TX	0.28 ± 0.02	11.2 ± 1.3
Lycidae (net-winged beetles)			
Lycus ferandezi (adults)	Brewster Co., TX	0.19 ± 0.01	5.4 ± 0.7
Scarabaeidae (scarab beetles)			
Dynastes titylus (larvae)	Highlands Co., FL	0.32 ± 0.04	8.9 ± 1.5

Table 1. Continued.

Species	Collection site	Mass (g)	Length (mm)
Pelidnota punctata (larvae)	Hillsborough Co., FL	0.27 ± 0.03	12.1 ± 2.3
(adults)	Hillsborough Co., FL	0.28 ± 0.05	9.2 ± 0.5
Tenebrionidae (tenebrionids)			
Alobates pennsylvanica (adults)	Hillsborough Co., FL	0.27 ± 0.04	8.2 ± 1.1
Tenebrio molitor (larvae)	Laboratory stock culture	0.12 ± 0.01	15.8 ± 2.2
(adults)	Lab. stock culture	0.29 ± 0.02	11.8 ± 0.8
Dictyoptera			
Blatellidae (German cockroach)			
Blatella germanica (nymphs)	Hillsborough Co., FL	0.17 ± 0.02	4.8 ± 0.6
Blattidae (American cockroach)			
Periplaneta americana (nymphs)	Hillsborough Co., FL	0.24 ± 0.03	7.8 ± 0.7
(adults)	Hillsborough Co., FL	0.87 ± 0.11	22.3 ± 3.4
Diptera (flies)			
Drosophilidae (fruit flies)			
Drosophila melanogaster (adults)	Laboratory stock culture	<0.01	3.6 ± 0.01
	Hillsborough Co., FL	<0.01	3.3 ± 0.01
Hemiptera			
Coreidae (leaf-footed bugs)			
Acanthocephala			
terminalis (adults)	Pinellas Co., FL	0.26 ± 0.05	7.2 ± 1.5
Homoptera			
Cicadidae (cicadas)			
Tibicen canicularis (adults)	Polk Co., FL	1.56 ± 0.24	31.3 ± 3.4
Isoptera			
Rhinotermitidae			
Reticultermes hesperus (workers)	Presidio Co., TX	0.06 ± 0.01	3.7 ± 0.3
Lepidoptera			
Heliconiidae (zebra butterflies)			
Heliconius			
charitonius (adults)	Hillsborough Co., FL	0.65 ± 0.21	12.4 ± 1.4
(larvae)	Hillsborough Co., FL	1.21 ± 0.08	18.2 ± 2.4
Sphingidae (sphinx moths)			
Pandora pandorus (adults)	Hillsborough Co., FL	0.72 ± 0.17	14.4 ± 1.6
(larvae)	Hillsborough Co., FL	1.32 ± 0.22	20.3 ± 3.5
Neuroptera			
Chrysopidae (lacewings)			
Chrysopa carnia (adults)	Hillsborough Co., FL	0.17 ± 0.02	10.3 ± 0.8
Orthoptera			
Acrididae (grasshoppers)			
Schistocerca obscura (nymphs)	Leon Co., FL	0.41 ± 0.27	14.7 ± 2.8
Gryllidae (crickets)			
Acheta domesticus (adults)	Polk Co., FL	0.22 ± 0.01	12.2 ± 2.3
	Terrell Co., TX	0.24 ± 0.01	11.4 ± 1.8
	Laboratory stock culture	0.25 ± 0.01	12.5 ± 0.9
Gryllus assimilis (adults)	Pinellas Co., FL	0.17 ± 0.02	11.7 ± 0.3

[a] All arachnids were adult females.
[b] All adult insects were females.

citation wavelength = 280 nm; emission wavelength > 310 nm). Retinol was determined at 325 nm. External standards were compared to sample extracts for final vitamin concentrations. Vitamin A activity was calculated as 0.3 μg retinol = 1 IU, and vitamin E activity as 1.0 mg α-tocopherol = 1.49 IU, 1.0 mg γ-tocopherol = 0.15 IU, and 1.0 mg δ-tocopherol = 0.05 IU.

Tissue samples were analyzed for mineral analyses according to the atomic absorption methods described by Perkin-Elmer (1982). Total nitrogen was analyzed using the macro-Kjeldahl method with a copper catalyst (Ellis, 1984). Acid detergent fiber nitrogen (ADF-N), which is an index of chemically-bound nitrogen, was determined using the acid detergent fiber method described by Frye and Calvert (1989). Tissue samples were boiled in an acid detergent solution for 1.5 hr, filtered using Whatman # 54 paper, and rinsed with water. The subsequent filtrate was analyzed by the Kjeldahl method (Ellis, 1984).

Statistical procedures—Data were expressed as means ± SD. Differences among means within each group were assessed using unpaired *t*-tests and analysis of variance (ANOVA) (Sokal and Rohlf, 1995). LSD values were calculated using the Tukey test with $P < 0.05$.

RESULTS AND DISCUSSION—The water content and nutrient composition (crude fat, total nitrogen, ADF-N, NDF, ash) of the insects and arachnids analyzed in this study are shown in Table 2. There were some significant differences among field-collected and laboratory-reared species for all nutrient categories except NDF.

Among the arachnids, the spiders, *A. aurantia, M. sagittata, K. hibernalis, H. carolinensis, A. hentzi, L. mactans, T. pictipes,* and *M. formosipes* contained the highest percentage composition of water. No significant differences in water content were found for any of the scorpions, solifugids or whip scorpions analyzed. With respect to the insects, the termite *R. hesperus,* nymphs of the grasshopper *S. obscura,* and the crickets *A. domesticus* and *G. assimilis* exhibited the highest water content. Presumably, prey with a higher water content would provide more moisture for insectivores, and this would be most important for predators associated with xeric habitats (Punzo, 1998a; Punzo and Henderson, 1999). In this study, the spiders *A. hentzi* and *M. formosipes* were collected in the Chihuahuan Desert, although *M. formosipes* can be found in more mesic habitats. The insects *R. hesperus* (termite) and one group of the cricket *A. domesticus* were collected from xeric habitats as well.

Crude fat composition also varied among the arachnids and insects sampled in this study (Table 2). This may be due to differences in food procurement ability or reproductive status, although all of the arthropods were collected at the same time of the year. It is also interesting to note that some larval insects, including the beetle *P. punctata,* the moth *P. pandorus,* and the butterfly *P. charitonius*), contained a higher fat content than adults of the same species. This is in agreement with previous studies which showed that larval waxworms (*Galleria mellonella*) and mealworms (*Tenebrio molitor*) and the alates of ants and termites had significantly higher fat content than adults or workers (Redford and Dorea, 1984; Pennino et al., 1991). This may be due to the fact that the larval stage of holometabolous insects is concerned primarily with feeding and growth, whereas the adult stage is associated primarily with dispersal and reproduction. In the case of ants and termites, the alates frequently fly over considerable distances in their search for new colony sites and require significant food reserves. Because the caloric value of fats (9 kcal/g) is higher than proteins and carbohydrates (4 kcal/g) (Scriber and Slansky, 1981;

TABLE 2. Nutrient composition of various insects and arachnids. Data expressed as means ± S.D. Sample sizes (SS) shown in parentheses. Species and life cycle stages for each nutrient class within a column with different superscripts are significantly different ($P < 0.05$). ADF-N (acid detergent fiber nitrogen); NDF (neutral detergent fiber).

Species	Water (%)	Crude fat	Percent Dry Matter			
			Total nitrogen	ADF-N	NDF	Ash
ARACHNIDA						
Araneae (spiders)						
Argiope aurantia (Araneidae) (16)	66.7 ± 7.8[a]	57.2 ± 37[c]	8.1 ± 2.1[a]	0.6 ± 0.2	15.9 ± 3.1	8.9 ± 1.3[a]
Micrathena sagittata (Ctenidae) (10)	59.5 ± 7.7[b]	33.1 ± 5.7[b]	5.8 ± 0.8[a]	0.5 ± 0.1	13.3 ± 2.7	6.7 ± 1.5[a]
Ctenus captiosus (22)	60.8 ± 9.3[b]	47.4 ± 4.9[c]	5.4 ± 1.1[a]	0.4 ± 0.1	12.2 ± 0.9	3.3 ± 0.4[b]
Deinopis spinosa (Deinopidae) (9)	58.3 ± 6.3[b]	40.3 ± 5.9[b]	7.6 ± 0.8[a]	0.4 ± 0.1	11.3 ± 2.4	3.1 ± 0.5[b]
Kukulcania hibernalis (Filistatidae) (12)	67.5 ± 8.4[a]	18.3 ± 3.2[a]	8.8 ± 1.5[a]	0.9 ± 0.2	15.8 ± 2.6	4.9 ± 1.1[a]
Hogna carolinensis (Lycosidae) (8)	63.3 ± 6.9[a]	36.4 ± 4.4[b]	2.9 ± 1.2[b]	0.4 ± 0.1	9.9 ± 1.3	5.1 ± 0.7[a]
Trochosa parthenus (10)	61.8 ± 4.8[b]	48.8 ± 3.6[c]	5.8 ± 1.4[a]	0.5 ± 0.2	11.7 ± 2.4	3.9 ± 0.5[b]
Oxyopes salticus (Oxyopidae) (14)	62.4 ± 5.7[b]	45.8 ± 4.7[c]	4.9 ± 1.3[a]	0.5 ± 0.1	13.5 ± 3.2	3.2 ± 0.4[b]
Aphonopelma hentzi (Theraphosidae) (10)	66.5 ± 8.2[a]	41.7 ± 3.5[b]	3.8 ± 0.7[b]	0.7 ± 0.2	11.4 ± 3.3	5.9 ± 1.5[a]
Latrodectans mactans (Theridiidae) (22)	62.1 ± 6.9[b]	27.3 ± 3.3[b]	6.4 ± 1.1[a]	0.5 ± 0.1	13.2 ± 2.6	7.2 ± 2.6[a]
Theridion pictipes (18)	70.4 ± 2.9[a]	23.8 ± 4.1[b]	10.1 ± 2.2[a]	0.6 ± 0.3	17.4 ± 3.1	5.3 ± 1.2[a]
Misumenoides formosipes (Thomisidae) (12)	65.1 ± 2.1[b]	40.2 ± 3.5[b]	9.9 ± 0.8[a]	0.4 ± 0.1	12.2 ± 2.2	5.5 ± 0.6[a]
Scorpionida (scorpions)						
Centruroides hentzi (Buthidae) (12)	61.4 ± 8.2[b]	50.3 ± 5.4[c]	5.8 ± 0.8[a]	0.4 ± 0.1	11.9 ± 3.2	3.3 ± 0.7[b]
Paruroctonus gracilior (Vaejovidae) (10)	62.6 ± 6.6[b]	45.5 ± 6.1[c]	6.7 ± 1.1[a]	0.5 ± 0.2	10.4 ± 2.1	3.5 ± 1.0[b]
Solifugae (wind scorpions)						
Ammotrechella stimpsoni (Ammotrechellidae) (10)	65.2 ± 7.8[b]	39.9 ± 7.3[b]	6.2 ± 1.4[a]	0.6 ± 0.2	11.1 ± 1.9	3.4 ± 0.5[b]
Uropygi (whip scorpions)						
Mastigoproctus giganteus (Thelyphonidae) (14)	58.3 ± 6.4[b]	34.7 ± 5.5[b]	7.7 ± 1.3[a]	0.4 ± 0.1	10.4 ± 2.6	3.2 ± 0.4[b]
INSECTA						
Coleoptera (beetles)						
Carabidae (ground beetles)						
Calasoma scrutator (adults) (12)	62.2 ± 6.9[b]	46.3 ± 3.7[c]	6.3 ± 0.8[a]	0.3 ± 0.1	11.1 ± 3.3	3.1 ± 0.7[b]

Table 2. Continued.

Species	Water (%)	Percent Dry Matter				
		Crude fat	Total nitrogen	ADF-N	NDF	Ash
Omophron obliteratum (larvae) (10)	60.2 ± 6.2^b	54.1 ± 3.8^c	5.9 ± 1.4^a	0.4 ± 0.1	10.8 ± 2.1	2.9 ± 1.1^b
(adults) (10)	61.8 ± 5.8^b	49.5 ± 6.1^c	6.7 ± 1.2^a	0.5 ± 0.2	11.9 ± 2.6	3.3 ± 0.4^b
Cerambycidae (longhorn beetles)						
Coenopaeus palmeri (adults) (10)	59.9 ± 5.8^b	46.8 ± 4.4^c	6.2 ± 1.1^a	0.7 ± 0.3	11.1 ± 2.5	3.2 ± 1.2^b
Lycidae (net-winged beetles)						
Lycus ferandezi (adults) (14)	62.1 ± 7.1^b	49.8 ± 4.8^c	6.6 ± 0.8^a	0.4 ± 0.1	11.8 ± 2.7	3.5 ± 1.3^b
Scarabaeidae (scarab beetles)						
Dynastes titylus (larvae) (22)	61.9 ± 6.6^b	50.8 ± 5.5^c	6.8 ± 0.9^a	0.3 ± 0.1	12.1 ± 3.1	3.2 ± 0.8^b
Pelidnota punctata (larvae) (10)	61.4 ± 8.3^b	27.8 ± 3.4^b	7.9 ± 1.8^a	0.4 ± 0.1	12.6 ± 2.3	3.6 ± 1.1^b
(adults) (14)	60.4 ± 5.5^b	21.1 ± 3.3^a	6.6 ± 2.2^a	0.5 ± 0.2	11.8 ± 1.7	3.3 ± 0.5^b
Tenebrionidae (tenebrionids)						
Alobates pennsylvanica (adults) (12)	61.3 ± 7.4^b	29.9 ± 5.8^b	6.3 ± 1.6^a	0.3 ± 0.1	12.8 ± 3.3	3.6 ± 0.5^b
Tenebrio molitor (larvae) (34)	64.2 ± 7.7^b	31.4 ± 1.8^b	6.8 ± 1.1^a	0.3 ± 0.1	13.2 ± 3.1	3.9 ± 0.8^b
(adults) (26)	63.1 ± 5.2^b	27.4 ± 2.7^b	7.3 ± 1.4^a	0.5 ± 0.2	12.5 ± 2.8	3.3 ± 1.8^b
Dictyoptera						
Blatellidae (German cockroach)						
Blatella germanica (nymphs) (16)	62.8 ± 4.8^b	50.2 ± 2.9^c	6.2 ± 1.3^a	0.4 ± 0.1	11.6 ± 2.1	3.1 ± 0.7^b
Blattidae (American cockroach)						
Periplaneta americana (nymphs) (12)	59.7 ± 3.6^b	47.3 ± 3.2^c	5.5 ± 1.1^a	0.6 ± 0.2	10.2 ± 1.4	2.8 ± 0.3^b
(adults) (10)	61.4 ± 5.3^b	49.1 ± 4.6^c	5.1 ± 0.4^a	0.5 ± 0.1	10.8 ± 1.2	2.6 ± 0.5^b
Diptera (flies)						
Drosophilidae (fruit flies)						
Drosophila melanogaster (adults) (44)	68.2 ± 4.1^a	16.4 ± 1.5^a	7.9 ± 0.9^a	0.9 ± 0.2	14.7 ± 3.4	3.9 ± 0.4^b
Hemiptera						
Coreidae (leaf-footed bugs)						
Acanthocephala terminalis (adults) (12)	62.5 ± 5.1^b	50.8 ± 4.7^c	4.9 ± 1.7^a	0.7 ± 0.2	11.2 ± 2.4	2.3 ± 0.3^b

Table 2. Continued.

Species	Water (%)	Percent Dry Matter				
		Crude fat	Total nitrogen	ADF-N	NDF	Ash
Homoptera						
Cicadidae (cicadas)						
Tibicen canicularis (adults) (14)	58.2 ± 3.3[b]	40.4 ± 3.1[b]	7.4 ± 1.2[a]	0.3 ± 0.1	10.7 ± 1.1	2.9 ± 0.5[b]
Isoptera						
Rhinotermitidae						
Reticulitermes hesperus (22)	67.4 ± 3.6[a]	17.5 ± 2.7[a]	9.2 ± 0.8[a]	0.9 ± 0.3	16.7 ± 1.3	5.1 ± 0.5[a]
Lepidoptera						
Heliconiidae (zebra butterflies)						
Heliconius charitonius (adults) (10)	60.8 ± 4.1[b]	51.4 ± 3.3[c]	6.8 ± 1.8[a]	0.4 ± 0.1	12.4 ± 2.9	3.3 ± 1.1[b]
(larvae) (14)	62.3 ± 5.4[b]	55.3 ± 2.8[c]	5.4 ± 1.3[a]	0.3 ± 0.1	11.3 ± 1.6	2.5 ± 0.7[b]
Sphingidae (sphinx moths)						
Pandora pandorus (adults) (8)	59.9 ± 3.8[b]	51.4 ± 3.5[c]	7.8 ± 2.2[a]	0.4 ± 0.1	10.8 ± 1.6	3.1 ± 0.4[b]
(larvae) (10)	61.1 ± 4.6[b]	55.7 ± 2.8[c]	6.9 ± 0.8[a]	0.3 ± 0.1	11.6 ± 2.1	2.8 ± 1.1[b]
Neuroptera						
Chrysopidae (lacewings)						
Chrysopa carnia (adults) (12)	58.3 ± 4.1[b]	39.8 ± 2.8[b]	7.2 ± 0.3[a]	0.4 ± 0.2	10.7 ± 1.9	3.2 ± 0.4[b]
Orthoptera						
Acrididae (grasshoppers)						
Schistocerca obscura (nymphs) (10)	65.9 ± 6.7[a]	10.5 ± 1.2[a]	8.6 ± 2.1[a]	0.6 ± 0.2	15.9 ± 2.5	9.2 ± 1.1[a]
Gryllidae (crickets)						
Acheta domesticus (adults) (32)	71.6 ± 4.2[a]	20.6 ± 2.5[a]	8.9 ± 1.1[a]	0.6 ± 0.1	18.5 ± 3.1	4.4 ± 0.9[a]
Gryllus assimilis (adults) (24)	68.9 ± 3.8[a]	18.9 ± 2.2[a]	8.2 ± 1.7[a]	0.5 ± 0.2	16.8 ± 2.4	5.1 ± 1.1[a]

Simpson and Raubenheimer, 1995), insectivores could maximize their caloric intake and energy budgets by selectively feeding on larval insects when they are available in the field. In captivity, growth rates could be enhanced by utilizing diets high in non-toxic larval insects. In addition, when oxidized, fats provide twice the amount of metabolic water than carbohydrates (Downer and Mathews, 1976) thus enhancing the dietary source of water. This may be especially important for insectivores found in xeric habitats.

Among the arachnids, the spiders *A. aurantia, C. captiosus, T. parthenus,* and *O. salticus,* and the scorpions *C. hentzi* and *P. gracilior,* contained crude fat levels approaching the highest concentrations found in some insects (Table 2).

Total nitrogen values ranged from 2.9–10.1% dry matter (DM) for arachnids, and 5.1–9.2% DM for insects (Table 2). Only 3–9% of total nitrogen was measured as chitin-bound nitrogen (ADF-N). This is in agreement with the 3–8% range for ADF-N reported for other species of insects by Barker and co-workers (1998) and Studier and co-workers (1991).

Insects have been described as a good source of dietary nitrogen; studies have reported nitrogen values ranging from 3–19% DM in several orders of flying insects (Studier and Sevick, 1992), and 14–23% DM in the cocoons of several lepidopteran species (Studier et al., 1991). Barker and co-workers (1998) reported values ranging from 6.9–8.3% DM for several species of mealworms, 8.8–10.3% DM for juvenile and adults, respectively, of the cricket, *Acheta domesticus,* 6.6% for the waxworm *Galleria mellonella,* and 9.0% DM for the fruit fly, *Drosophila melanogaster.*

Ash values ranged from 3.1–8.9% DM in arachnids, and 2.3–9.2% DM in insects (Table 2). Ash is an index of dietary mineral content, and previous studies have reported similar ash levels in other species of insects (Scriber and Slansky, 1981; Studier and Sevick, 1992; Barker et al., 1998).

NDF, an index of dietary fiber (in the cell walls of plants and in chitin) comprised 9.9–17.4% of DM in arachnids, and 10.7–18.5% of DM in insects (Table 2). This is in agreement with values ranging from 12–19% reported for other insect species (Frye and Calvert, 1989; Pennino et al., 1991; Barker et al., 1998). Although some small mammals can digest up to 20% of chitin (Allen and Oftedal, 1989), chitin is typically difficult to digest. However, indigestible chitin can play an important role in nutrient absorption in the gastroinestinal tracts of a variety of insectivores (Van Soest, 1994).

The concentrations of selected minerals and trace elements in the arachnids and insects analyzed in this study are shown in Table 3. Significant differences were found between the various taxa for calcium, magnesium, phosphorus, copper, iron, manganese, and zinc. Calcium requirements for birds and mammals range from 0.4–2.5% (Robbins, 1993), with lower requirements reported for insects (Nation, 2002). Only the cockroaches *B. germanica* and *P. americana,* the hemipteran *A. terminalis,* the homopteran *T. canicularis,* the neuropteran *C. carnia,* and the orthopterans *S. obscura, A. domesticus,* and *G. assimilis* meet these requirements. In general, insects have been reported to be inadequate sources for dietary calcium (Frye and Calvert, 1989; Keeler and Studier, 1992), and all of the arachnids tested in this study as well as most of the insects had low calcium content.

