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Author(s): Henry B. Floyd and Thomas A. Jenssen

Reviewed work(s):

Source: *Copeia*, Vol. 1983, No. 2 (May 6, 1983), pp. 319-331

Published by: [American Society of Ichthyologists and Herpetologists \(ASIH\)](http://www.asih.org/)

Stable URL: <http://www.jstor.org/stable/1444374>

Accessed