All of the arachnids and insects analyzed in this study exhibited Mg and P levels (0.03–0.15% DM and 0.3–0.6% DM, respectively) adequate to meet the dietary needs of birds and mammals (Robbins, 1993) and most insects (House, 1974; McFarlane, 1991; Nation, 2002). Similarly, the trace element requirements of most vertebrates and insects (ranging from 1.0–6.0 mg/kg Cu; 2.4–47.5 mg/kg Mn; 17–180 mg/kg Fe; 7.1–30.0 mg/kg Zn) (Gordon, 1959; Waldbauer and Friedman, 1991; Robbins, 1993) were met by the taxa sampled in this study (Table 3).

Concentrations of vitamin E and A were quite variable among the taxa (Table 4). In spiders, vitamin E concentrations ranged from 43.2–201.2 IU/kg, whereas vitamin A levels ranged from144.5–426.3 IU/kg. Scorpions and whip scorpions had significantly lower levels of vitamin E as compared to the other arachnids. In insects, vitamin E concentrations ranged from 17.7–512.5 IU/kg, and vitamin A concentrations from lows of 11.4 IU/kg in the fruit fly *D. melanogaster*, and 21.7 IU/kg in the termite *R. hesperus*, to a high of 803.2 IU/kg in adults of the mealworm, *T. molitor*. Vitamin A requirements for domestic carnivores and wildlife range from 6000–15,000 IU/kg while vitamin E requirements range from 20–80 IU/kg (National Research Council, 1985, 1986; Robbins, 1993). All of the taxa analyzed in this study fall well below these levels, indicating that arachnids and insects may provide only a limited dietary source of vitamin E and A for insectivores.

Minimum vitamin requirements of insects are poorly understood and are thought to be quite variable depending upon the species and life cycle stage (House, 1974; Nation, 2002). Vitamin E is required for spermatogenesis in male crickets of *A. domesticus* (House, 1974), and by some female insects to attain sexual maturity and oviposit eggs (Nation, 2002). Vitamin A is required by insects for normal pigmentation and eye function, and has been shown to accelerate growth in the fly *Agria affinis* and the silkworm *Bombyx mori* (Waldbauer and Friedman, 1991; Nation, 2002).

In conclusion, these data provide a baseline for understanding the nutritional quality of arthropods found in the diets of naturally-occurring insectivores. The nitrogen, ash, minerals, trace elements, and dietary fiber content of arthropod tissues can be quite variable between species, and may reflect seasonal variations in micronutrient environments (Keeler and Studier, 1992). In addition, insects are known to be poor sources of preformed vitamin A and E (Allen and Oftedal, 1989; Barker et al., 1998; Finke, 2002) leading some to suggest that insectivores may be able to convert carotenoid precursors to help meet the dietary demand for this nutrient (Dierenfeld et al., 1995). Although the effects of dietary deficiencies in vitamin E on insectivores are poorly understood, it is a well known antioxidant and is involved in cellular homeostatic processes (Robbins, 1993; Nation, 2002). In captivity, insectivores are typically provided with insect diets that are supplemented with calcium and vitamins A, D, and E, in amounts that vary according to the types of invertebrates in the diet (Finke, 2002). More information is required to understand how wild-ranging insectivores may compensate for nutrient deficiencies that may vary seasonally.

TABLE 3. Selected macrominerals and trace elements in representative arachnids and insects. Sample sizes are the same as listed in Table 2. Values expressed as % or means ± S.D. Species and life cycle stages for each nutrient class within columns with different superscripts are significantly different ($P < 0.05$).

Species[†]		Mineral concentrations					
	Ca (%)	Mg (%)	P (%)	Cu (mg/kg)	Fe (mg/kg)	Mn (mg/kg)	Zn (mg/kg)
ARACHNIDA							
Araneae							
A. aurantia	0.22[a]	0.08[a]	0.78[a]	11.7 ± 3.4[a]	137.4 ± 8.8[a]	26.3 ± 2.1[a]	175.5 ± 16.2[a]
M. sagittata	0.23[a]	0.11[a]	0.59[a]	15.4 ± 2.2[a]	134.7 ± 4.7[a]	24.1 ± 0.8[a]	168.9 ± 13.1[a]
C. captiosus	0.11[b]	0.19[b]	1.41[b]	14.9 ± 3.1[a]	35.2 ± 5.5[b]	5.8 ± 1.3[b]	121.6 ± 8.8[b]
D. spinosa	0.14[b]	0.24[b]	1.37[b]	16.7 ± 3.4[a]	37.4 ± 8.8[b]	6.3 ± 2.1[b]	125.5 ± 10.2[b]
K. hibernalis	0.13[b]	0.21[b]	1.29[b]	15.4 ± 2.2[a]	34.7 ± 4.7[b]	6.1 ± 0.7[b]	118.9 ± 13.1[b]
H. carolinensis	0.14[b]	0.21[b]	1.32[b]	17.2 ± 3.2[a]	36.4 ± 5.5[b]	5.8 ± 2.2[b]	131.1 ± 14.3[b]
T. parthenus	0.12[b]	0.19[b]	1.25[b]	14.7 ± 2.7[a]	31.6 ± 6.4[b]	7.2 ± 1.9[b]	117.8 ± 12.4[b]
O. salticus	0.14[b]	0.22[b]	1.31[b]	15.9 ± 4.1[a]	27.7 ± 3.7[b]	6.1 ± 1.4[b]	109.3 ± 13.5[b]
A. hentzi	0.11[b]	0.14[a]	1.27[b]	13.3 ± 3.6[a]	35.9 ± 5.1[b]	5.7 ± 0.9[b]	124.6 ± 15.8[b]
L. mactans	0.21[a]	0.12[a]	0.72[a]	12.2 ± 2.3[a]	151.2 ± 20.1[a]	24.1 ± 4.3[a]	171.5 ± 17.4[a]
T. pictipes	0.19[b]	0.13[a]	0.68[a]	11.6 ± 1.7[a]	135.6 ± 9.6[a]	26.1 ± 3.2[a]	168.5 ± 11.6[a]
M. formosipes	0.10[b]	0.17[a]	1.22[b]	14.5 ± 2.2[a]	30.4 ± 3.7[b]	5.7 ± 0.6[b]	112.6 ± 10.4[b]
Scorpionida							
C. hentzi	0.13[b]	0.20[b]	1.35[b]	16.4 ± 2.3[a]	41.1 ± 5.9[b]	6.1 ± 1.5[b]	124.3 ± 9.9[b]
P. gracilior	0.12[b]	0.24[b]	1.27[b]	18.1 ± 3.6[b]	37.6 ± 4.4[b]	5.7 ± 0.6[b]	130.6 ± 14.5[b]
Solifugae							
A. stimpsoni	0.14[b]	0.21[b]	1.33[b]	16.5 ± 4.1[a]	34.7 ± 3.7[b]	4.9 ± 0.5[b]	114.3 ± 10.3[b]
Uropygi							
M. giganteus	0.17[b]	0.15[a]	0.79[a]	11.8 ± 2.1[a]	40.3 ± 5.3[b]	6.1 ± 0.7[b]	124.7 ± 13.6[b]
INSECTA							
Coleoptera							
C. scrutator	0.14[b]	0.25[b]	1.37[b]	16.3 ± 4.3[a]	32.5 ± 4.7[b]	5.9 ± 0.6[b]	136.2 ± 14.2[b]
O. obliteratum (L)	0.11[b]	0.24[b]	1.32[b]	17.4 ± 3.4[a]	33.8 ± 2.6[b]	6.3 ± 1.4[b]	135.2 ± 15.1[b]
(A)	0.12[b]	0.27[b]	1.40[b]	16.6 ± 2.9[a]	37.5 ± 4.4[b]	5.9 ± 0.7[b]	131.8 ± 12.5[b]
C. palmeri	0.13[b]	0.25[b]	1.33[b]	17.1 ± 4.2[a]	35.3 ± 2.6[b]	6.4 ± 2.5[b]	129.8 ± 13.6[b]

TABLE 3. Continued.

Species[†]	Mineral concentrations						
	Ca (%)	Mg (%)	P (%)	Cu (mg/kg)	Fe (mg/kg)	Mn (mg/kg)	Zn (mg/kg)
L. ferrandezi	0.11[b]	0.27[b]	1.35[b]	15.8 ± 1.9[a]	33.7 ± 2.7[b]	6.5 ± 1.1[b]	132.5 ± 10.6[b]
D. titylus	0.12[b]	0.25[b]	1.36[b]	16.7 ± 2.2[a]	34.9 ± 3.8[b]	6.4 ± 1.7[b]	128.9 ± 7.8
P. punctata (L)	0.13[b]	0.24[b]	1.32[b]	17.2 ± 3.4[a]	36.5 ± 5.2[b]	6.6 ± 1.5[b]	130.8 ± 11.8[b]
(A)	0.14[b]	0.22[b]	1.33[b]	16.4 ± 3.1[a]	32.8 ± 3.6[b]	5.9 ± 0.8[b]	128.5 ± 8.5[b]
A. pennsylvanica	0.13[b]	0.26[b]	1.38[b]	15.9 ± 3.4[a]	35.7 ± 2.9[b]	6.3 ± 1.7[b]	131.7 ± 10.8[b]
T. molitor (L)	0.12[b]	0.28[b]	1.41[b]	17.5 ± 2.5[a]	38.7 ± 4.7[b]	6.8 ± 0.7[b]	134.5 ± 11.5[b]
(A)	0.12[b]	0.25[b]	1.39[b]	16.8 ± 3.3[a]	36.9 ± 6.1[b]	6.4 ± 1.3[b]	129.9 ± 13.3[b]
Dictyoptera							
B. germanica	1.23[c]	0.15[a]	0.81[a]	8.4 ± 1.8[c]	169.5 ± 25.7[a]	40.6 ± 6.7[c]	162.2 ± 12.4[a]
P. americana	1.27[c]	0.16[a]	0.77[a]	9.4 ± 0.8[c]	183.4 ± 34.2[a]	48.4 ± 8.8[c]	157.4 ± 15.3[a]
Diptera							
D. melanogaster	0.14[b]	0.15[a]	1.17[a]	8.5 ± 1.2[c]	298.3 ± 21.1[c]	17.3 ± 2.9[a]	151.3 ± 10.6[a]
Hemiptera							
A. terminalis	1.22[c]	0.19[b]	0.88[a]	7.7 ± 1.3[c]	89.8 ± 11.1[a]	41.2 ± 5.5[c]	131.5 ± 14.6[b]
Homoptera							
T. canicularis	1.25[c]	0.16[a]	0.79[a]	8.8 ± 1.6[c]	157.3 ± 13.1[a]	29.3 ± 5.5[a]	144.3 ± 11.6[a]
Isoptera							
R. hesperus	0.14[b]	0.17[a]	2.11[b]	8.1 ± 1.5[c]	234.6 ± 33.5[c]	13.6 ± 3.3[a]	127.4 ± 20.3[b]
Lepidoptera							
H. charitonius (A)	0.08[d]	0.09[a]	1.31[b]	3.1 ± 0.4[d]	70.5 ± 7.3[a]	4.6 ± 0.6[b]	69.7 ± 9.5[c]
(L)	0.07[d]	0.09[a]	1.29[b]	2.9 ± 0.5[d]	67.7 ± 5.9[a]	4.4 ± 0.4[b]	66.8 ± 6.7[c]
P. pandorus	0.07[d]	0.08[a]	1.33[b]	3.2 ± 0.3[d]	71.3 ± 7.1[a]	3.9 ± 0.5[b]	63.7 ± 4.7[c]
Neuroptera							
C. carnia	1.23[c]	0.16[a]	0.74[a]	7.9 ± 1.3[c]	135.3 ± 9.9[a]	7.8 ± 1.4[b]	107.3 ± 11.3
Orthoptera							
S. obscura	1.33[c]	0.17[a]	0.79[a]	9.5 ± 1.1[c]	187.6 ± 17.1[b]	50.3 ± 7.3[c]	162.1 ± 18.2[a]
A. domesticus	1.28[c]	0.16[a]	0.82[a]	8.8 ± 0.9[c]	192.1 ± 11.3[b]	45.9 ± 6.2[c]	149.5 ± 13.6[a]
G. assimilis	1.30[c]	0.17[a]	0.74[a]	9.1 ± 2.1[c]	179.3 ± 9.9[b]	43.7 ± 4.8[c]	155.7 ± 10.3[a]

† Taxa as listed in Table 2.

TABLE 4. Fat soluble vitamins in representative arachnids and insects. Sample sizes are the same as listed in Table 2. Values expressed as means ± S.D. Species and life cycle stages (for each vitamin within a column with different superscripts are significantly different ($P < 0.05$).

Species[†]	Vitamin E (IU/kg)	Vitamin A (IU/kg)
ARACHNIDA		
Araneae		
A. aurantia	201.2 ± 20.1[a]	401.2 ± 29.3[a]
M. sagittata	55.3 ± 5.8[b]	197.6 ± 19.3[b]
C. captiosus	71.1 ± 5.2[b]	307.6 ± 27.4[c]
D. spinosa	64.3 ± 4.9[b]	144.5 ± 20.5[b]
K. hibernalis	68.5 ± 7.9[b]	201.5 ± 19.4[b]
H. carolinensis	102.4 ± 17.8[c]	239.7 ± 30.5[c]
T. parthenus	92.4 ± 8.8[c]	219.9 ± 18.6[b]
O. salticus	69.5 ± 6.7[b]	152.3 ± 20.2[b]
A. hentzi	43.2 ± 7.3[d]	291.1 ± 23.4[c]
L. mactans	151.8 ± 5.6[e]	441.3 ± 20.5[a]
T. pictipes	134.7 ± 6.3[e]	426.3 ± 31.4[a]
M. formosipes	71.2 ± 4.6[b]	266.8 ± 17.4[c]
Scorpionida		
C. hentzi	31.9 ± 5.7[d]	234.6 ± 18.2[c]
P. gracilior	35.2 ± 4.9[d]	228.8 ± 21.5[b]
Solifugae		
A. stimpsoni	62.5 ± 8.1[b]	378.2 ± 25.5[d]
Uropygi		
M. giganteus	32.4 ± 6.8[d]	247.8 ± 21.3[c]
INSECTA		
Coleoptera		
C. scrutator	31.6 ± 5.1[d]	725.2 ± 44.1[e]
O. obliteratum (L)	40.2 ± 5.7[d]	509.6 ± 41.7[f]
(A)	19.3 ± 6.3[f]	244.7 ± 21.5[c]
C. palmeri	30.5 ± 3.9[d]	417.7 ± 18.6[a]
L. ferandezi	28.4 ± 4.4[d]	353.7 ± 26.8[d]
D. titylus	31.6 ± 5.9[d]	684.2 ± 40.1[e]
P. punctata (L)	39.4 ± 6.6[d]	428.6 ± 35.8[a]
(A)	17.7 ± 3.3[f]	209.5 ± 12.6[b]
A. pennsylvanica	40.2 ± 6.7[d]	657.4 ± 22.6[e]
T. molitor (L)	29.6 ± 4.1[d]	771.8 ± 33.6[g]
(A)	31.7 ± 7.1[d]	803.2 ± 44.7[g]
Dictyoptera		
B. germanica	74.6 ± 7.3[b]	438.2 ± 20.6[a]
P. americana	82.3 ± 8.4[b]	425.5 ± 24.1[a]
Diptera		
D. melanogaster	25.3 ± 7.6[d]	11.4 ± 2.6[h]
Hemiptera		
A. terminalis	36.7 ± 6.6[d]	562.2 ± 41.1[f]
Homoptera		
T. canicularis	40.3 ± 4.5[d]	548.7 ± 28.4[f]
Isoptera		
R. hesperus	32.2 ± 3.9[d]	21.7 ± 5.2[h]
Lepidoptera		
H. charitonius (A)	212.5 ± 14.2[a]	109.3 ± 10.2[i]
(L)	512.5 ± 34.2[g]	161.4 ± 11.4[i]

TABLE 4. Continued.

Species[†]	Vitamin E (IU/kg)	Vitamin A (IU/kg)
P. pandorus	241.2 ± 22.4[a]	104.3 ± 13.6[i]
Neuroptera		
C. carnia	44.7 ± 7.7[d]	397.8 ± 31.1[a]
Orthoptera		
S. obscura	67.7 ± 11.5[b]	739.8 ± 36.4[g]
A. domesticus	79.7 ± 10.3[b]	754.6 ± 64.2[g]
G. assimilis	70.4 ± 12.4[b]	772.5 ± 47.5[g]

[†] Taxa as listed in Table 2.

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HERBIVORY AND POSTGRAZING RESPONSE IN *HYPERICUM CUMULICOLA*

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ABSTRACT: *We describe patterns of mammalian herbivory and examine possible fitness consequences of herbivory on* Hypericum cumulicola, *an herbaceous perennial endemic to Florida scrub. We noted the presence or absence of mammalian herbivory on 1841* H. cumulicola *individuals, from 23 populations in two study sites. At Archbold Biological Station, we found the presence of herbivory to be positively correlated to the number of conspecific neighbors, and negatively correlated with time-since-fire. At Arbuckle Tract of Lake Wales Ridge State Forest, presence of herbivory was affected by habitat (scrub or roadside) and negatively associated with the number of conspecific neighbors. We performed a clipping treatment on naturally occurring* H. cumulicola *individuals to simulate mammalian herbivory. The results indicated that* H. cumulicola *appears to undergo compensatory regrowth following defoliation. The one-year fitness consequences of herbivory appear to be neutral although the long-term fitness consequences of herbivory on the perennial* H. cumulicola *can not be known from this study. We hypothesize that in addition to disturbance tolerance (through increased regrowth rate), patchy distribution and low density may reduce the impact of mammalian herbivory on* H. cumulicola.

Key Words: compensatory growth, Florida scrub, herbivory, *Hypericum cumulicola*, overcompensation

HERBIVORY reduces plant biomass, and can affect growth and reproduction (McNaughton, 1983; Bergelson and Crawley, 1992a,b). In intensive grazing systems, selection pressure should favor plant individuals with traits allowing them to attenuate the negative effects of tissue loss. Belsky and co-workers (1993) grouped such adaptations as (1) strategies that allow the plant to avoid herbivory, such as escape from discovery through non-apparent, patchy distribution and chemical and mechanical defenses and (2) overcompensatory growth following an herbivory event. Compensatory response can be divided into three classes (Maschinski and Whitham, 1989): overcompensatory growth, compensatory growth and undercompensatory growth. In overcompensation, grazed plants produce more fruits and seeds than control plants. Compensation occurs when grazed and control plants produce similar numbers of fruits and seeds. Undercompensation occurs when grazed plants produce fewer fruits and seeds than control plants. Overcompensatory growth has been controversial, with studies in support of this phenomenon (McNaughton, 1983; Paige and Whitham, 1987; Paige, 1992, 1999) and studies

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finding no support for it (Belsky, 1986, 1987; Bergelson and Crawley, 1992a,b; Bergelson et al., 1996). An array of compensatory responses has been documented, with undercompensatory growth and overcompensatory growth at the extremes (Maschinski and Whitham, 1989). One explanation for compensatory growth is that rapid regrowth following defoliation is an evolved response of the plant to minimize the effects of structural damage, which can come from many sources including fire, trampling, and herbivory (Belsky, 1986; Belsky et al., 1993; Rosenthal and Kotanen, 1994). A meta-analysis of the impact of herbivory on plants in different resource conditions indicates that overcompensation is more likely in high resources for monocots and in low resources for dicot herbs (Hawkes and Sullivan, 2001).

This work examines mammalian herbivory on *Hypericum cumulicola*, a perennial herbaceous species restricted to sandy gaps in the Florida rosemary scrub. The study consists of two parts: (1) an observational study, relating mammalian (presumably deer *Odocoileus virginianus seminolus* and rabbit *Sylvilagus floridanus floridanus*) herbivory rates on *H. cumulicola* to demographic parameters and environmental variables, and (2) a clipping experiment testing *H. cumulicola* compensatory response to herbivory. The objectives of this study are to explore patterns of mammalian herbivory across different populations of *H. cumulicola* and to examine possible fitness consequences.

METHODS—*Study species*—*Hypericum cumulicola* ((Small) P. Adams) is a small, short-lived, perennial herb endemic to the Lake Wales Ridge of Polk and Highlands Counties in central Florida (Quintana-Ascencio et al., 1995). Though largely limited to gaps in Florida rosemary scrub, *H. cumulicola* can also be found along roads and firelanes and, infrequently, in well-drained openings in scrubby flatwoods. *H. cumulicola* branches from the base and grows to heights of 20–70 cm. Vegetative in the winter and spring, most plants become reproductive during the summer, growing reproductive stalks (1–17) with up to thousands of flowers and fruits per plant. Fire kills *H. cumulicola* individuals, but populations are able to recover through persistent seed banks and/or dispersal from nearby populations (Quintana-Ascencio et al., 1998). Fruit production, recruitment rates, and survivorship are highest for the first few years after fire, with these traits decreasing with increased time-since-fire (Quintana-Ascencio and Morales-Hernández, 1997; Quintana-Ascencio et al., 2003).

Study Sites—We conducted this study at Archbold Biological Station (Archbold) and the Arbuckle Tract of Lake Wales Ridge State Forest (Arbuckle) in south-central Florida. All study sites at Archbold were in Florida rosemary scrub. We organized the Archbold sites by time-since-fire based on records of natural, accidental, and prescribed fires kept since 1967 (Main and Menges, 1997). Study sites at Arbuckle encompassed a larger range of *H. cumulicola* habitats. These habitats included natural (rosemary scrub and oak scrub), and human disturbed (roadside and tram). The rosemary scrub and oak scrub patches in Arbuckle were within areas burned in the last decade. However, the large size of Florida rosemary (*Ceratiola ericoides*), an obligate seeder, in the Florida rosemary scrub sites indicated that fire did not reach these Florida rosemary scrub patches.

Rosemary scrub occurs on sandy, well-drained soils of ridges and knolls and is characterized by sometimes large, open gaps in the vegetation (Abrahamson et al., 1984). Florida rosemary (*Ceratiola ericoides*) often dominates the shrub layer. Other species often present include oaks (*Quercus* spp.), and palmettos (*Serenoa repens* and *Sabal etonia*). The sub-shrub *Licania michauxii*, lichens (*Cladonia* spp.), spike moss (*Selaginella arenicola*), and several herbaceous species including *H. cumulicola* grow in open gaps in the vegetation. Oaks (*Quercus* spp.), and palmettos (*Serenoa repens* and *Sabal etonia*) are dominant species in oak scrub. Though not characterized by them, oak scrub sometimes does contain scattered open gaps, which support similar vegetation as the gaps in rosemary scrub. Roadside sites were

on active sand roads, which contain *H. cumulicola* populations. Tram sites lie on berms of old railroad lines. Tram sites are characterized by large gaps and a lower water table than the surrounding areas. Though the railroad tracks are no longer present, the berms now lie along side sand roads.

Fire plays a major role in determining Florida scrub community composition and dynamics (Menges and Hawkes, 1998; Menges, 1999). Fires in oak and rosemary scrub are often heterogeneous, producing gaps in the unburned vegetation. Gap specialists (such as *H. cumulicola*) are most abundant shortly after fire, but become less abundant as shrubs and lichens increase with time-since-fire. Thus, gap specialist species residing in oak and rosemary scrub depend on fire for their persistence.

Sampling methods of the observational study—At Archbold, in August 2001, we noted the mammalian herbivory on 956 *H. cumulicola* plants from 15 rosemary scrub patches, representing a gradient of time-since-fire (4 to 34 years after fire), patch size, and north-south distribution along the station. Within each patch/site, we sampled at least 70 individuals in a stratified random fashion along 1 m wide belt transects, if greater than 100 plants were present at the site. If fewer than 100, the entire population was included in the sample. At Arbuckle, we sampled 885 individuals from 8 sites: 2 oak scrub sites (n = 236), 2 rosemary scrub sites (n = 201), 2 road sites (n = 236), and 2 tram sites (n = 212). We recorded, for each plant sampled, maximum height, number of conspecifics within 15 cm, number of reproductive structures (flowering buds, flowers and fruits), and presence or absence of mammalian herbivory. Presence of mammalian herbivory was associated with complete branch removal. Insect herbivory was also present on some *H. cumulicola* individuals but was not recorded and was readily distinguished from mammalian herbivory as branches, flowers or fruits eaten by insects were not entirely removed.

We conducted forward stepwise (Wald) logistic regressions to determine the significance of the association of time-since-fire, and number of conspecific neighbors (data log-transformed) to the presence of herbivory in *H. cumulicola* at Archbold. We conducted forward stepwise (Wald) logistic regressions to determine the significance of the association of habitat, and number of conspecific neighbors (data log-transformed) to the presence of herbivory in *H. cumulicola* at Arbuckle. We then tested the significance of contrasts among habitats.

Clipping experiment—We selected three Archbold rosemary scrub patches with known populations of *H. cumulicola* and of varying time since fire (15, 8, and <1 years since fire) for the clipping experiment. Three levels of simulated herbivory were imposed on the plants between 18 and 19 August 2001, with 10 individuals sampled per treatment, per patch. Control plants had no clipping imposed, 50% treatment had one clipping made on ~half of reproductive stalks, and 100% treatment had one clipping made on each reproductive stalk. These clipping treatments mimicked the amount and type of tissue removal observed in plants with naturally occurring herbivory. We imposed clipping on a haphazardly chosen piece of stalk, at the point of the first branching event (only one stalk was present in 5 of 30 plants under the 50% herbivory treatment; clipping was imposed on this stalk). Within gaps at each scrub patch, we sampled plants along 1 m wide belt transects, running at a random distance from the edge, perpendicular to the longest axis of open sand in the gap. At 1-m increments along the belt transect, the three closest plants (without prior herbivory) were chosen for sampling. For each sampled plant, we recorded the height of the tallest stalk (pre- and post-clipping), cumulative height of the stalks (pre- and post-clipping), and the number of reproductive structures (pre- and post-clipping). Treatments were assigned left to right with respect to the tape, in a rotational fashion. At completion of sampling, plants were enclosed in cages made of wire chicken cooping, successfully preventing the subsequent occurrence of natural herbivory.

We resampled the treated plants between 15 and 17 September 2001. For each plant, height of the tallest stalk, cumulative height of stalks, and number of reproductive structures were recorded. Maschinski and Whitham's (1989) definitions of compensatory growth involve only the differences in fruit and seed production, between grazed and ungrazed plants. This study also looks at changes in plant height, as height has been found to be the best predictor of fecundity in *H. cumulicola* (Quintana-Ascencio et al., 2003).

We conducted univariate analysis of covariance to test for significance of differences among clipping treatments on *H. cumulicola*. We tested for significance of treatment, site, and their interactions

TABLE 1. Coefficients of forward (Wald) logistic regression models of presence of herbivory in *H. cumulicola* at Arbuckle State Forest, and Archbold Biological Station.

Source of variation	Beta	s.e.	df	P
Arbuckle				
Constant	−0.713	0.110	1	<0.001
Tram-Road	0.608	0.283	1	0.031
Tram-Oak scrub	3.058	0.275	1	<0.001
Oak scrub-Road	−2.450	0.234	1	<0.001
Rosemary scrub-Tram	−1.084	0.274	1	<0.001
Rosemary scrub-Road	−0.476	0.239	1	0.046
Rosemary scrub-Oak scrub	1.974	0.229	1	<0.001
Ln(neighbors)	−0.496	0.110	1	<0.001
Archbold				
Constant	1.023	0.144	1	<0.001
Years since last fire	−0.126	0.011	1	<0.001
Ln(neighbors)	0.141	0.052	1	0.007

on change in maximum height, cumulative stalk height, and number of reproductive structures over the month-long treatment. We statistically controlled for differences in initial size using original maximum height, original cumulative stalk height, and initial number of reproductive structures as covariates, respectively. We adjusted and compared linear models describing the relationship between height and number of reproductive structures for individuals with and without herbivory (or clipping). All statistical analyses were performed using SPSS 10.1.0.

RESULTS—*Observational study*—Across all rosemary scrub patches at Archbold, the presence of herbivory on *H. cumulicola* was positively correlated to number of conspecific neighbors within 15 cm, and negatively correlated with years-since-last fire (Table 1, Fig. 1). Presence of herbivory on *H. cumulicola* at Arbuckle was affected by habitat and negatively correlated to the number of conspecific neighbors within 15 cm (Table 1, Fig. 2). Presence of herbivory was significantly different among all habitats in the following descending order: oak scrub, rosemary scrub, road, and tram (Table 1, Fig. 2).

Clipping experiment—Clipped plants (at both the 50% and 100% treatments) did not differ significantly from unclipped plants with respect to final height of the tallest reproductive stalk, final accumulated height of reproductive stalks, or number of reproductive structures during the one month treatment period (Tables 2–4). Final height, when adjusted by the pre-clipping height of the tallest stalk, was still not significantly affected by clipping treatments (Table 2). Similarly, final number of reproductive structures, when statistically adjusted by the initial number of reproductive structures, was not significantly affected by clipping treatments (Table 4).

To test how closely the clipping regime mimicked natural herbivory in *H. cumulicola*, we compared growth function models describing the association between the number of reproductive structures and the height of the plant for both *H. cumulicola* individuals with natural herbivory and experimentally clipped individuals. There was a significant correlation between plant height and number of reproductive structures (logarithmic transformed), with $r^2 > 0.465$ for all curves.
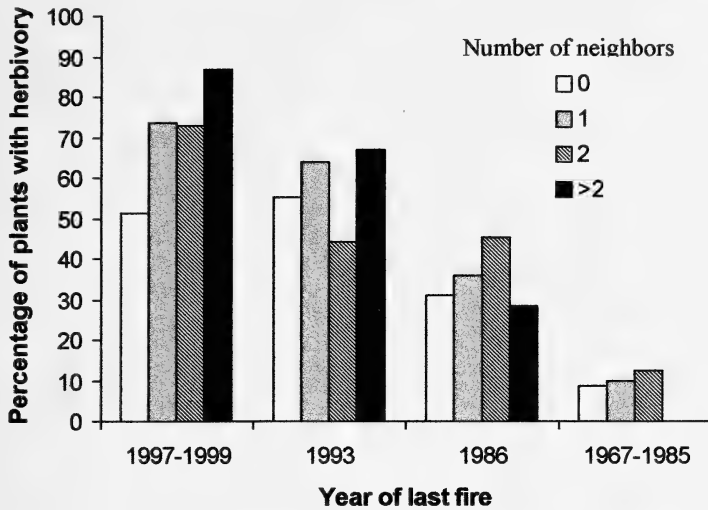
FIG. 1.   Percentage of plants with herbivory in 2001 by year of last fire and number of conspecific neighbors in Rosemary scrub patches at Archbold Biological Station.

There was always overlap among standard errors of the slopes for individuals with and without herbivory or clipping (Table 5).

DISCUSSION—*Hypericum cumulicola* responded to biomass removal with compensatory growth (*sensu* Maschinski and Whitham, 1989), as experimentally grazed and ungrazed plants did not produce significantly different numbers of reproductive structures. Additionally, experimentally grazed and ungrazed plants did not show significantly different stalk heights. Although *H. cumulicola* did not exhibit overcompensatory growth, increased growth (and reproductive structure production) rate was present in clipped plants, resulting in compensatory growth. We do not see any immediate reproductive consequences of simulated herbivory on *H. cumulicola*, as clipping did not reduce or increase fruit yield. Though, as *H. cumulicola* is a perennial, the long-term fitness consequences of herbivory can not be known from this study.

    In previous studies, Bergelson and Crawley (1992 a,b) and Bergelson and co-workers (1996) found no evidence for overcompensatory growth following mammalian herbivory in *Ipomopsis aggregata*, despite previous findings which supported overcompensatory growth in *I. aggregata* (Paige and Whitham, 1987; Paige, 1992; 1994; 1999). Despite the contention by Bergelson and co-workers (1996) that there is no compelling evidence for overcompensatory growth in *I. aggregata*, or any other plant species, the debate continues to rage. Hawkes' and Sullivan's (2001) review indicates that resource availability differentially affects plant recovery after herbivory in monocot and dicot herbs. These authors argue that these differences among functional groups may explain, at least in part, contradictory evidence on plant response to herbivory in the literature (Hawkes
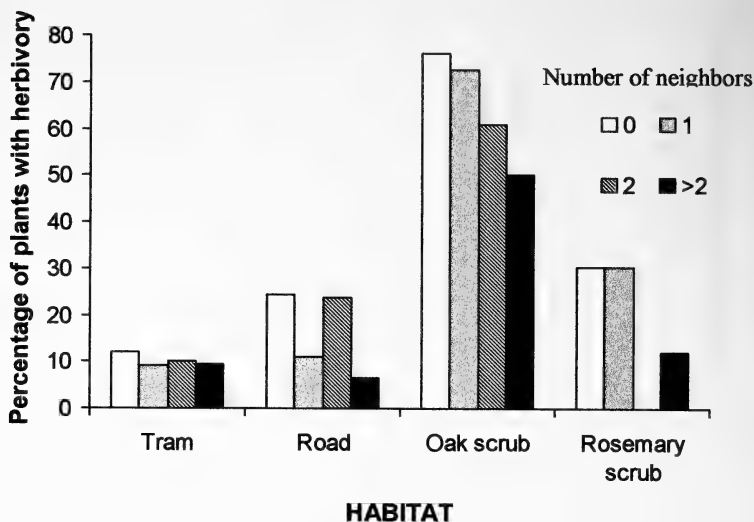
FIG. 2.   Percentage of plants with herbivory in 2001 by habitat and number of conspecific neighbors at Arbuckle State Forest.

and Sullivan, 2001). Our present study lends support to those who argue for compensatory growth (Bergelson et al., 1996; for example), as we saw no evidence in support of overcompensatory growth in *H. cumulicola*.

Our study raises the question of which general anti-herbivory strategies (see Belsky et al., 1993) are employed by *H. cumulicola*, if any. These are grouped into strategies or circumstances that allow a plant to avoid herbivory and strategies that allow a plant to recover from herbivory. This study shows that *H. cumulicola* exhibits increased growth rate following an herbivory-like disturbance (clipping). Although it has been proposed that there is a resource tradeoff between herbivory tolerance and herbivory avoidance strategies (van der Meijden et al., 1988; Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999), *H. cumulicola* may avoid herbivory in addition to tolerating it. Apparency theory (Feeny, 1976) hypothesizes that if the distribution of a plant species is patchy, it can be harder for herbivores to find and plants may avoid discovery. This may explain a circumstance reducing herbivory in *H. cumulicola*, as it resides predominantly in the rosemary scrub phase of sand pine scrub, which is patchy in distribution throughout the Florida scrub ecosystem (Abrahamson et al., 1984).

The observational experiment at Archbold showed a strong correlation between herbivory rates and time-since-fire, with *H. cumulicola* receiving the highest herbivory rates in recently burned areas. Herbivory rates have been shown to be higher in woody species in recently burned areas as herbivores favor the green vegetative resprouts that woody species grow after being burned (see for example Singer and Harter, 1996). However, one might not expect a perennial herb killed by fire and that does not have large storage organs to show this trend. Why, then, would herbivory rates be higher in recently burned areas for an herbaceous species,

TABLE 2. Results of an ANCOVA of final maximum height of *Hypericum cumulicola* with clipping treatment and site as fixed factors, and initial maximum height as covariate.

Source of variance	df	Mean square	F	P
Clipping treatment	2	4.5	0.8	0.468
Site	2	2.6	0.4	0.643
Initial maximum height	1	35.5	6.1	0.016
Clipping treatment*Initial height	2	2.8	0.5	0.623
Site*Initial height	2	3.2	0.5	0.582
Clipping treatment*Site	4	10.0	1.7	0.156
Clipping treatment*Site*Initial height	4	11.8	2.0	0.099
Error	72	5.8		

which produces green shoots every year? One possibility is that *H. cumulicola* may be a focal forage species, that is, mammalian herbivores are actively seeking out *H. cumulicola* for consumption. If this were the case, plants in recently burned areas should be most highly consumed, as *H. cumulicola* individuals are most productive and most abundant in recently burned areas (Quintana-Ascencio and Morales-Hernández, 1997). Herbivores would concentrate their foraging in these areas.

However, due to the small and patchy population sizes of *H. cumulicola*, it makes more sense that *H. cumulicola* is a supplementary forage species, with the following situation taking place: In recently burned areas, most woody species rapidly resprout new shoots (Menges and Kohfeldt, 1995), which are heavily browsed by herbivores (Singer and Harter, 1996). In addition, several herbaceous species, including *H. cumulicola*, increase their densities after fire (Menges and Kimmich, 1996, Quintana-Ascencio et al., 2003). Herbivores may be attracted by all these species, but feed on *H. cumulicola*, once they have reached the site. As time-since-fire increases and woody species resume their normal aboveground vegetative state and herb abundance declines, herbivores are no longer attracted to the area and *H. cumulicola* is not consumed. A study of habitat preferences within pine flatwoods using infrared-triggered cameras indicated that white-tailed deer and all other mammals captured on film were present more frequently in a 24 months post-fire site than in an adjacent site 48 months post-fire (Main and Richardson, 2002).

TABLE 3. Results of an ANCOVA of final cumulative stalk height of *Hypericum cumulicola* with clipping treatment and site as fixed factors, and initial cumulative stalk height as covariate.

Source of variance	df	Mean square	F	P
Clipping treatment	2	26.1	0.1	0.874
Site	2	377.3	2.0	0.150
Initial stalk height	1	102.5	0.5	0.469
Clipping treatment*Initial stalk height	2	6.5	0.03	0.967
Site*Initial stalk height	2	190.7	1.0	0.379
Clipping treatment*Site	4	89.2	0.5	0.765
Clipping treatment*Site*Initial stalk height	4	66.8	0.3	0.847
Error	72	193.7		

TABLE 4. Results of an ANCOVA of final number of reproductive structures of *Hypericum cumulicola* with clipping treatment and site as fixed factors, and initial number of reproductive structures as covariate.

Source of variance	df	Mean square	F	P
Clipping treatment	2	0.2	0.6	0.527
Site	2	0.6	1.7	0.195
Initial number of reproductive structures	1	6.2	16.3	<0.001
Clipping treatment*Initial fruits	2	0.2	0.5	0.630
Site*Initial fruits	2	0.3	0.9	0.416
Clipping treatment*Site	4	0.6	1.5	0.219
Clipping treatment*Site*Initial fruits	4	0.5	1.3	0.261
Error	71	0.4		

The presence of mammals increased to levels observed in the 24 months post-fire site after 8 weeks following a prescribed fire in the site previously 48 months post-fire (Main and Richardson, 2002).

The proportion of *H. cumulicola* plants with herbivory at Arbuckle was higher in rosemary scrub and oak scrub sites than it was in road and tram sites. This can be looked at in two ways, which are difficult to distinguish since habitats are identical for each case. First, herbivory rates were higher in natural sites than in man-made sites. Second, there was more herbivory away from roads than near roads. The reason for this is unclear, but may be due to mammalian herbivores (deer and rabbits) favoring covered areas (such as scrubby sites) with places to hide, over open areas (such as roadside and tram sites).

This study has shown that herbivory is correlated to number of conspecifics. This correlation was negative at Arbuckle and positive at Archbold, in 2001. *H. cumulicola* survivorship in Florida rosemary scrub has been shown to be positively correlated to number of conspecifics (1995: $p < 0.001$ slope $= 0.369$, 2001: $p < 0.001$ slope $= 0.185$; Quintana-Ascencio and Morales-Hernández, 1997; Quintana-

TABLE 5. Parameters (and their standard error) of growth functions ($\ln y = a + b * x$) of height and number of reproductive structures (logarithmic transformed) of individuals clipped (before and after a month of treatment), untreated (control), with herbivory, and without herbivory (from the observational study, vegetative individuals not included).

Treatment	r^2	a	s.e.	b	s.e.	n
Pre-clipped (all)	0.538	1.848	0.251	0.06	0.006	90
Pre-clipped (control)	0.642	1.846	0.361	0.06	0.009	30
Post-clipped (control)	0.565	2.167	0.402	0.06	0.009	30
Post-clipped (clipped)	0.463	1.481	0.382	0.07	0.010	60
Arbuckle						
Without herbivory	0.643	1.012	0.113	0.08	0.003	557
With herbivory	0.565	0.693	0.210	0.08	0.005	238
Archbold						
Without herbivory	0.629	0.577	0.129	0.100	0.003	483
With herbivory	0.465	0.126	0.207	0.104	0.006	341

Ascencio, unpublished data). This raises a paradox, as high density areas may have higher survival despite higher herbivory. However, neither herbivory nor conspecific density have a consistent impact on *H. cumulicola* survival. Instead, it appears that other microhabitat attributes are ultimately determinant of *H. cumulicola* survival, to the point where favorable habitat allows plants to overcome the ill-effects of herbivory and competition by conspecific neighbors.

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EFFECT OF SHEAR FORCES ON THE RELEASE
OF BREVETOXINS FROM *KARENIA BREVIS*

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ABSTRACT: *The forces associated with a culture of* Karenia brevis *with a magnetic stirrer were calculated and related to the release of toxins by the affected organism. Even under seemingly mild conditions (3.5 rpm with a 2.5 cm stirring bar) enough shearing energy was provided to release toxins. Parameters calculated were: the Reynolds Number, tangential velocity, mean velocity gradient, and the power.*

Key Words: Red tide, *Karenia brevis*, HABs, Florida, Reynolds Number

RED TIDE is the discoloration of water in the marine environment associated with the proliferation of organisms, and is a world-wide phenomenon. In Florida, red tides are associated with the unarmored dinoflagellate *Karenia brevis* (formerly *Gymnodinium breve* Davis or *Ptychodiscus brevis*). Typically the outbreaks have been observed on the west coast of Florida from Cape Sable to Cape San Blas. Blooms of *Karenia brevis* have been associated with mass mortalities of marine animals, more than 100 species having been identified (Steidinger and Ingle, 1972; Steidinger, 1983; Steidinger and Melton Penta, 1999). The dinoflagellate causes deaths directly through the production and release of neurotoxins called brevetoxins (Steidinger and Ingle, 1972; Lin et al., 1981; Baden, 1989) and indirectly through oxygen deprivation when large numbers of the dinoflagellates die (Simon and Dauer, 1972).

Presumably, the brevetoxins are released when *K. brevis* cells are destroyed. It has been a matter of conjecture as to the conditions under which this will occur. Heavy metal ions, notably from copper salts, can destroy *K. brevis* cells (Rounsefell and Nelson, 1966). Available evidence showed that allelochemicals can account for the destruction of *K. brevis* cells (Taft and Martin, 1986; Martin and Taft, 1998). And presumably physical effects could be responsible. The release of toxins in the surf, for example, has not seemed reasonable, considering that the surf on the west coast of Florida, in contrast with the east coast, is not considered to be a high energy surf.

The present study examines the forces involved when a culture of *Karenia*

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TABLE 1. Summary of calculated parameters for stirring of *Karenia brevis* culture*.

Parameter	Calculated value
Reynolds Number	400
Tangential velocity	7 cm/sec
Mean velocity gradient	28 sec^{-1}
Power	2.19×10^{-4} ft-lb/sec

* 50 mL culture in a 250 mL Erlenmeyer flask stirred with a 2.5 cm bar at a rate of 3.5 rpm.

brevis was subjected to mild stirring with a magnetic stirrer. Previous research (Derby, 2002; Derby et al., 2002) demonstrated toxin release under these mild conditions. Thus, it seemed pertinent to calculate what forces were involved under these experimental conditions.

METHODS—Standard methods (Streeter and Wylie, 1985) were used to calculate the various parameters, given the following characteristics of the experiment. A 50-mL sample of a culture of *Karenia brevis* was placed in a 250 mL Erlenmeyer flask equipped with a 2.5 cm magnetic stirrer and stirred at the rate of 3.5 rpm. The base of the flask was 7.0 cm in diameter, and the height of the medium was 1.6 cm.

Toxicities of control (unstirred) and test samples (stirred) had been tested using a Microtox® 500 system (Derby, 2002; Derby et al., 2002).

RESULTS AND DISCUSSION—The calculated parameters are listed in Table 1. Certain general comments seem appropriate.

First of all, the Reynolds Number is used in fluid mechanics as a criterion of laminar flow. The number is the ratio of $\rho vd/\mu$ of the inertial force ρvd to viscous force μ, where ρ is the fluid density, v is the velocity, and d is a characteristic of the medium (Streeter, 1966; Streeter and Wylie, 1985). In a pipe, laminar flow would be characterized by a Reynolds value of less than 2000 and turbulent flow by a value greater than 3000 (Streeter, 1966). The calculated value of the Reynolds Number in our case was 400, which is diagnostic of a comparatively low degree of laminar flow.

In contrast, the tangential velocity of 7 cm/sec is comparatively high and indicates a degree of shear force, despite the casual observation that a stirring rate of 3.5 rpm with a 2.5-cm magnetic stirrer does not seem to produce a visually impressive stirring rate. The casual observation is misleading, however, and the significant degree of shear force is confirmed by the mean velocity gradient. This parameter is a measure of mixing, and the calculated value was 28. It is recognized that this value is low in comparison with values of the order of 200, which are frequently encountered in water treatment coagulation situations, but it is a significant value, especially when taken with the values of the two other parameters.

Finally, the power level, 2.19×10^{-4} ft-lb/sec is quite low.

In summary, the calculations of the parameters listed in Table 1 indicate that laminar flow occurs with a degree of shear force of comparative low power that was sufficient to cause release of brevetoxins in separately reported experiments (Derby, 2002; Derby et al., 2002). Specifically, we measured the effect of a culture of

Karenia brevis on the bacterium *Vibrio fischeri* using a Microtox® analyzer (Derby et al., 2002). Non-stirred cultures provided a toxicity value of $-20 \pm 0.15\%$ (the minus sign is indicative of stimulation of growth), whereas the cultures that were stirred (as described in Table 1) for 24 hours, had a toxicity value of $45 \pm 1\%$, indicating that half the bacteria were eliminated in a five-minute test. Thus, while the power level was low, the shear effect was evidently significant, and allows us to understand the result more clearly.

Other workers (Hemmert, 1975; Asai et al., 1982) have noted that red tides in the near-shore environment are associated with such unpleasant respiratory effects as non-productive cough, asthma-like symptoms, air hunger and the like, associated with release of brevetoxins and conversion to aerosols. The process whereby the red tide cells are destroyed remained uncertain, and perhaps still does. However, the action of fish gills could be consistent with laminar flow and shear effects such as we have observed and report here. On the other hand, when *Karenia brevis* cells are in a wave that is washing ashore, it is not so evident that the laminar flow conditions match those we have described, and further consideration of this matter seems in order.

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TEMPORAL DIVERSITY AND ABUNDANCE OF DRIFT MACROPHYTES AND ASSOCIATED ORGANISMS IN MOSQUITO LAGOON, VOLUSIA COUNTY, FLORIDA

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ABSTRACT: *In terms of biomass, drift algal communities are often the dominant organisms in estuaries. On the east coast of central Florida, drift communities have been studied primarily in the southern reaches of the Indian River Lagoon system. To determine the abundance and diversity of floating drift macrophytes and associated fauna in Mosquito Lagoon, the northernmost region of the Indian River Lagoon, monthly observations were run for a 2-year period, beginning in April 1998. For each 24-hr sampling period, all drift was collected every 4 hr, brought into the laboratory, sorted by species, and weighed. Environmental data (salinity, wind speed, water motion, water and air temperatures) was also recorded every 4 hr. During the two-year survey, 26 species of drift macrophytes were collected in Mosquito Lagoon. Red algae of the genus* Gracilaria *and the seagrass* Halodule wrightii *were found in the greatest abundances, representing 51.7% and 23.7%, respectively, of all macrophyte biomass collected. Invertebrates and fishes (e.g. the code goby* Gobiosoma robustum*) were, at times, found in high densities attached or closely associated with these topographically complex, drift communities. No correlations between macrophyte abundance and wind speed or flow rate were found. Additionally, no consistent temporal patterns of macrophyte abundances were observed.*

Key Words: drift algae, *Gracilaria*, *Halodule wrightii*, Indian River Lagoon, Canaveral National Seashore

MANY species of macroalgae incorporate drifting into their life-histories as mechanisms for dispersal and survival in areas where predators or storm events are common (e.g. Norton and Mathieson, 1983; Bushing, 1994). For some species of algae, dislodged fragments can rapidly attach to benthic organisms or to sand (e.g. Walters and Smith, 1994; Smith and Walters, 1999; Walters and Beach, 2000). Dislodged fragments of other species of macroalgae never reattach, but can survive long periods of time floating or tumbling over the benthos (Kain and Norton, 1990; Astill and Lavery, 2001). Clumps of drift algae may remain viable for months, decomposing only when physical conditions change or the clumps are washed above the high tide line (Highsmith, 1985; Virnstein and Carbonara, 1985).

Many mobile and sessile invertebrates and a few fish species (i.e. the code goby *Gobiosoma robustum* and the gulf pipefish *Syngnathus scovelli*) are frequently found in high densities attached or closely associated with these topographically complex, drift algal communities (e.g. Kulczycki et al., 1981; Lewis, 1987;

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Virnstein and Howard, 1987; Ingolfsson and Olaffson, 1997; Knowles and Bell, 1998; Brooks and Bell, 2001). For example, Norkko and co-workers (2000) counted over 1100 mobile invertebrates/g algal dry weight on mixed species clumps of drift algae in the Baltic Sea. Kulczycki and co-workers (1981) counted 6300 amphipods in a 600 g sample of drift algae in a Florida estuary. Numerous species of anemones, molluscs, amphipods, echinoderms, sponges and bryozoans have also been observed moving offshore in the California current system on kelp blades (Bushing, 1994). For sessile organisms, the colonization of drift macroalgae occurs either by larval recruitment onto drift macrophytes or settlement on attached plants that subsequently break off and enter the drift (Jackson, 1986). Abgrall (2002) looked at the importance of the drift alga *Gracilaria* on the dispersal of the sessile bryozoan *Bugula neritina* and found that *Bugula* larvae settled in large numbers on drift individuals, but avoided attached plants of the same species.

Both positive and negative interactions have been documented between drift macrophytes and associated fauna (e.g. Kingsford, 1992). Drift algal mats can act as floating rafts or marine tumbleweeds that aid in the dispersal of fishes and invertebrates (Highsmith, 1985; Virnstein and Howard, 1987; Holmquist, 1994; Helmuth et al., 1994; Kingsford, 1995; Brooks and Bell, 2001; Abgrall, 2002). Dispersal potentials over 1.0 km/d have been estimated for Tampa Bay, FL (Brooks and Bell, 2001). Predation on invertebrates by fish is frequently significantly reduced in drift algae clumps due to high habitat complexity and increased number of refuges (Kulczycki et al., 1981; Aarnio and Mattila, 2000). Additionally, some invertebrates can forage directly on drift macrophyte hosts or it's epiphytes (Zimmerman et al., 1979). Negative faunal impacts of individuals in contact or close proximity to drift algal clumps include: 1) losses associated with being in drift clumps that become stranded by ebbing tides (Highsmith, 1985; Virnstein and Carbonara, 1985), and 2) mortality due to low levels of dissolved oxygen. For example, in the northern Baltic Sea, researchers have found hypoxic conditions and reduced biodiversity in soft-bottom communities under ephemeral mats of drift algae (Norkko, 1998; Norkko et al., 2000). Likewise, Astill and Lavery (2001) found hypoxic conditions and increased ammonia levels under drift algae within 24 hr of the arrival of the macroalgal mats in the Swan-Canning Estuary in western Australia. Alternatively, Sundbaeck and co-workers (1996) did not find any adverse effects of the green alga *Enteromorpha* covering benthic microbial mats.

In the Indian River Lagoon (IRL), on the east coast of central Florida, algal biomass exceeds seagrass biomass in many places, especially during the winter and spring months (Thompson, 1978; Benz et al., 1979; Virnstein and Carbonara, 1985). Epiphytic, free-standing attached, and drift forms of many algal species can all be found in these waters (Walters et al., 2001). In particular, Virnstein and Carbonara (1985) found that in the southern reaches of the IRL near Fort Pierce, FL, drift algae, primarily *Gracilaria* spp., was temporally and spatially very abundant, and in some sheltered, shallow water locations in spring months, drift algae biomass exceeded 15,000 g/dry wgt/m^2. The goal of the present study is to better understand the diversity of flora and fauna that moves in the surface drift in Mosquito Lagoon, the northernmost part of the IRL. This is the first time temporal diversity of drift has
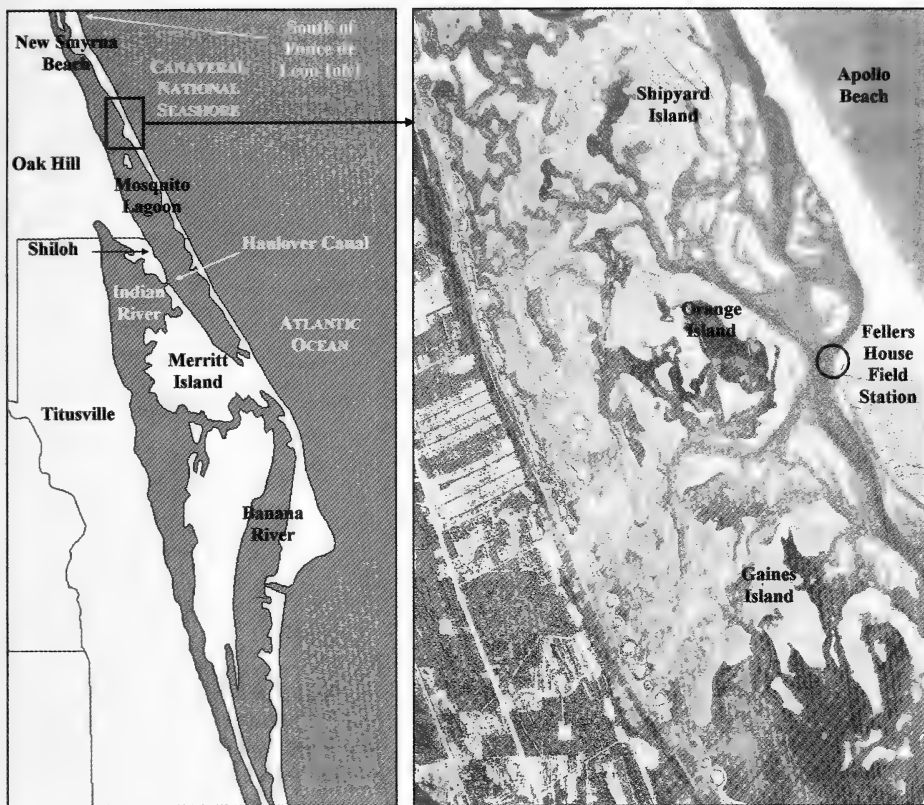
Fig. 1.   Map of the east coast of central Florida and the Indian River Lagoon system (left), and map of the location of Fellers House Field Station in Canaveral National Seashore (right).

been quantified in these waters. For this study, monthly 24-hr observations were made for a 2-year period, beginning in April 1998.

METHODS—All drift collections were made in northern Mosquito Lagoon, immediately seaward of the University of Central Florida Field Station dock (28°54′N; 80°49′W) (Fig. 1). This site is directly south of Eldora State House in Canaveral National Seashore. At its southern end, Mosquito Lagoon is connected to the Indian River via Haulover Canal; at its northern end, it is connected to the Atlantic Ocean through Ponce de Leon Inlet (Fig. 1). At this site, the average depth is 1.5 m. Throughout the year, salinity ranges from 30–46 ppt, mean water temperature ranges from 17–28 degrees C, and 122–142 cm of rain falls on an annual basis (Walters et al., 2001, unpublished data). Waters in Mosquito Lagoon are moved by both the wind and tides; the former dominates and it is classified as a wind-driven system (Walters et al., 2001).

Twenty-four hour surveys were run once a month for two years, beginning in April 1998. On each sampling date, all floating macrophytes and associated organisms were collected from our nets every four hours. Twelve collectors were created from 0.1 cm fiberglass screen mesh that was sewn together with 100 lb. test fishing line to create 84 cm long × 33 cm diameter nets (Fig. 2). Groups of three collectors were attached to two 160 cm PVC pipes (diameter: 1.9 cm) with cable ties (Fig. 2). The first collector was attached 50 cm from the end of the PVC pipe and the remaining two collectors were then spaced 30 cm apart. To keep the opening of each net circular, the open end of each collector was reinforced with
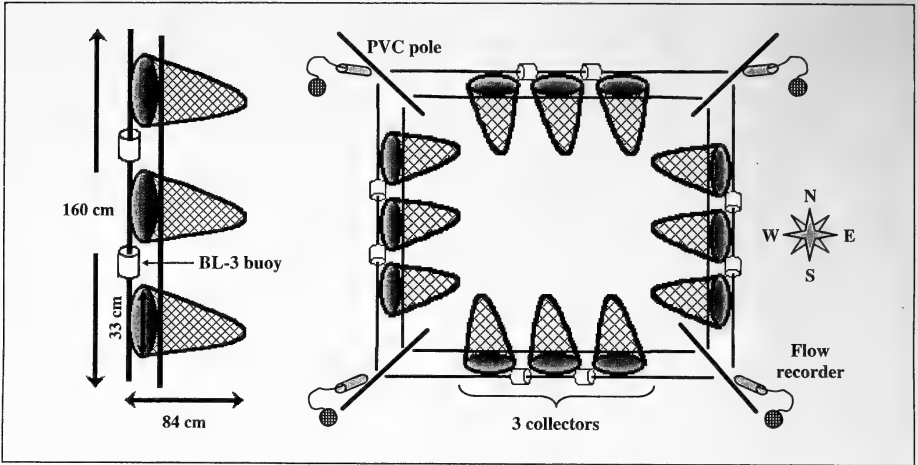
FIG. 2.   Design of drift macrophyte collectors.

20 × 33 cm wide strips of rigid plastic mesh (Vexar: 0.6 cm mesh openings) covered by fiberglass screen mesh. Two BL-3 styrofoam buoys helped maintain the opening of the nets near the surface of the water (Fig. 2).

Four sets of algal collectors were arranged in a square (Fig. 2). Six nets were placed parallel to the shore with their open ends facing north and south and the other six were placed perpendicular to the shore with their openings facing east and west (Fig. 2). Each PVC pipe of the set had its ends loosely attached to two 160-cm PVC poles (diameter: 2.5 cm) submerged 45 cm perpendicular to the substrate, allowing the surface algal collectors to move up and down with the tides. These PVC poles were placed at a distance of 180 cm seaward of the dock and 165 cm from each other. They remained in the water for the two years of this study.

Accumulated drift organisms were removed from the nets every 4 hours during each 24-hr sampling period. All organisms were sorted to species and identified. Counts were made for invertebrates, seeds and fishes for each 4-hr period. After sorting collected macrophytes (macroalgae, seagrasses), all were blotted dry, and weighed. Wet weights were made by first spinning off excess water with a salad spinner for 45 s and then weighing the algae or seagrass biomass on an electronic, top-loading balance (Ohaus Scout II, Model SC2020). The number of attached, sessile organisms on each piece of drift was also recorded and removed before the algal biomass was weighed. Algal identifications were made using two reference collections made for Mosquito Lagoon, one from winter 1998 and one from summer 1998. Dr. Clinton Dawes, University of South Florida, confirmed the identification of all specimens from these collections.

Immediately before removing accumulated drift every four hours, environmental data were collected at the study site. The maximum flow rate in water adjacent to the collectors was determined using four pre-calibrated maximum velocity flow recorders (Bell and Denny, 1994). One device was placed on each vertical PVC pole of the drift collectors (Fig. 2). Salinity was measured using a refractometer, water and air temperatures were measured using a mercury-filled glass thermometer, and the wind speed was recorded using a Kestrel 2000 wind gauge. Spearman's correlation coefficient tests ($\alpha = 0.05$) were used to determine if there was a significant linear relationship between the abundance of collected drift macrophytes and the wind speed and between drift abundance and maximum flow rate on each sampling date.

RESULTS—During the two-year field survey, 26 species of drift macrophytes were collected in our nets in Mosquito Lagoon. Red algae of the genus *Gracilaria* and the seagrass *Halodule wrightii* were found in the greatest abundances, representing 51.7% and 23.7% respectively, of all macrophyte biomass collected
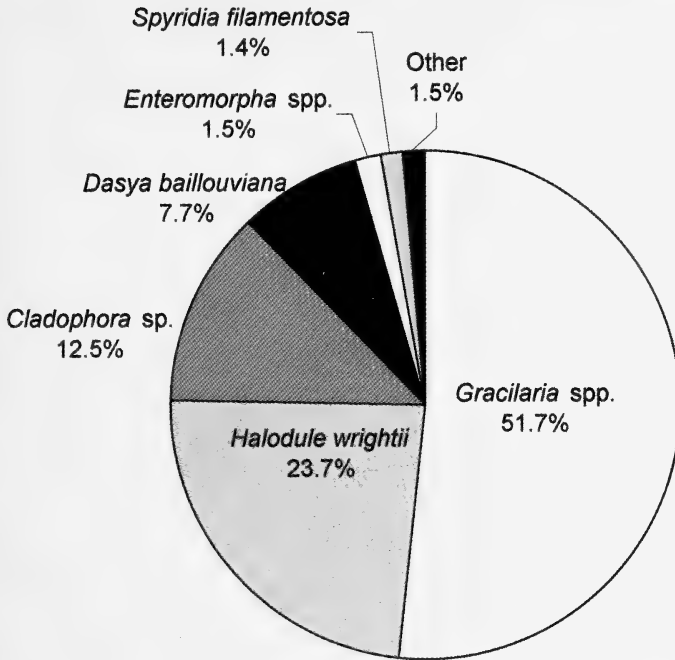
FIG. 3.   Overall percentage of drift macrophytes found in nets during monthly 24-hour collections for a 2-year period, beginning April 1998. The species *Gracilaria armata, G. tikvahiae, G. cylindrica, G. blodgettii, G. compressa,* and *G. verrucosa* are grouped under the genus *Gracilaria. Enteromorpha compressa, E. intestinalis,* and *E. prolifera* are grouped under the genus *Enteromorpha.* Other = *Acanthophora spicifera* (0.7%), *Hypnea spinella* (0.5%), *Agardhiella subulata* (0.2%) and *Chondria littoralis* (0.1%).

(Fig. 3). Among the various species of *Gracilaria* collected, *G. armata* and *G. tikvahiae* were most commonly found. Various size fragments of *G. verrucosa, G. compressa* and *G. blodgettii* were also found on some sampling dates. Representing 12.5% of all macrophytes collected, the green alga *Cladophora* sp. was frequently found entangled with *Gracilaria.*

The red alga *Dasya baillouviana* was not observed as drift or attached in Mosquito Lagoon in 1998. However, in 1999 and 2000, large clumps of this feathery alga were collected, representing 7.7% of the total biomass (Fig. 3). Among the species of *Enteromorpha* collected (1.5% total biomass), *E. intestinalis* was most frequently found. *Enteromorpha compressa* and *E. prolifera* were collected on a few occasions. *Spyridia filamentosa* was found primarily as an epiphyte on other algae and accounted for 1.4% of the total biomass (Fig. 3). The red alga *Acanthophora spicifera, Hypnea spinella, Agardhiella subulata* and *Chondria littoralis* were rarely collected and combined represented 1.5% of the total biomass (Fig. 3).

No consistent temporal patterns were observed over the course of the 2-year study. Most *Gracilaria* biomass was recorded during April 1998 (Fig. 4). At this time, a mean amount of 185.1 g was collected every 4 hours (Fig. 4). Smaller peaks of *Gracilaria* abundance were found in August 1998 (9.6 g/ 4 hr) and February 1999
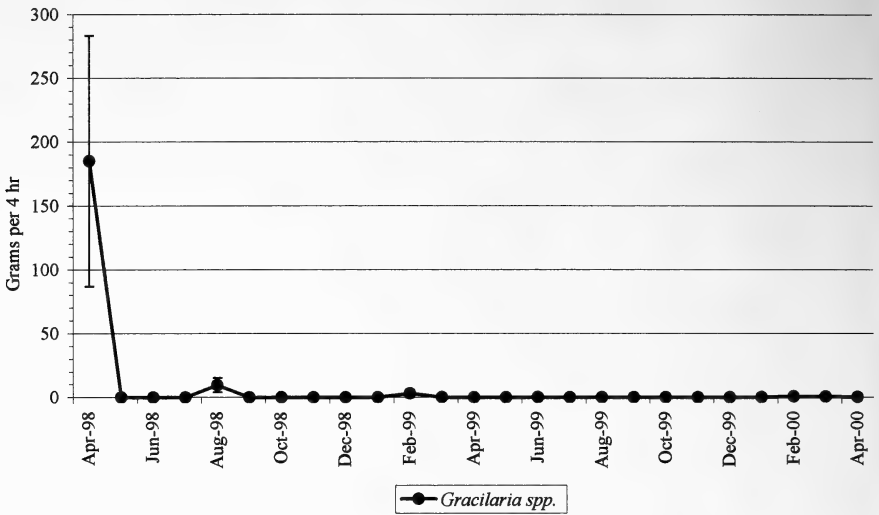
FIG. 4. Mean abundance of drift macrophytes (±S.E.) found in nets during monthly 24-hr collections for a 2-year period. *Gracilaria* spp. includes *G. armata*, *G. blodgettii*, *G. compressa*, *G. cylindrica*, *G. tikvahiae* (two morphs), and *G. verrucosa*.

(3.1 g/ 4 hr) (Fig. 4). With the exception of December 1999, *Halodule wrightii* was found every month, with greatest abundances during July 1999 (59.4 g/ 4 hr) and August 1999 (10.1 g/ 4 hr) (Fig. 5). The macroalga *Cladophora* sp. was not ob-served in the nets in 1998, but was found in 1999 and 2000 (Fig. 5). *Cladophora* sp. was generally found during the winter months, especially February 2000 (40.5 g/ 4 hr) (Fig. 5). The abundance of *Acanthophora spicifera*, *Enteromorpha* spp., and *Spyridia filamentosa* also varied temporally (Fig. 6).

No consistent temporal patterns were observed for either flow rate or wind speed during the monthly 24-hr collections (Fig. 7). Despite high wind speeds recorded in April 1998 (7.1 ± 1.87 m/s), June 1998 (8.9 ± 1.0 m/s), November 1999 (13.0 ± 1.0 m/s), and February 2000 (6.7 ± 2.6 m/s), there was no significant linear correlation between overall abundance of drift biomass and wind speed (Spearman's correlation coefficient test: p value = 0.306). Thus, an increase in wind speed did not predict the abundance of macrophyte biomass during the monthly survey or the subsequent month. Likewise, the months with highest maximum flow rates did not correlate with the months with largest macrophyte biomass (Spearman's correlation coefficient test: p value = 0.435). Thunderstorms occurred during collections in August 1998, July 1999, August 1999 and September 1999. These storms (maximum duration: 2 hours) potentially impacted the abundance of drift macrophytes during these sampling periods. However, neither strong winds nor increased flow rates were recorded during these collections.

Invertebrates and fishes were found in nets during the 24-hr collections and as with the drift macrophytes, faunal abundances varied temporally and no consistent patterns were observed (Tables 1–3). Sessile invertebrates were infrequently collected attached to drift (Table 1). The bryozoan *Scrupocellaria bertholleti* was
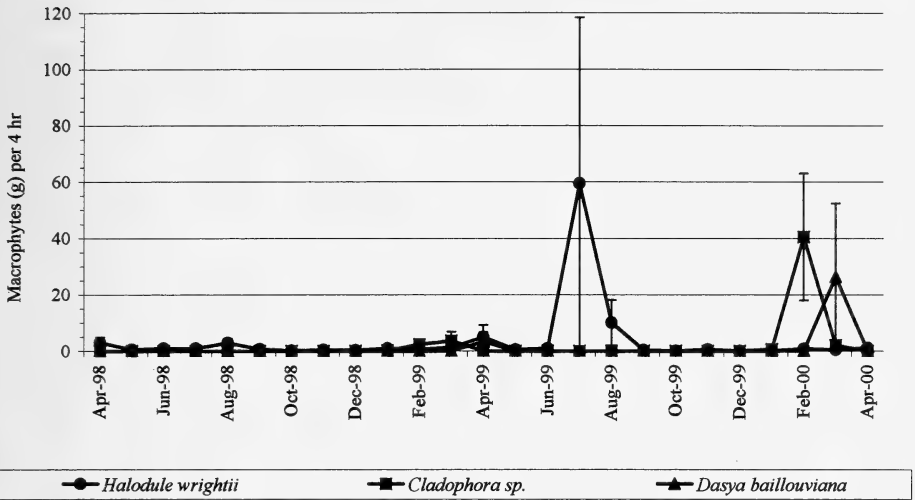
FIG. 5.   Mean abundance of drift macrophytes (±S.E.) found in nets during monthly 24-hr collections for a 2-year period.

occasionally found attached to *Gracilaria* sp. Other sessile invertebrates collected in the drift included the feather duster worm *Sabella melanostigma* (primarily attached to *Gracilaria* sp.), *Spirobis* sp. attached to the red alga *Hypnea*, and the stoloniferous ascidian *Perophora viridis* attached to *Gracilaria* and *Hypnea* fragments (Table 1).

Unattached invertebrates either moving on the surface alone or associated, but not attached to drift plants, included members of a wide range of taxa. Huge numbers of the comb jelly *Mnemiopsis mccradyi* were found in October and November 1998, April, May, July, and October 1999, and March and April 2000 (Table 1). A few snails (*Littorina irrorata*) and one sea slug (*Doriopsilla pharpa*) were collected crawling on fragments of *Gracilaria* sp. Many crustaceans, including isopods, amphipods, shrimp and crabs were collected in nets with drift algae (Table 2). The number of isopods (valiferans, anthurideans, and flabelliferans), amphipods (gammarids and caprellids), and the shrimp *Palaemonetes* sp. were extremely variable over time (Table 2). December 1999 was the only sampling date when all three small crustacean taxa were found in large quantities (Table 2). Porcelain crabs (*Megalobrachium soriatum*), blue crabs (*Callinectes sapidus*), and hermit crabs (*Clibanarius vittatus*) of various sizes were also collected in nets and their numbers varied over time (Table 2).

Various species of fish and fish larvae were observed in nets during the 24-hr collections (Table 3). Total numbers of these fish varied temporally (Table 3). More than 50% of the code gobies (*Gobiosoma robustum*) were collected during April and August 1998, two dates when large amounts of drift algae were also collected (Fig. 3). The spotted sea trout *Cynoscion nebulosus*, the pinfish *Lagodon rhomboides*, the pigfish *Orthopristis chrysoptera*, and the seahorse *Hippocampus* sp. were infrequently found in nets (Table 3).
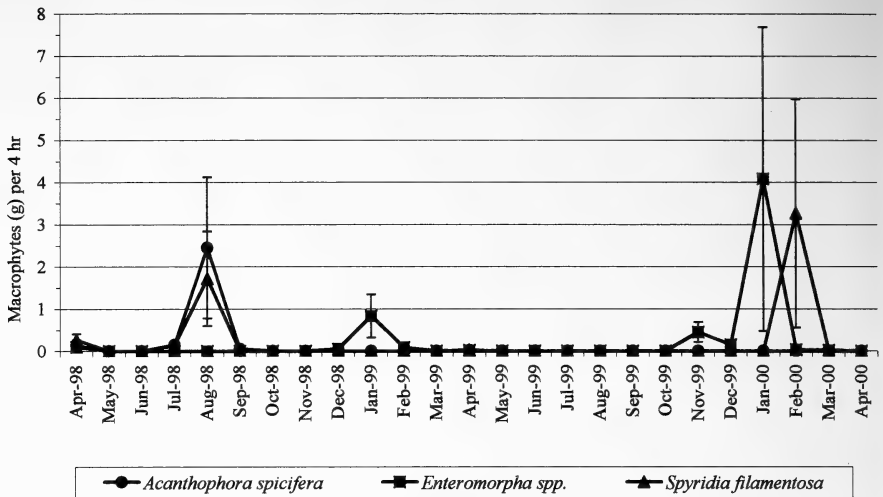
FIG. 6.   Mean abundance of drift macrophytes (±S.E.) found in nets during monthly 24-hr collections for a 2-year period. *Enteromorpha* spp. includes *E. compressa*, *E. intestinalis*, and *E. prolifera*.

A few fragments (<5 individuals total) of coastal, upland angiosperms, including the glasswort *Salicornia perennis* and the sea purselane *Sesuvium portulacastrum*, were found in September and October 1999. This coincides with stormy weather on these sampling dates. Several seeds of the black mangrove *Avicennia germinans* were also collected, mostly in November 1999 (Table 1).

DISCUSSION—In terms of biomass, drift algal communities are often the dominant communities in sandy bays and estuaries (e.g. Eiseman and Benz, 1975; Norton and Mathieson, 1983, Virnstein and Carbonara, 1985). This is especially true in the Indian River Lagoon system, where hard substratum for attachment of algae is extremely limited (Virnstein and Carbonara, 1985; Walters et al., 2001). In these waters, attached algae were only found on oyster shells, mangrove roots and man-made substrates, including jetties, pilings, floats and seawalls (Eiseman and Benz, 1975; pers. obs.). While most macroalgae begin their lives as attached individuals, macroalgae do not need to be attached to survive (Kain and Norton, 1990). Based on observations made by Eiseman and Benz (1975), almost any species of macroalgae observed in the Indian River Lagoon may be found in the drift community at some time. They found 31 species of drift macroalgae. Twenty-six species of drift macrophytes were observed in the present study and drift clumps were frequently composed of multiple species.

Similar to findings in the southern reaches of the IRL (Virnstein and Carbonara, 1985), we found *Gracilaria* sp. dominated the drift community in the northern IRL. However, our values do not come close to the biomass measures they report: 15,000 g/ dry weight/m^2 (Virnstein and Carbonara, 1985). Although the collection locations were similar in depth, our site was over 100 km further north and significantly cooler
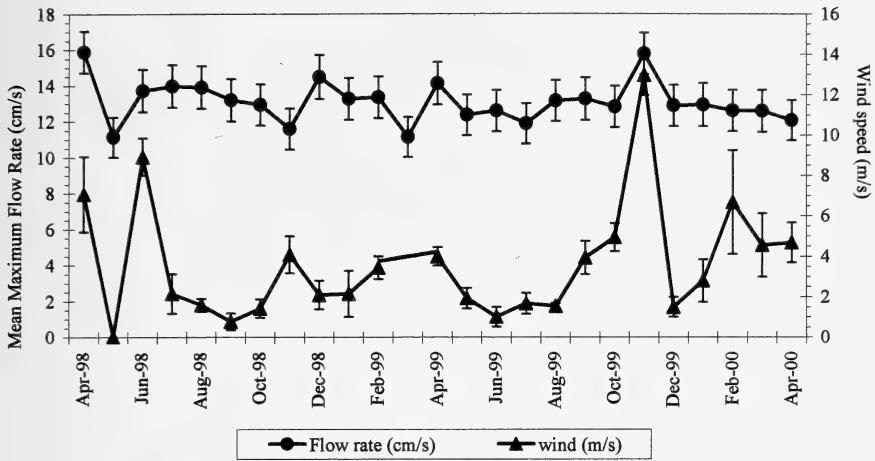
FIG. 7.   Mean maximum flow rate ($\pm$S.E.) and wind speed ($\pm$S.E.) recorded during monthly 24-hr collections during the 2-yr study. Wind speed data was not collected in March 1999 due to equipment failure.

in winter months (Walters et al., 2001). Additionally, we only collected surface drift, while Virnstein and Carbonara (1985) collected drift throughout the water column. The abundance of the green alga *Cladophora* sp. was much greater in the present study than in previous collections (Eiseman and Benz, 1975; Fig. 3). Although present in the southern IRL, the red algae *Jania adherens* and *Laurencia* sp. and the brown algae *Rosenvingea intricata* and *Dictyota dichotoma* were not collected in Mosquito Lagoon (Eiseman and Benz, 1975; Virnstein and Carbonara, 1985). Representing 7.7% of the total biomass collected, the red alga *Dasya baillouviana* appeared to be an important new addition to the drift algal community in the Indian River Lagoon system (Fig. 3). Only a few epiphytic individuals of this genus were previously recorded (Benz et al., 1979).

Virnstein and Carbonara (1985) found that the drift alga abundance varied significantly over time. They also found most high-density carpets of drift algae (thickness: 15–30 cm) between mid-December and early May, and by late July, drift algae near Fort Pierce, FL was sparse and mostly decomposed (Virnstein and Carbonara, 1985). They suggested that, in the spring, drift algae may be trapped by the fast-growing seagrass beds, forming large, stationary accumulations (Virnstein and Carbonara, 1985). Reduced light penetration, higher temperatures, increased precipitation, greater freshwater runoff, and competition with seagrasses for nutrients may have also been responsible for the decline of drift algae during the summer months (Benz et al., 1979; Virnstein and Carbonara, 1985). Similar temporal differences were found in our collections (Figs. 4–6).

Collection dates with high abundances of drift algae were also dates with high abundances of both sessile and mobile invertebrates and fishes (Figs. 4–6, Tables 1–3). Although we can not eliminate the potential that some mobile species, such as the blue crab *Callinectes sapidus*, were collected because they were attracted to the

TABLE 1. Number of invertebrates and angiosperms found in nets during monthly 24-hr collections. For all species in which >5 individuals were recorded, 24-hr totals are presented.

Date	Scrupocellaria bertholleti (bryozoan) No. colonies	Sabella melanostigma (feather-duster polychaete) No. individuals	Mnemiopsis mccradyi (comb jelly) No. individuals	Littorina irrorata (gastropod snail) No. individuals	Avicennia germinans (black mangrove) No. seeds
April-98	9	17	6	0	0
May-98	0	0	0	0	0
June-98	0	0	0	0	0
July-98	4	0	8	0	0
August-98	0	22	8	4	0
September-98	0	0	20	2	0
October-98	0	0	>200	1	0
November-98	0	0	>50	0	0
December-98	0	0	5	0	0
January-99	0	0	25	0	0
February-99	0	0	2	0	0
April-99	0	0	>50	0	0
May-99	0	0	>50	0	0
June-99	0	0	3	0	0
July-99	0	0	>50	0	0
August-99	0	0	12	0	0
September-99	0	0	0	0	0
October-99	0	0	>200	0	0
November-99	0	0	1	0	13
December-99	0	0	0	0	0
January-00	0	0	9	0	0
February-00	0	0	>10	0	1
March-00	0	0	>50	0	0
April-00	0	0	>50	0	0
Total	13	39	>809	7	14

TABLE 2. Crustaceans found in nets during monthly 24-hr collections. Presence or absence of individuals was recorded for smaller crustaceans (isopods, amphipods, the grass shrimp *Palaemonetes* sp.) and recorded as 0 = none, + = few, and ++ = abundant. Counts were used for all other species. Isopods were not identified to species and members of the suborders Valvifera, Anthuridea, and Flabellifera are grouped together. Amphipods were not identified to species and members of the suborders Gammaridea and Caprellidae are grouped together.

Date	Isopods	Amphipods	*Palaemontes* sp. (grass shrimp)	*Penaeus* sp. (penaeid shrimp)	*Megalobrachium soriatum* (porcelain crab)	*Callinectes sapidus* (blue crab)	*Clibanarius vittatus* (hermit crab)
April-98	++	++	0	18	0	0	0
May-98	0	0	0	0	0	0	0
June-98	0	0	0	0	0	0	0
July-98	+	0	0	3	0	0	0
August-98	0	0	0	76	0	1	1
September-98	+	0	++	27	3	2	6
October-98	+	0	++	2	0	1	2
November-98	0	0	++	2	0	1	0
December-98	0	+	++	3	0	1	0
January-99	0	++	0	4	1	0	0
February-99	0	0	0	1	2	0	0
April-99	0	++	0	7	2	0	0
May-99	0	0	+	1	0	0	0
June-99	0	0	++	5	0	1	2
July-99	0	0	++	3	0	0	0
August-99	+	0	0	9	0	0	0
September-99	0	0	+	0	0	0	0
October-99	0	0	0	0	0	0	0
November-99	0	0	++	0	0	0	0
December-99	++	++	++	1	0	0	0
January-00	++	++	0	15	0	0	0
February-00	++	++	+	1	0	2	0
March-00	++	++	0	17	0	0	0
April-00	+	0	0	1	0	0	0
Total				196	8	9	11

TABLE 3. Number of fishes found in nets during monthly 24-hr collections.

Date	Gobiosoma robustum (code goby)	Cynoscion nebulosus (spotted sea trout)	Lagodon rhomboides (pinfish)	Orthopristis chrysoptera (pigfish)	Syngnathus sp. (pipefish)	Hippocampus sp. (seahorse)	Fish larvae
April-98	10	0	0	0	0	0	0
May-98	0	0	0	0	0	0	0
June-98	0	0	0	0	0	0	0
July-98	0	0	0	1	0	0	2
August-98	6	1	1	0	0	0	3
September-98	7	0	2	0	3	0	0
October-98	0	0	0	0	0	0	0
November-98	0	0	0	0	0	0	0
December-98	0	0	0	0	0	0	0
January-99	0	0	0	0	0	0	0
February-99	0	0	0	0	0	0	0
April-99	0	0	0	0	2	0	1
May-99	1	0	0	0	0	0	0
June-99	3	0	0	0	1	0	0
July-99	0	0	0	0	0	0	0
August-99	1	0	0	0	1	0	0
September-99	0	0	0	0	0	0	0
October-99	0	0	0	0	0	0	0
November-99	0	0	0	0	0	1	2
December-99	0	0	0	0	0	0	0
January-00	0	0	0	0	0	0	0
February-00	1	0	0	0	0	0	0
March-00	2	0	0	0	0	0	0
April-00	1	0	0	0	0	0	0
Total	32	1	3	1	7	1	8

structure of the collectors, much of the high diversity of fauna is likely due to the fact that the drift macrophytes provided refuge from predators (e.g. Lenanton et al., 1982; Norkko et al., 2000). Protection may have been both physical (i.e. topographical complexity) and via secondary metabolites associated with the macrophytes (e.g. Walters and Wethey, 1991). Although some marine algae may produce chemicals that are toxic to settling larvae (Walters et al., 1996), this anti-fouling protection may be lost when the alga enters the drift (Abgrall, 2002). Abgrall (2002) found that larvae of the bryozoan *Bugula neritina* avoided attached *Gracilaria armata*, but settled in large numbers on drift forms of the same species.

Rafting on drift macrophytes can significantly impact the dispersal potential for some animals. For example, Abgrall (2002) examined the impact of rafting on *Gracilaria armata* on the dispersal potential for the arborescent sessile bryozoan *Bugula neritina*. Larvae of *Bugula* are approximately 167 microns, ciliated spheres that move passively with the current (Walters and Wethey, 1996). The larvae are also non-feeding and have approximately 24 hours before stored food reserves are depleted (Woollacott and Zimmer, 1971). Near the study site in Mosquito Lagoon, water movement averaged 5 cm/s (pers. obs.). Thus, larvae of *B. neritina* could potentially disperse 0.43 km from the source in 24 hr. If larvae settle on drift macrophytes, over 15-d period, they could potentially disperse 7.3, 12.9 or 87.5 km at wind speeds of 0.4 m/s, 3.5 m/s, and 6.7 m/s, respectively (Abgrall, 2002). Thus, rafting would significantly increase dispersal of this bryozoan. Likewise, Brooks and Bell (2001) found that drift clumps of *Hypnea cervicornis* acted as mobile corridors across a seagrass bed landscape for amphipods, enabling them to disperse over 1.1 km/d.

In summary, 26 species of drift macrophytes were collected in the surface drift in Mosquito Lagoon during the two-year survey. Although no consistent temporal patterns were evident, *Gracilaria* spp. and the seagrass *Halodule wrightii* dominated the drift biomass. Invertebrates and fish were, at times, found in high densities attached to or closely associated with these topographically complex, drift communities. No correlations were found between macrophyte abundance and wind speed or macrophyte abundance and maximum flow rate.

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WILDLIFE MORTALITY ON U.S. HIGHWAY 441 ACROSS PAYNES PRAIRIE, ALACHUA COUNTY, FLORIDA

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ABSTRACT: *Wildlife mortality was documented for one year on a 3.2 km section of U.S. Highway 441 in Alachua County, Florida, prior to construction of a wildlife barrier/underpass system. A total of 1,821 vertebrates, representing 62 species, were recorded dead on the road during 105 sampling days; counts were conducted weekly for 52 consecutive weeks. The most common species killed were green treefrog (*Hyla cinerea; n = 296*), southern leopard frog (*Rana sphenocephala; 230*), Florida water snake (*Nerodia fasciata pictiventris; 194*), pig frog (*Rana grylio; 145*), and green water snake (*Nerodia floridana; 119*). U.S. Highway 441 at Paynes Prairie appears to have one of the highest levels of snake road mortality ever reported; dead snakes were observed at a rate of 1.854 individuals per km surveyed (336 km surveyed/623 snakes killed).*

Key Words: Paynes Prairie, Reptiles, Amphibians, Snakes, Roads, Mortality

THERE have been numerous reports of significant mortality of amphibians and reptiles on U.S. Highway 441 across Paynes Prairie in Alachua County, Florida [Beck, 1938; Carr, 1940; 1974; Hellman and Telford, 1956; Kauffeld, 1957; Franz and Scudder, 1977; unpubl. data Florida Department of Transportation (FDEP), Gainesville, FL]. Anecdotal accounts suggested that there was a declining trend in snake populations in the vicinity of the road, most likely related to long term road mortality (Carr, 1974). In addition to mortality of individual animals, the roadway was thought to act as a nearly impenetrable barrier to snake movements (Franz and Scudder, 1977). Although snakes and frogs comprised the majority of kills on U.S. 441, more than 60 species of vertebrates have been reported killed on this 3.2-km stretch of highway (unpubl. data FDEP, Gainesville, FL).

In January 2000, the Florida Department of Transportation (FDOT) began construction of a barrier wall and underpass system (ecopassage) to reduce wildlife mortality by physically preventing access to the roadway and by directing snakes and other vertebrates through culverts beneath the road. Prior to construction of the ecopassage system, we conducted a year-long survey to determine pre-construction mortality levels. These data, and those of a post-construction survey, will be used to evaluate the effectiveness of the ecopassage system in decreasing or preventing vertebrate mortality. A concurrent monitoring study at existing and new culverts will determine whether snakes and other vertebrates use culverts to pass under the roadway. Results of the pre-construction road mortality study are presented here.

Paynes Prairie is a large highland freshwater marsh along the central Florida Ridge in Alachua County. Highland marshes are shallow wetlands characterized by unstable drainage patterns (Kushlan, 1980). Depending on rainfall and drainage, Paynes Prairie may be a dry prairie, marsh, or shallow lake. Water on the prairie flows east where it drains into Alachua Sink. The prairie basin encompasses an area nearly 5,000 ha in size and was designated as a State preserve in 1970. The prairie is transected by two major roads, Interstate 75 (I-75) and U.S. Highway 441 (U.S. 441). U.S. 441 was built in 1923 and was expanded from two to four lanes in 1957. Fill for the roadway was taken from the adjacent marsh, which created shallow canals that parallel the road. The highway is ca. 50 m wide (including a grassy clear zone, paved lanes, and grassy median) and it traverses 1.8 km of the prairie basin. There are four box culverts beneath the highway for drainage (2- 1.8 $\times$ 1.8 m and 2- 2.4 $\times$ 2.4 m). The current speed limit on Hwy 441 is 97 km/h (65 mph).

METHODS—The study took place from August 19, 1998 through August 13, 1999. Surveys consisted of a researcher walking the entire 3.2-km length of the road on three consecutive days per week for 52 weeks. The start date each week was chosen using a computer-generated random numbers table based on Julian date. On day 1, a researcher went out and spray painted all dead animals found, and on days 2 and 3 (sample days) all unmarked roadkills were counted and subsequently marked. By marking dead animals, we were able to obtain a count of the number of dead animals that had accrued during two 24-hour periods per week.

The road was divided into 100-m sections for a length of 3.2 km. The area surveyed consisted of the entire road surface (north and southbound lanes) and extended 3–4 m onto the grassy shoulders (1 pass on each side of the road). The median also was surveyed on foot or mountain bicycle (1 pass). Surveys were conducted at dawn and all live and dead animals were recorded. Dead animals were marked with spray paint so that they were not counted more than once. The paint used was both lead and toluene-free (Forestry Suppliers, Jackson, MS). Locations of animals also were recorded, e.g., north or southbound lane, right-of-way, median, and 100-m section. Environmental data were collected midway across the prairie basin and near the south rim. Air temperature (AT), water temperature (WT), relative humidity (RH), and barometric pressure (BP) were measured with computer data loggers (Onset Computer Corporation, Bourne, MA).

Water level and rainfall data at Alachua Sink, located in the northwest portion of Paynes Prairie, were provided by FDEP. At the beginning of the study (August 1998) the water level on the prairie was 59.90' NGVD (National Geodetic Vertical Datum). Water levels peaked in early October at 60.72' following rains associated with Tropical Storm Georges and declined steadily thereafter, and reached a 12-month low of 56.62' at the end of the study (Fig. 1). Total rainfall for the year was 924 mm (unpubl. data FDEP, Gainesville, FL).

Data Analysis—Kill rates were calculated as the number of kills per 24-hour sampling period (day 2 and 3). A genmod procedure (SAS, 2001) was used to examine interactions between environmental variables (rainfall, AT, WT, BP, and RH), water level (NGVD) and road kill counts for reptiles and amphibians. Mean AT, WT, BP, and RH and total rainfall for the 24-hour period prior to the road survey were used in calculations. Traffic counts for the 3.2-km section were conducted by the Florida Department of Transportation for one 24-hour period per month through the course of the study.

RESULTS—During the 24-hour surveys (n = 105), 1,821 dead vertebrates representing 62 different species were counted (Table 1). Most of the kills could be identified to the species level (87.4%); however, 7.4% could only be identified to the generic level, and 5.2% could only be categorized by class. Most of the roadkills
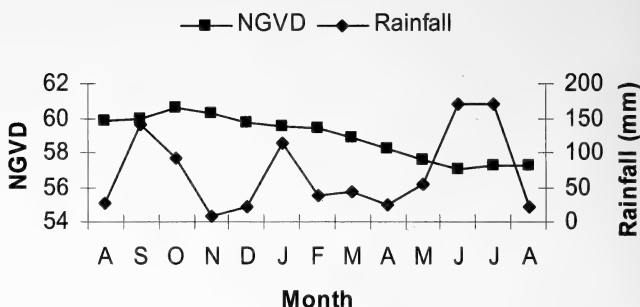
━■━ NGVD ━◆━ Rainfall

FIG. 1. Mean monthly water levels and rainfall totals on Paynes Prairie, Alachua County, Florida from August 1998–August 1999.

were frogs (45.7%) and snakes (34.2%), whereas turtles, birds, mammals, and alligators comprised 20% of the sample. The green tree frog (*Hyla cinerea*) was the most commonly observed species (n = 296), followed by the southern leopard frog (*Rana sphenocephala*; 230), Florida water snake (*Nerodia fasciata pictiventris*; 194), pig frog (*Rana grylio*; 145), and green water snake (*Nerodia floridana*; 119). These five species represented 54% of all animals killed. An additional 1,545 dead vertebrates (500 frogs, 669 snakes, 1 lizard, 187 turtles, 17 alligators, 126 birds, 45 mammals, including an additional 16 species) were counted on day 1 of the surveys. The total road length surveyed was 336 km (3.2 km × 105 24-hour sampling units); the number of roadkills per km was 5.41. The 24-hour kill rate (mean number of kills per 24-hour sampling unit) for all vertebrates was 17.3 (SD = 15.5; range = 0–79) (Table 2).

Roadkills occurred in all months of the year; however, seasonal patterns in the kill rates were evident. With the exception of birds, most road kills occurred from April through November (Fig. 2). Very high kill rates for frogs and snakes were observed in July and August 1999 (15.8 snakes/day and 30.2 frogs/day, respectively). The monthly kill rates for the five most common species are presented in Figs. 3a and 3b. Among the frogs, green treefrogs were most abundant in June, July and August 1999, whereas most pig frogs were killed in April and May. The majority of the pig frogs observed in April and May (88%) were subadults that may have been dispersing after completing metamorphosis in response to declining water levels on the prairie. Southern leopard frogs were killed in the greatest numbers from November through February, although large numbers also were killed in August 1999. The greatest number of Florida water snake kills occurred in August 1998, when water levels were at their highest for the period of record. Large numbers of green water snakes were recorded in July and August 1999. Three gravid green water snakes with 8–24 fully developed young were killed in mid-July. Approximately 50% of the green water snakes killed in July and August were neonates (<30 cm snout-vent length).

The kill rate for birds was highest in March (3.6 birds/day) and November (3.1/day). The most common birds killed were those that inhabited shrubs along the right-of-way, including yellow-rumped warbler (*Dendroica coronata*; 19.4%) and

common yellowthroat (*Geothlypis trichas*; 7.9%). Two wetland species, the common moorhen (*Gallinula chloropus*) and least bittern (*Ixobrychus ixilis*) comprised 13.7% of the sample. A black-bellied plover (*Pluvialis squatarola*) was found dead on the road in May 1999 (on day 1 of the survey week); this represents the first record of this species for the Preserve. Mammals represented only 1.5% of the sample. Raccoons (*Procyon lotor*), opossums (*Didelphis virginianus*), and round-tailed muskrats (*Neofiber alleni*) represented the majority of mammals killed (66.7%).

A summary of the interactions between environmental variables and the number of road kills is presented in Table 3. The variables AT and WT were highly correlated, therefore, only AT was used in the analysis. Significant interactions were detected between BP, RH, and NGVD and number of roadkill frogs. There was a significant relationship between RAIN and turtle kills and NGVD and snake kills. Although there was no clear pattern between the environmental variables measured in this study and the daily kill rate, the numbers of snakes and frogs observed from year to year on the prairie probably is related to local weather conditions (see Main and Allen, 2002). For example, Carr (1974) recalled finding more than 700 snakes on the road and right-of-way following a hurricane in 1941 (at least two thirds of which were injured or dead). Hellman and Telford (1956) also described an event where more than 200 juvenile mud snakes were killed following a 1950 hurricane.

The average annual daily traffic volume on U.S. 441 across Paynes Prairie (including both north and southbound traffic) was $12,165 \pm 994$ (FDOT, 1999). Peak traffic in the northbound lanes occurred between 0700 and 0730 hrs and in the southbound lanes from 1630–1700 hrs (Fig. 4). Daily traffic volumes ranged from 11,120 in September 1998 to 14,139 in November 1998. We found no relationship between traffic volume and mean monthly kill rate ($t = 0.85$, $P = 0.417$, $df = 12$, $r^2 = 0.067$). However, traffic data were collected just one day per month and did not necessarily correspond with road sampling.

Most carcasses were located on the paved surface of the road (93.9%), whereas only a few were found on the grassy right-of-way (4.56%) and median (1.5%). Carcasses were not evenly distributed on the paved surface of the road, e.g., bicycle, outside, or inside lanes ($\chi^2 = 65.09$; $P < 0.0001$); most were located in outside lanes. Although kills of most taxa were concentrated in the outside lanes, alligators and birds were more evenly distributed on the roadway (Fig. 5). Nearly twice as many frogs were found in the west (southbound) lanes as compared to east (northbound) lanes, and the reverse was the case for turtles. The number of snake kills was slightly higher in the northbound lanes.

The kills were not evenly distributed along the length of the roadway ($\chi^2 = 9.75$; $P < 0.005$) and it seems likely that the number of kills per 100-m road section was related to the adjacent habitat. The greatest number of kills occurred adjacent to flooded pasture at the base of the north rim of the prairie and the fewest kills occurred in sections which were adjacent to open water habitat.

Only 26 live animals were observed during morning road surveys. Eleven were simply basking on the right-of-way [e.g., American alligator (*Alligator mississippiensis*) and Florida cottonmouth (*Agkistrodon piscivorus*)]; however, the remainder was observed attempting to cross the road. Of the 15 vertebrates that tried to

TABLE 1. Vertebrate species recorded dead on U.S. Highway 441 across Paynes Prairie, Alachua County, Florida, August 19, 1998–August 13, 1999.

Scientific Name	Common Name	Total
Frogs		
Bufo terrestris	southern toad	6
Hyla cinerea	green treefrog	296
Hyla squirella	squirrel treefrog	1
Hyla sp.	unidentified hylid	72
Rana grylio	pig frog	145
Rana sphenocephala	southern leopard frog	230
Rana sp.	unidentified ranid	62
	unidentified frog	21
	Total:	833
Crocodilians		
Alligator mississippiensis	American alligator	12
Turtles		
Apalone ferox	Florida softshell	4
Chelydra serpentina	common snapping turtle	8
Kinosternon bauri	striped mud turtle	77
Kinosternon subrubrum	eastern mud turtle	15
Pseudemys floridana	peninsula cooter	16
Pseudemys nelsoni	Florida redbelly turtle	13
Sternotherus odoratus	common musk turtle	26
Terrapene carolina bauri	Florida box turtle	1
Trachemys scripta scripta	yellowbelly slider	4
	unidentified turtle	23
	Total:	187
Snakes		
Agkistrodon piscivorus conanti	Florida cottonmouth	68
Crotalus adamanteus	eastern diamondback rattlesnake	1
Elaphe guttata guttata	corn snake	3
Elaphe obsoleta quadrivittata	yellow rat snake	3
Farancia abacura	mud snake	33
Nerodia fasciata pictiventris	Florida water snake	194
Nerodia floridana	Florida green water snake	119
Nerodia taxispilota	brown water snake	1
Opheodrys aestivus	rough green snake	2
Regina alleni	striped crayfish snake	67
Seminatrix pygaea	black swamp snake	83
Storeria dekayi victa	Florida brown snake	11
Tantilla relicta neilli	central Florida crowned snake	1
Thamnophis sauritus sackenii	peninsula ribbon snake	29
Thamnophis sirtalis sirtalis	eastern garter snake	1
	unidentified snake	7
	Total:	623
Birds		
Agelaius phoeniceus	red-winged blackbird	1
Bubulcus ibis	cattle egret	4
Ceryle alcion	belted-kingfisher	1
Coccyzus americanus	yellow-billed cuckoo	1

TABLE 1. Continued.

Scientific Name	Common Name	Total
Cathartes aura	turkey vulture	1
Dendroica coronata	yellow-rumped warbler	27
Dendroica palmarum	palm warbler	1
Dumetella carolinensis	gray catbird	1
Fulica americana	American coot	2
Gallinago gallinago	common snipe	1
Gallinula chloropus	common moorhen	10
Geothlypis trichas	common yellowthroat	11
Ixobrychus exilis	least bittern	9
Melospiza georgiana	swamp sparrow	10
Mimus polyglottos	northern mockingbird	1
Otus asio	eastern screech owl	1
Porzana carolina	sora	2
Quiscalus major	boat-tailed grackle	2
Rallus limicola	Virginia rail	1
Sialia sialis	eastern bluebird	1
Spizella passerina	chipping sparrow	3
Sayornis phoebe	eastern phoebe	1
Tachycineta bicolor	tree swallow	4
Thryothorus ludovicianus	Carolina wren	3
Zenaida macroura	mourning dove	1
	unidentified bird	39
	Total:	139
Mammals		
Canis familiaris	domestic dog	1
Myotis austroriparius	southeastern myotis	1
Dasypus novemcinctus	nine-banded armadillo	1
Didelphis virginianus	opossum	6
Neofiber alleni	round-tailed muskrat	5
Procyon lotor	raccoon	7
Sigmodon hispidus	hispid cotton rat	1
	unidentified mammal	5
	Total:	27
	Grand Total:	1,821

cross the road, seven were injured or killed, five turned away from the road and returned to the prairie, and three crossed successfully. The three animals that successfully crossed the road were a red fox (*Vulpes vulpes*), a Florida box turtle (*Terrapene carolina bauri*), and a common snapping turtle (*Chelydra serpentina*). The red fox crossed quickly during a break in heavy traffic, whereas the two turtles crossed on weekend days, when traffic volume was quite low.

Boat-tailed grackles (*Quiscalus major*) were the most common diurnal scavengers observed in the vicinity of the road. They were seen feeding on the carcasses of a Florida water snake, common musk turtle (*Sternotherus odoratus*), and green treefrog. Nine boat-tailed grackles and one turkey vulture (*Cathartes aura*) were found dead on the road and presumably were hit while foraging on

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TABLE 2. Total number of kills and kill rates for vertebrates on U.S. Highway 441 across Paynes Prairie, Alachua County, Florida, from August 1998–August 1999.

	Number Killed	Kills/km	24-hour Kill rate
Frogs	833	2.48	7.93
Alligators	12	0.04	0.11
Turtles	187	0.55	1.78
Snakes	623	1.85	5.93
Birds	139	0.41	1.32
Mammals	27	0.08	0.26
Total	1821	5.42	17.33

the roadway. Nocturnal scavengers could include Florida cottonmouth, raccoon (*Procyon lotor*), and opossum (*Didelphis virginianus*), all of which were found dead on the road.

DISCUSSION—Based on the mean kill rate determined in this study (17.3 vertebrates/day), the estimated mortality for the year (1998–1999) was 6,314 animals (2,894 frogs; 2,164 snakes; 650 turtles; 482 birds; 95 mammals; and 40
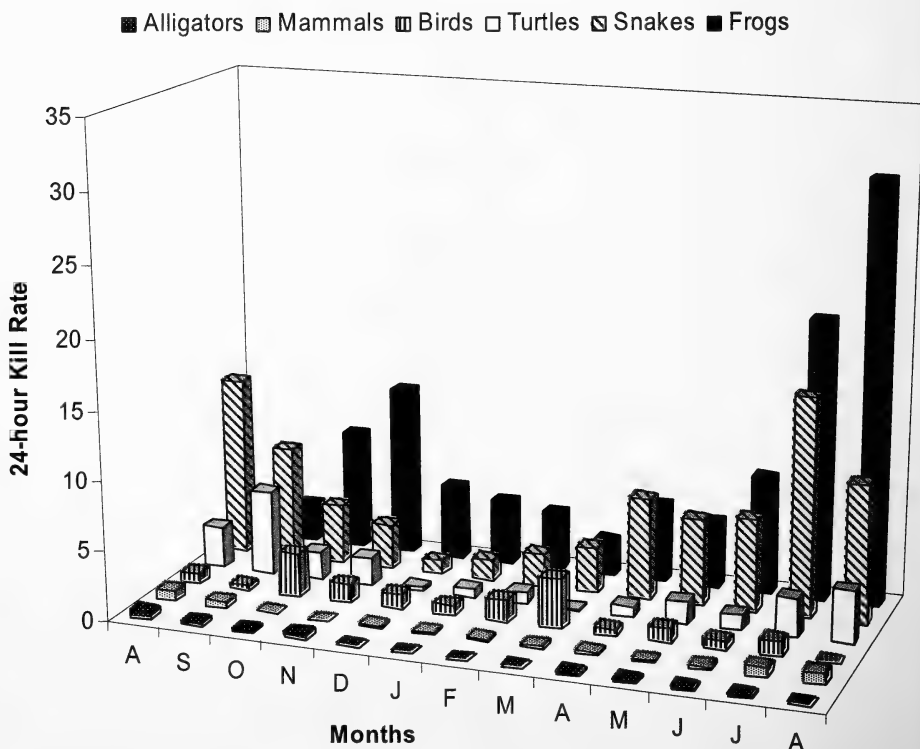
FIG. 2. Monthly distribution of road kills on U.S. Highway 441 across Paynes Prairie (August 1998–August 1999).
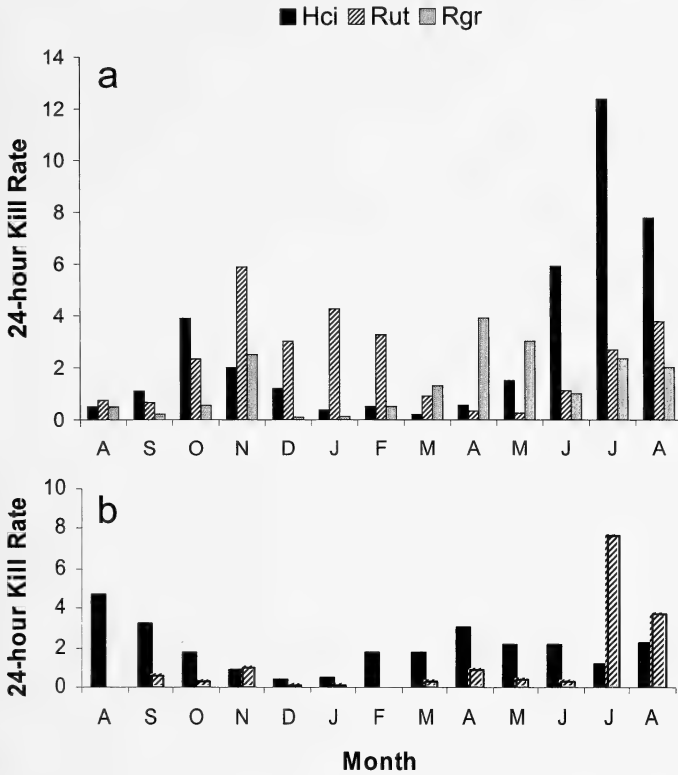
FIG. 3. (a) Monthly distribution of *Hyla cinerea* (Hci), *Rana sphenocephala* (Rut), and *Rana grylio* (Rgr) kills on U.S. Highway 441 across Paynes Prairie, Alachua County, Florida. (b) Monthly distribution of *Nerodia fasciata pictiventris* (Nfa) and *Nerodia floridana* (Nfl) kills on U.S. Highway 441 across Paynes Prairie, Alachua County, Florida.

alligators). Although these estimates should be interpreted with caution because of the high degree of variation in the kill rate among sampling periods, we suspect they may be an underestimate of actual mortality levels. Scavengers undoubtedly consumed some of the sample and some animals may have left the roadway after being hit. Prior to our survey, staff at Paynes Prairie State Preserve documented more than 25,000 dead vertebrates on U.S. 441 over a nine-year period (unpubl. data FDEP, Gainesville, FL). Again, we suspect that these numbers are an underestimate of the true mortality levels, because the FDEP surveys were opportunistic rather than systematic. Furthermore, these surveys were conducted from moving vehicles and smaller vertebrates probably went unseen. Nonetheless, these estimates are impressive.

To our knowledge, U.S. 441 at Paynes Prairie appears to have one of the highest levels of mortality of road-killed snakes ever reported; snakes were observed at a rate of 1.854 individuals per km surveyed (336 km surveyed/623 snakes killed). This rate is much greater than that reported for Paynes Prairie by Franz and Scudder (1977), who observed 0.295 snakes/km over a 58-month period. The difference in the

TABLE 3. Interactions between environmental variables and number of road kills for frogs, turtles, and snakes on U.S. Highway 441 across Paynes Prairie. Data were collected two days per week from 18 August 1998–13 August 1999. Environmental variables included: AT = air temperature, WT = water temperature, BP = barometric pressure, RH = relative humidity, NGVD = national geodetic vertical datum, RAIN = rainfall. Mean AT, WT, BP, and RH and total rainfall for the 24-hour period prior to the road survey were used in calculations.

Variable	N	Frogs		Turtles		Snakes	
		F Value	Pr > F	F Value	Pr > F	F Value	Pr > F
AT	103	2.17	0.1445	0.14	0.7130	1.52	0.2203
BP	103	11.64	0.0010	0.79	0.3764	0.44	0.5094
RH	103	48.29	<0.0001	2.23	0.1394	0.05	0.8318
NGVD	103	5.87	0.0174	0.42	0.5183	4.22	0.0429
RAIN	103	0.65	0.4216	6.23	0.0145	0.91	0.3421

observation rates between the two surveys may be due to the fact that Franz and Scudder (1977) conducted surveys from a moving vehicle, whereas we walked the entire paved roadway, median, and right-of-way. Furthermore, the daily traffic volume on U.S. 441 has more than doubled since the Franz and Scudder study (FDOT, unpubl. data.), thus more snakes are likely being killed than in the past. In other snake roadkill studies, observation rates were lower still. For example, Dodd and co-workers (1989) reported an observation rate of only 0.007 snakes/km in northwestern Alabama and observation rates of 0.010 and 0.016 have been reported for roads in New Mexico (Campbell, 1953; Price, 1983). Rosen and Lowe (1994) reported slightly higher values for snakes in the Sonoran Desert 0.0322 (3.22 DOR/100km). Bernardino and Dalrymple (1992) found large numbers of dead snakes on a stretch of road through a seasonally inundated prairie in Everglades National Park (784 dead snakes in one year on an 11.5-km stretch of highway). However, the number of survey passes conducted in this study is not reported. Main and Allen (2002) recorded 0.0103 DOR snakes/km along a 48 km highway corridor in Lee County, Florida.

Unfortunately there is no way to make a direct comparison between our results and those of past studies to determine if snake numbers on Paynes Prairie are declining. However, anecdotal accounts seem to suggest that this may be the case. For example, Beck (1938) reported finding 588 dead Florida green water snakes in just six visits to the road. Carr (1974) describes the observation of more than 700 snakes on U.S. 441 across Paynes Prairie following a 35.5-cm rain event in 1941. There have been no recent accounts of such concentrations of snakes along the roadway.

Roadkills have long been used as a source of information about the distribution and biology of species (Fitch, 1949; Campbell, 1953; van Gelder, 1973; Case, 1978; Sullivan, 1981). The long-term study on snake movements on the prairie performed by Franz and Scudder (1977) and our more recent survey provides the opportunity to make general comparisons of changes in species composition over time. For example, we recorded 15 species of snakes as compared to 12 found by Franz and Scudder (1977) during their 5-year survey. All of the five "new" species recorded in our study were rare (<5 occurrences). Two of the five species, the eastern
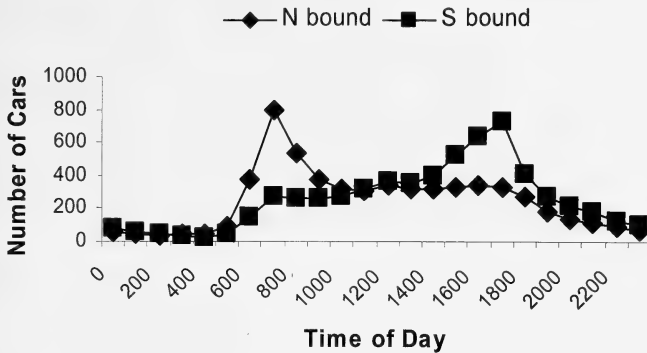
FIG. 4.   Average hourly traffic volume on U.S. Highway 441 at Paynes Prairie State Preserve, from September 1998–August 1999 (FDOT, 1999).

diamondback rattlesnake (*Crotalus adamanteus*) and the Florida crowned snake (*Tantilla relicta neilli*) are upland species that were found on the rim of the prairie. Franz and Scudder's (1977) survey was confined to the prairie basin, thus explaining the lack of these species in their sample. A third species, the corn snake (*Elaphe guttata guttata*), also typically occurs in terrestrial habitats, but two of the three specimens found in our study were located in the prairie basin. A fourth species, the rough green snake (*Opheodrys aestivus*) inhabits vegetation lining streams or lakes (Conant and Collins, 1998). Both of these species might be expected to use edge habitat created by the road. The fifth "new" species recorded in our study, the brown water snake (*Nerodia taxispilota*) is a highly arboreal aquatic species that typically occurs along the banks of rivers or streams; its occurrence on the prairie basin is somewhat unusual. The only species reported by Franz and Scudder (1977) that was not found in our study was the eastern kingsnake (*Lampropeltis getula*). Franz and Scudder found only one eastern kingsnake in 1975; however, Carr (1940) and Kauffeld (1957) described the ease with which this species was collected in the past. Most observations of eastern kingsnakes occurred prior to the highway being widened to four lanes in 1957. Prior to 1957, the road shoulder contained exposed lime rock that may have offered ideal habitat for kingsnakes or their prey (Franz, 1998).

Five species—the Florida banded water snake, Florida green water snake, striped crayfish snake (*Regina alleni*), black swamp snake (*Seminatrix pygaea*), and mud snake (*Farancia abacura*)—dominated the sample during the Franz and Scudder (1977) surveys, although the ranking within this group varied among years. The most obvious difference between our survey and that of Franz and Scudder is the increase in numbers of Florida cottonmouth killed. This species represented <5% of the sample in all 5 years of the Franz and Scudder study, whereas it represented nearly 16% of our sample. Again, changes in the habitat along the right-of-way may favor this species. Striped crayfish snake numbers were quite variable in the Franz and Scudder survey (53.6% of the sample in 1974 versus 2.6% of the sample in 1975). Striped crayfish snakes represented approximately 11% of our sample, but immediately prior to the study (Spring 1998), during a period of extremely high water, large numbers of striped crayfish snakes were killed (Weimer, 1998).

Fig. 5.   Location of kills by lane on U.S. Highway 441 across Paynes Prairie, Alachua County, Florida. F = frogs, C = alligators, T = turtles, S = snakes, B = birds, M = mammals; ROW = grassy right-of-way, BL = bicycle lane, OUT = outside traffic lane, CL = center line; IN = inside traffic lane, MED = grassy median.

Given the extremely high traffic volume on Highway 441, we suspect that virtually all animals that attempt to cross the road during peak traffic hours are killed, regardless of minor fluctuations in daily traffic levels. The few animals observed crossing the road successfully in this study did so during non-peak hours or were extremely swift-footed (e.g., red fox). It seems likely that slow-moving species such as most aquatic snakes, ranid frogs, or turtles would be especially susceptible to being hit by motor vehicles. Franz and Scudder (1977) monitored the fate of 132 snakes attempting to cross U.S. 441 at night. They found that only eight of the snakes survived, and that they did so by returning to the prairie, roughly where they left it. In addition, they reported finding very few snakes in the median during their weekly surveys, and suggested that few snakes were able to successfully reach the median. The low number of carcasses found in the median during our study further supports this conclusion.

The majority of the species killed on U.S. 441 at Paynes Prairie were "common", widely distributed species and road mortality is unlikely to impact these species at more than a local level. However, since the road may present an impenetrable barrier to some species, there may be important demographic and genetic consequences (Forman and Alexander, 1998). There has been concern in the scientific community about the effects of roads on wildlife for a number of years (Stoner, 1925; Dickerson, 1939). However, the magnitude of the impacts of roads on animal populations has proven difficult to quantify, primarily because impacts cannot be assessed without corresponding data on species abundance.

Transportation managers and engineers have conceived of a variety of ways to prevent or reduce highway-related wildlife mortality because animals killed on roads represent a drain on adjacent populations, and because of increasing public pressure to do something about the problem. These efforts are most advanced in Europe, where the problems associated with road-related wildlife mortality have long been recognized (Langton, 1989; ALASV, 1994; Percsy, 1995). Rather than simply cataloguing mortality, biologists are now in a position to recommend solutions based on carefully collected life history data, particularly on habitat use and activity patterns. These data will prove more vital in the design of ecopassages and barriers to reduce or prevent road-related mortality.

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DISTRIBUTION OF THE INTRODUCED BLACK SPINY-TAILED IGUANA (*CTENOSAURA SIMILIS*) ON THE SOUTHWESTERN COAST OF FLORIDA

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ABSTRACT: *The black spiny-tailed iguana (*Ctenosuara similis*) was introduced onto Gasparilla Island in southwestern peninsular Florida ca. 30 years ago. Since then, this exotic species has undergone both natural and human-mediated range expansion, and it is presently found in Placida, Cape Haze, Gulf Cove, Cayo Costa, Keewaydin Island, and Little Marco Island. Although* C. similis *is primarily herbivorous, it will feed opportunistically on small animals, including insects, crabs, rodents, fishes, nestling birds, bird eggs, and hatchling sea turtles. Because of the possible ecological impacts of* C. similis *on Florida's native flora and fauna, population monitoring and/or eradication efforts should be conducted on* C. similis.

Key Words: Iguana, *Ctenosaura similis*, Ecology, Florida, Gasparilla Island, Keewaydin Island

THE IGUANID genus *Ctenosaura* consists of 13 species native to central and southern Mexico, the Yucatan Peninsula, and Central America (Köhler et al., 2000). Ctenosaurs or spiny-tailed iguanas have been introduced into the United States in southern Texas and southern peninsular Florida (Eggert, 1978; Behler and King, 1979; Wilson and Porras, 1983; Stiling, 1989; Conant and Collins, 1991; Dalrymple, 1994; Angell, 1996; Butterfield et al., 1997; Bartlett and Bartlett, 1999; McKercher, 2001). The black spiny-tailed iguana (*Ctenosuara similis*) was first reported to have an established population along Old Cutler Road in Miami-Dade County (Eggert, 1978). However, Wilson and Porras (1983) stated that this population was misidentified and consisted of the Mexican spiny-tailed iguana (*C. pectinata*). Nonetheless, recent surveys on and near Gasparilla Island on the southwestern coast of Florida have identified established populations of *C. similis* that are undergoing natural and human-mediated range expansion. Herein, we present records of *C. similis* from Charlotte, Collier, and Lee counties, Florida.

METHODS—Gasparilla Island, an approximately 10.5-km long barrier island southwest of Port Charlotte, is separated from the mainland by Charlotte Harbor and Gasparilla Sound. Gasparilla Island is connected to the mainland at Placida via the Boca Grande Causeway, which stretches over two small uninhabited causeway islands and three bridges before reaching Gasparilla Island. The approximate

TABLE 1. Black spiny-tailed iguanas (*Ctenosaura similis*) collected from southwestern peninsular Florida.

County	Location	Date	Collector(s)	Voucher
	This Study			
Lee	Gasparilla Island	25 June 2002	K.L. Krysko, F.W. King, K.M. Enge	UF 133211–17
Lee	Gasparilla Island	27 June 2002	K.L. Krysko, F.W. King, K.M. Enge	UF 133254
	Other Specimens			
Charlotte	Gasparilla Island	June 1994	P.E. Moler	UF 91662
Collier	Keewaydin Island, Rookery Bay Estuarine Research Reserve	20 June 2000	S.M. Bertone	UF 128412
Lee	Gasparilla Island	2 June 2000	K. Mebert	UF 121140–43

northern one-third of Gasparilla Island is situated in Charlotte County, whereas the southern two-thirds is in Lee County.

Records of *C. similis* are based on recent captures and observations during three survey days on the southwestern Florida coast between December 2000 and June 2002. Additional records were gathered by querying the Department of Environmental Protection (DEP) personnel and exotic species database (Florida Department of Environmental Protection, 2002). Captures were made during the daytime using noose carpets and blowguns with tapered corks. Because only *C. pectinata* has been previously reported from Gasparilla Island (Angell, 1996; Bartlett and Bartlett, 1999; McKercher, 2001), the possibility of encountering this species was also considered, and we attempted to verify species identification via observation if an individual was not collected.

Ctenosaura similis and *C. pectinata* are closely related species but differ in a number of morphological and molecular characters (Köhler and Streit, 1996; Köhler et al., 2000). *Ctenosaura similis* has 0–2 (usually zero) scales separating the dorsal and caudal crests, two complete rows of intercalaries between whorls of enlarged caudal scales near the base of the tail, and some (usually a high) degree of dark dorsal crossbands (Köhler and Streit, 1996). *Ctenosaura pectinata* has 2–14 scales separating the dorsal and caudal crests, three complete rows of intercalary scales between whorls of enlarged caudal scales near the base of the tail, and no dark dorsal crossbands. Identification of juveniles is more problematic, as both species tend to be green to gray with dark crossbands. However, the number of scales separating the dorsal and caudal crests, as well as the intercalary characters, hold for all age classes and were used for species identification of juveniles. Voucher specimens and photographs were deposited in the Florida Museum of Natural History (FLMNH), University of Florida (UF collection).

RESULTS—We recorded >200 *C. similis* on Gasparilla Island. Eight specimens were collected (Table 1) consisting of juveniles and adults of both sexes. We observed at least two individuals on each Boca Grande Causeway island (26°48.907′N, 082°16.439′W and 26°49.543′N, 082°16.223′W) and three individuals on the mainland at Placida (26°49.790′N, 082°16.172′W). No *C. pectinata* were recorded in our surveys. Five additional *C. similis* from Gasparilla Island and one from Keewaydin Island, Collier County, were found in the UF collection. Eighteen individuals from Gasparilla Island and one from Cayo Costa were recorded in the DEP exotic species database (Florida Department of Environmental Protection, 2002), and numerous individuals were recorded from Keewaydin Island (Bertone, 2002).

DISCUSSION—Because no *C. pectinata* were recorded in our surveys, we believe that the Gasparilla Island population was misidentified in earlier reports. McKercher (2002) assumed *C. pectinata* was the species found on Gasparilla Island based entirely on the field guide identification by Bartlett and Bartlett (1999), yet she collected no voucher specimens during her study. Photographs labeled as *C. pectinata* by Angell (1996) and Bartlett and Bartlett (1999) are misidentified and clearly *C. similis*. Four individuals labeled as green iguanas (*Iguana iguana*) in the DEP exotic species database are undoubtedly *C. similis* as described in their remarks (Florida Department of Environmental Protection, 2002). Despite the fact that ctenosaurs on Gasparilla Island have been consistently identified as *C. pectinata*, there is no evidence that *C. pectinata* ever existed in this area.

Ctenosaura similis on Gasparilla Island appears to have originated from a single introduction. In the late 1970s–early 1980s an island resident brought back from Mexico three *C. similis* (McKercher, 2001; Amen, 2002; Middleton, 2002), which were raised by his children for the next few years before being released near the Range Light House (Amen, 2002; Middleton, 2002). The ctenosaurs remained localized for several years but began to reproduce and slowly spread from the point of introduction (Middleton, 2002). Presently, our data illustrate a large, well-established population of *C. similis* throughout the entire island, on both Boca Grande Causeway islands, and on the mainland at Placida. Individuals have also been found dead-on-road (DOR) after being hit by vehicles on the Boca Grande Causeway bridges (McKercher, 2002), suggesting that the species reached the mainland naturally. Additionally, individuals have been taken from Gasparilla Island to the mainland by workers (Middleton, 2002), which could assist in a more rapid range expansion of *C. similis* on the mainland. Middleton (2002) found a ctenosaur under the hood of her car after driving home from Gasparilla Island State Park on a cold afternoon. Individuals have now been reported from Cape Haze north of Placida (Middleton, 2002), Gulf Cove, Cayo Costa to the south of Gasparilla Island (Florida Department of Environmental Protection, 2002), and Keewaydin Island in the Rookery Bay Estuarine Research Reserve ca. 80 km south of Gasparilla Island (Bertone, 2002) (Table 1).

Ctenosaura similis was probably transported purposely to Cayo Costa, which is accessible only by boat. *Ctenosaura similis* on Keewaydin Island also appears to have originated from a single introduction. A private landowner on Keewaydin Island released 5–30 *C. similis* on his property on the southern end of the island in the summer of 1995 (Bertone, 2002). No *C. similis* were reported until April 1998, when island residents began reporting ctenosaurs causing landscape destruction ca. 1 km north of the introduction site (Bertone, 2002). In the summer of 1998, numerous hatchling and adult *C. similis* were reported from the southern tip of the island north to Johns Pass on the northern half of the island ca. 8 km north of the introduction site (Bertone, 2002). Presently, *C. similis* is found on the entire Keewaydin Island and adjacent Little Marco Island.

The range expansion and ecological status of *C. similis* should be of particular interest to conservationists in Florida. *Ctenosaura similis* has been reported to produce 5–8 clutches annually (Ojasti, 1996), each consisting of 12–88 (mean 43)

eggs (Wiewandt, 1982). One specimen (UF 131496) collected by us on 27 March 2002 at Crandon Park on Key Biscayne had 82 well-developed eggs in her oviducts. Ctenosaurs are primarily herbivorous but will feed opportunistically on small animals, including insects, crabs, rodents, fishes, nestling birds, bird eggs, and hatchling sea turtles (Evans, 1951; Fitch et al., 1971; Alvarez del Toro, 1982; Smith, 1990; Smith et al., 1992; Rodriguez-Juarez and Cepeda, 1998; Arndt, 1999; Durtsche, 2000; McKercher, 2001). *Ctenosaura similis* on Keewaydin Island pose a threat to eggs and nestlings of the least tern (*Sterna antillarum*) (Zambrano, 2002), a threatened species in Florida. On 16 June 1998, Rookery Bay National Estuarine Research Reserve staff observed an adult *C. similis* chasing baby and adult least terns on the beach on the southern tip of Keewaydin Island (Bertone, 2002). Least terns, Wilson's plovers (*Charadrius wilsonia*), and snowy plovers (*C. alexandrinus*) nest on the northern end of Gasparilla Island, which is also inhabited by ctenosaurs (Douglass, 2002). Keewaydin Island is also used by nesting loggerheads (*Caretta caretta*) (Meylan et al., 1995), but their eggs are probably safe from ctenosaurs because of the depth at which they are laid. On Gasparilla Island, *C. similis* occupies the same habitats and feeds on the same native vegetation as gopher tortoises (McKercher, 2001). It also utilizes tortoise burrows but has not been observed to cohabit with tortoises (McKercher, 2001). If *C. similis* ever becomes established in Cape Coral, Lee County, it could impact the largest population of burrowing owls (*Athene cunicularia floridana*) in Florida (Millsap and Bear, 2000) by competing for burrows or even preying upon nestlings. Although *C. similis* is considered an attraction by some residents and visitors on Gasparilla Island, the species has also proven a nuisance, as evidenced by the lizard foraging on native plants and the thousands of dollars spent each year by homeowners because of damage to their houses and landscape vegetation (Angell, 1996; McKercher, 2001). We believe that the *C. similis* populations and their ecological impacts should be monitored and efforts should be initiated to control populations in areas where detrimental impacts on sensitive native flora and fauna are documented.

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SEED DISPERSAL BY *GOPHERUS POLYPHEMUS* AT ARCHBOLD BIOLOGICAL STATION, FLORIDA

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ABSTRACT: *We investigated the potential for the gopher tortoise (*Gopherus polyphemus*) to act as an agent of seed dispersal at Archbold Biological Station, Florida. Scat dissections, as well as foraging observations, were used to determine the seed species and plant taxa consumed by the tortoises during June and July 2001. The diet of the gopher tortoise consisted mainly of grasses and sedges, and these, as well as* Pinus elliottii, Galactia *sp.,* Vaccinium myrsinites, *and* Gaylussacia dumosa, *comprised the majority of the plant matter identified in the scat. Germination tests were performed on digested and undigested seed of the two most abundant seed species found in the scat, the exotic grass* Paspalum notatum *(bahiagrass) and its native congener,* P. setaceum. *The percent germination of digested* P. notatum *seeds was significantly lower than the germination of undigested* P. setaceum *(<1% vs. 27%). In contrast, many seeds of* P. setaceum *germinated after digestion, and there was no significant difference between digested and undigested seeds of this species. Gopher tortoises disperse seeds of the exotic* P. notatum *but suppress immediate germination. They disperse the native grass* P. setaceum, *which is able to germinate immediately after tortoise digestion.*

Key Words: Gopher tortoise, *Paspalum notatum*, *Paspalum setaceum*, Lake Wales Ridge, diet, herbivory, seed survival

THE GOPHER tortoise (*Gopherus polyphemus*) lives in upland xeric habitats throughout most of the Southeastern Coastal Plain of the United States (Auffenberg and Franz, 1982). Like all other members of the genus *Gopherus*, gopher tortoises dig and maintain burrows, which protect inhabitants from extreme temperatures, fire, desiccation, and predators (Cox et al., 1987). Gopher tortoise burrows provide habitat for over 350 different vertebrate and invertebrate species, and because of this, the tortoise is considered a keystone species (Cox et al., 1987; Jackson and Milstrey, 1989). The burrows and adjacent mounds of extracted sand also influence the vegetation in these communities by providing favorable microsites for certain plant species (Kaczor and Hartnett, 1990). Though these and many other aspects of the tortoise's natural history have been well studied, the potential role of the gopher tortoise as a seed disperser has been largely uninvestigated.

Seed dispersal by reptiles, or saurochory, is not entirely uncommon, yet has received considerably less attention than dispersal syndromes associated with other

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vertebrates, such as birds and mammals (Moll and Jansen, 1995; Traveset, 1998; Traveset et al., 2001). A growing body of evidence suggests a number of turtles and tortoises play a role in seed dispersal. Two species of herbivorous turtles in Costa Rica (Moll and Jansen, 1995), and the box turtle (*Terrapene carolina*) (Braun and Brooks, 1987) are known to disperse viable seeds. Furthermore, the germination of seeds was enhanced by passage through the gut of the Galapagos tortoise (*Geochelone nigra*) (Rick and Bowman, 1961) and *Gopherus berlandieri* (Rose and Judd, 1982).

The herbivorous diet and foraging habits of *G. polyphemus*, as well as evidence that other tortoises disperse seeds, suggest that the gopher tortoise could very well be dispersing viable seeds. Furthermore, as grasses make up the greatest portion of the tortoise's diet (Garner and Landers, 1981; MacDonald and Mushinsky, 1988), it is likely that grass seeds would be the most frequently consumed, and therefore, would possess the greatest potential to be dispersed. In a study of the diet of gopher tortoises in a sandhill community, seeds were found in 90% of the examined scat samples, and many of these seeds were identified as grass seeds (MacDonald and Mushinsky, 1988). Gopher tortoises may be agents of dispersal for wiregrass (*Aristida* sp.), which burns readily and is an important fuel for ground fires in the southeastern U.S. (Auffenberg, 1969). In this way, the gopher tortoise's role as a seed disperser may contribute to the maintenance of the fire-adapted communities in which it is found.

Though it is known that gopher tortoises frequently consume seeds, the viability of seeds found in scat is almost entirely unknown. *Ximenia americana*, or tallowwood, is the only species to have been tested and found to germinate post-gopher tortoise digestion (Hayes and LeCorff, 1989). However, in Hayes and LeCorff's study, no comparisons were made between the germination of undigested and digested tallowwood seeds, and hence, it remains unknown if tortoise digestion alters germination percentages in tallowwood seeds, or in seeds of any species. Furthermore, the fleshy tallowwood fruits, which become ripe in the fall, have only been found in the scat of tortoises located in southern Florida (Hayes and LeCorff, 1989).

In order to determine if gopher tortoise digestion alters the germination of seed species commonly found in the scat, as well as to examine its overall diet, we addressed the following questions: 1) What plant foods do gopher tortoises eat at Archbold Biological Station in the months June and July? 2) Which seed species are most frequently found in scat? 3) Do the most frequently consumed seeds germinate after passing through a gopher tortoise gut? 4) Is seed germination increased or decreased after passage through the tortoise?

STUDY SITE—Archbold Biological Station is located on the southern end of the Lake Wales Ridge, 12.9 km south of Lake Placid in Highlands County, Florida. The normal maximum and minimum temperatures for June and July are 33.4° C and 20.1° C, with 20.6-cm rainfall. All data for this study were collected on the 2,081 ha main property. We studied gopher tortoises along firelanes running through or near various xeric and upland vegetation types: flatwoods, scrubby flatwoods, southern ridge sandhill and human-modified old-field vegetation communities (see Abrahamson et al., 1984, for descriptions of native habitat types). Invasive grasses such as *Paspalum notatum* (bahiagrass), *Panicum* sp. and *Sporobolis*

indica dominated two human-modified old fields on the property. The 10 to 15 m wide firelanes were typically mowed twice a year and often had ruderal species of grasses and forbs growing along the edges, in addition to species typical of adjacent vegetation types.

METHODS—Data on the diet and seed consumption of the gopher tortoise were obtained through the dissection and analysis of field-collected scat. We collected 91 scat samples in June and July 2001. We located gopher tortoises during 1–4 hour search intervals between 1000 and 1700 hours along firelanes through or adjacent to scrubby flatwoods, flatwoods, southern ridge sandhill and human modified old-fields. These time periods and locations were chosen in accordance with the periods of highest activity and the preferred habitat of tortoises at Archbold Biological Station (Douglass and Layne, 1978). The tortoises were followed or placed in a wire enclosure until defecation occurred, which usually took place in less than a half-hour. We collected fifty samples in this manner from 34 individuals; the other 41 scat samples were found post-deposition, in the absence of a tortoise, and were collected only if they were completely intact and relatively fresh.

We dissected all scat samples within one week of collection and identified plant fragments and seeds to the lowest taxonomic level possible using an on-location herbarium and a reference collection of common plant species found along firelanes and within the adjacent habitat on the station (nomenclature follows Wunderlin [1998]). The leaf and stem matter of grasses and sedges were difficult to tell apart in the scat and were combined into a Poaceae/Cyperaceae category. Though the majority of the grass-like leaves were positively identified as grasses, the presence of some questionable specimens made it necessary to combine the two families. Each plant taxon was counted on a presence or absence basis for each scat, and from this, we calculated the absolute frequency of occurrence of each taxon in the 91 scat samples.

To supplement scat analysis, we observed tortoises foraging along firelanes for periods of 10–20 minutes (n = 24) and recorded all plants consumed by the tortoises. The frequency of occurrence in an observation period was calculated using the same method as the scat samples. In order to facilitate comparisons, each observation period was equivalent to one scat sample in that we counted the consumption of a plant taxa only once per observation period. These observations provided information on food plants that were difficult to identify in tortoise scat and also gave another estimate of the plants consumed by the gopher tortoise.

We sorted and counted all seeds found in scat samples. For each seed taxon, we calculated the relative frequency of occurrence in the scat samples (number of occurrences of each taxon/total number of occurrences * 100) and the relative density (number of individuals in each taxon/total number of seeds * 100). When 20 or more seeds were found in a single scat sample, we placed seeds on moistened filter paper in petri dishes (10 seeds per dish) within 24 hours of their discovery and monitored subsequent germination. Only two seed species were found in sufficient numbers to be used in the germination trials, *Paspalum notatum* and *P. setaceum*. At the outset of each trial, we placed an equal number of fresh, undigested conspecific seeds into petri dishes, to determine if there was a difference in percent germination of digested and undigested seeds. We checked for germination and watered regularly; tests were run outdoors in June–August on a covered veranda. Each of the seven germination tests ran for 45 days, and in the data analysis, we combined all tests on a single species. Germination percentages were compared between digested and undigested seeds using a Fischer's Exact Chi-square test.

RESULTS—Grasses and sedges dominated the summer diet of the gopher tortoise; the leaves of Poaceae/Cyperaceae were present in 97% of the scat samples (Table 1). Three grass species were identified by seed, and these included *Paspalum notatum* (bahiagrass) and *P. setaceum* (slender paspalum). In terms of plant fragments, a total of 20 plant genera were found in the 91 scat samples. Slash pine (*Pinus elliottii*) needles were present in almost 50% of the samples, and *Galactia* sp. and *Vaccinium myrsinites* were each found in more than 25% of the scat samples. Of the remaining groups, the most important were *Quercus geminata* and

TABLE 1. Frequency of the plant taxa found in *Gopherus polyphemus* scat (n = 91) or during a 10–20 minute foraging observation (n = 24). Each plant taxon was counted only once per scat sample and/or once per foraging observation. Taxa with asterisks are grasses identified by seed; the presence of their leaf matter was included in Poaceae (Cyperaceae). Nomenclature follows Wunderlin (1998).

Plant Taxon	Frequency in Scat (n = 91)	Frequency in Foraging Observations (n = 24)
Poaceae (Cyperaceae)	96.7%	70.8%
*Paspalum notatum**	19.8%	—
*Paspalum setaceum**	14.3%	—
Pinus elliottii	48.4%	8.3%
Galactia sp.	39.6%	4.2%
Vaccinium myrsinites	30.8%	8.3%
Quercus geminata	16.5%	—
Gaylussacia dumosa	15.4%	—
Roots	12.1%	8.3%
Selaginella arenicola	9.9%	—
Diodia teres	7.7%	16.7%
Smilax auriculata	5.5%	—
Myrica cerifera	5.5%	—
Digitaria sp.*	3.3%	—
Quercus myrtifolia	2.2%	—
Unknown herb	2.2%	—
Chamaesyce maculata	2.2%	4.2%
Quercus minima	1.1%	—
Carya floridana	1.1%	—
Lyonia lucida	1.1%	—
Lyonia fruticosa	1.1%	—
Opuntia humifusa	1.1%	—
Ximenia americana	1.1%	—
Froelichia floridana	—	4.2%
Pityopsis graminifolia	—	4.2%
Tephrosia chrysophylla	—	4.2%
Mimosa quadrivalvis	—	4.2%
Licania michauxii (fruit)	—	4.2%
Commelina erecta	—	4.2%

Gaylussacia dumosa. Nine genera were found in only one, two or three scat samples. In 89% of the scat samples, all of the plant matter was identified.

A comparison of the species composition of observed forage versus species composition of scat revealed many similarities and some notable differences (Table 1). Grasses and sedges were by far the most frequently observed plant taxa eaten by gopher tortoises, consumed in 17 of the 24 observation periods. The exotic bahiagrass was the most commonly consumed plant species, observed in eight of 24 observation periods, and we watched tortoises ingest the seed heads of this species during four of eight observations. The top five taxa of the foraging observation periods were also found in the scat, but their relative frequencies in the scat examinations and the foraging observations were often quite different. Foraging observations showed the highly digestible *Diodia teres* to be far more frequently consumed than the scat dissections indicated. Furthermore, tortoises were observed eating six plant species

TABLE 2. The seed taxa found in *Gopherus polyphemus* scat. For each taxon, the relative frequency of occurrence in the scat samples and the relative density were calculated.

Seeds Found in Scat	Relative Frequency (n = 52)	Relative Density (n = 1538)
Paspalum notatum	34.6%	72.9%
Paspalum setaceum	25.0%	12.6%
Diodia teres	13.5%	1.6%
Unknown seeds	7.7%	2.2%
Digitaria sp.	5.8%	2.3%
Pinus elliottii	5.8%	0.3%
Chamaesyce maculata	3.8%	8.1%
Quercus geminata	3.8%	0.2%

that were never identified in scat samples (Table 1). Each of these taxa was recorded only once during the 24 foraging observation periods.

Strong evidence exists that gopher tortoises were capable of dispersing plant seeds (Table 2). We found 1538 seeds in total, with seeds occurring in 45% of the scat samples. The vast majority, 85%, of seeds found were *Paspalum notatum* and *Paspalum setaceum*. The third most commonly found seed came from the low-growing forb *Diodia teres*; this species accounted for 1.6% of all the seeds and was found in a total of seven scat samples. Few of the other seeds were notably dense or frequent in the scat. Four unknown seed types were each encountered in 2 or fewer scat samples.

Germination results showed that the percent germination of digested *Paspalum notatum* seeds was significantly lower than that of the undigested seeds (p < 0.001 X^2 = 137.4 df = 1; Table 3). Only one of the 460 digested *P. notatum* seeds germinated, whereas 122 of 460 undigested seeds germinated. In contrast, passage through the gut of the gopher tortoise did not appear to greatly alter the germinability of the seeds of the native *P. setaceum* (p = 0.18 X^2 = 1.83 df = 1; Table 4).

DISCUSSION—Grasses predominated in the diet of gopher tortoises at Archbold Biological Station, in agreement with results from studies elsewhere (Garner and Landers, 1981; MacDonald and Mushinsky, 1988). *Paspalum notatum* was found to be frequently consumed along roadsides in this and other studies (Garner and Landers, 1981). *Galactia* species were the most frequently consumed forbs in MacDonald and Mushinsky's (1988) study as well as this study, and these and other legumes were the most important forbs according to Garner and Landers (1981). Tortoises may preferentially consume these herbaceous plants because they have high nutritional value, being relatively rich sources of calcium and protein (Garner and Landers, 1981).

Differences in the results of this and other studies on gopher tortoise feeding can largely be attributed to the short duration of this study compared to the year-long studies of other researchers. Though this study occurred during the season of peak activity for gopher tortoises (Douglass and Layne, 1978), annual fluctuations in

TABLE 3. Germination percentages of digested and undigested *Paspalum notatum* seeds. Each trial consisted of all of the *P. notatum* seeds found in one scat as well as an equal number of undigested seeds. There was a significant difference between the percent germination of digested seeds and that of undigested seeds for all the trials combined (n = 460 p < 0.001).

Dates	No. of Seeds per Treatment	Percent Germination of Digested Seeds	Percent Germination of Undigested Seeds
7/18–9/1	200	0	18.5
7/29–9/12	100	0	52.0
7/29–9/12	100	1	13.0
7/29–9/12	60	0	33.3
Total:	460	0	26.5

plant species abundance and subsequent presence in the diet were not captured in this two-month study. Furthermore, this study was conducted solely along firelanes, and hence it may over-represent the food plants of tortoises that frequently feed near roads and firelanes, as opposed to tortoises that spend more time away from the road.

Of the two seed species with the greatest potential to be dispersed by the tortoise (owing to their being the most commonly ingested in this study), only *Paspalum setaceum*, a native grass, was found to germinate after passing through the gopher tortoise gut. *Paspalum notatum*, or bahiagrass, is an introduced species that is now widespread throughout the southern United States. This species is adapted to heavy grazing in neotropical grasslands and has been shown to survive and even have increased germination after being digested by cattle (Gardener et al., 1993). However, after passage through gopher tortoise guts, bahiagrass seeds did not germinate. These seeds may still be viable and may in fact have been induced to dormancy by gut passage, as in a palm species ingested by box turtles in the Florida Keys (Liu et al., 2003). Digestion by vertebrates can alter germination rates and timing of plant species, with some species having accelerated and (less commonly) delayed germination (Traveset, 1998; Traveset et al., 2001). Longer experiments are needed to determine the effects of gopher tortoise digestion on bahiagrass. In contrast, *Paspalum setaceum*, which is native in gopher tortoise habitats, appears to be adapted to survive the rigors of tortoise digestion and germinate shortly after this passage. Germination responses among congeneric plant species to the same herbivore species often are often inconsistent (Traveset, 1998), as was the case in this study.

Estimates of the home ranges and movements of *Gopherus polyphemus* (Auffenberg and Iverson, 1979; McRae et al., 1981; Smith et al., 1997), in combination with a 13 day average seed passage time (Bjorndal, 1987), make it possible to consider the general magnitude of the distances seeds may be moved by tortoises. McRae and others (1981) found the majority (95%) of tortoise feeding and daily activity to be within 30 meters of the burrow for most of the year. Movement between burrows is not uncommon, however, and may serve to occasionally increase the dispersal distance. A number of additional factors, such as the sex of the individual, time of year, local food resource quality (Smith et al., 1997) and the surrounding habitat (McRae et al., 1981) also may play a role in determining the

TABLE 4. Germination percentages of digested and undigested *Paspalum setaceum* seeds. Each of the three trials ran for 45 days and consisted of all of the *P. setaceum* seeds found in one scat plus an equal number of undigested conspecifics. The difference between the total percent germination of digested and undigested *P. setaceum* seeds was not significant (n = 110 p = 0.18).

Dates	No. of Seeds per Treatment	Percent Germination of Digested Seeds	Percent Germination of Undigested Seeds
6/28–8/12	50	20.0	2.0
7/12–8/26	36	5.6	47.2
7/18–9/1	24	0	4.2
Total:	110	10.9	17.3

distance a seed may be displaced from its parent. To date, spatial aspects of seed dispersal by gopher tortoises remain uninvestigated.

It is not unusual for a local organism to spread the seeds of an exotic plant over a wide area, as is the case with some exotic *Lonicera* species dispersed by birds in the eastern United States (Hutchinson and Vankat, 1998). Though this mode of invasion is not always considered, especially in cases involving non-avian species, the seed dispersing capabilities of birds, mammals or reptiles could be a serious hindrance to successfully excluding certain exotics from a natural habitat. In the case of *P. notatum* and gopher tortoises, however, the exotic seeds do not germinate after tortoise digestion. If tortoise-dispersed bahiagrass seeds are still viable, their germination appears delayed by passage through gopher tortoise guts. Effects of gopher tortoises on the demography of plants they disperse will require more study.

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REVIEW

Gary Mullen and Lance Durden, eds. *Medical and Veterinary Entomology.* Academic Press, San Diego, CA. 2002. xvi + 597 pp, clothbound, $99.95.

STUDENTS of medical and veterinary entomology in the United States have been without a modern, up-to-date textbook for almost twenty years. After a nine-year gestation, Messrs. Mullen and Durden have midwifed a remarkable volume. Like many births, the labor was long and difficult, but the child all the more precious and beautiful to behold. The book is a well-organized team effort. Twenty-five contributing authors submitted chapters in their areas of expertise. Over 100 other people served as reviewers, or supplied photographs, illustrations, or literature (the Acknowledgments run almost three pages). The book begins with a short Preface, in which the editors explain how and why the book was written and the format of each chapter (there are 24 chapters). The first two are an Introduction (Chapter 1), and a discussion of Epidemiology of Vector-Borne Diseases (Chapter 2). The Introduction gives the reader suggestions for background reading, a short history of medical-veterinary entomology, and briefly presents some related areas, such as forensic entomology, contamination of foodstuffs, and phobias. This chapter has one of the most extensive bibliographies, with 242 references. The second chapter, on epidemiology, covers transmission cycles of arthropod-borne pathogens, modes of transmission, interseasonal maintenance, vector incrimination, and surveillance.

Each of the remaining 22 chapters is devoted to a group of medically or veterinarily important arthropods. These chapters are organized in an identical manner: taxonomy, morphology, life history, behavior and ecology, public health importance, veterinary importance, prevention and control, and references and further reading all are taken in turn. New terms are introduced with italic type. For most chapters, the number of references given does not exceed 50. This is not due to paucity of information, but rather to the need to maintain the book at a reasonable length. With the exception of the Introduction, each chapter in this book could well merit its own volume of similar length.

The chapters are presented more or less in phylogenetic order of taxonomic group discussed, beginning with Cockroaches (Chapter 3), then covering Lice (Chapter 4), and True Bugs (Chapter 5). A surprise awaits the reader at Chapter 6. Beetles are usually given short shrift in medical entomology texts. Here they receive their own fourteen-page treatment. Chapter 7 is devoted to Fleas. The next ten chapters (8 to 17) are given to a detailed treatment of flies (Diptera). Chapter 8 is a general introduction to flies and some families of minor importance are presented. Chapters 9 to 17 then cover in detail one of the major groups of medically or veterinarily important Diptera, viz., Psychodidae (Chapter 9), Ceratopogonidae (Chapter 10), Simuliidae (Chapter 11), Culicidae (Chapter 12), Tabanidae (Chapter 13), Muscidae (Chapter 14), Glossinidae (Chapter 15), Oestroidea (Chapter 16), and Hippoboscoidea (Chapter 17). Another surprise is found at Chapter 18. This chapter thoroughly discusses the Lepidoptera of medical and veterinary importance. This is

another group that generally receives little attention in texts. Not only are the usual urticating caterpillars included, but also there is an excellent presentation of the lachryphagous (tear-feeding) and haematophagous moths of Southeast Asia. Ants, wasps, and bees (Hymenoptera) occupy Chapter 19.

Arachnids have five chapters devoted to them. Chapter 20 covers scorpions, Chapter 21 the solpugids, Chapter 22 covers spiders, Chapter 23 the mites, and Chapter 24 the ticks. This coverage of arachnid groups is unusual for a medical or veterinary entomology textbook. Treatment of arachnids comprises about 20% of the chapters and about 24% of the pages in this text. The chapter on mites is the longest of all. The book ends with taxonomic and subject indices.

This book includes some truly remarkable illustrations. I counted 424, many of them in color. Particularly fascinating are photos of the lachryphagous moths. The cover illustration, a photomicrograph of the spinose ear tick, is an excellent choice. The text is free of typographic errors, and the layout, with profuse illustrations, makes for easy reading. Current topics, such as West Nile virus and Lyme disease, are included in the appropriate chapters. A wealth of information is summarized in the many tables found throughout the text. My complaints about the book are few and trivial. One photograph in chapter 19 appears to be slightly out of focus. Chapter 21, on solpugids, is only two pages long and perhaps should have been combined with the chapter on scorpions. An author index (for literature cited) would have been a nice addition to the book.

The editors have produced a book that will serve not only students, but also professionals in several disciplines, indeed anyone who encounters arthropods of medical or veterinary importance in their work. *Medical and Veterinary Entomology* is without doubt the finest book available in English on the subject today. The last medical entomology textbook published in the United States went through seven editions and was in print for over sixty years. I am confident this new work will equal or exceed the old.—Lawrence J. Hribar, Florida Keys Mosquito Control District, Marathon, lhribar@keysmosquito.org.

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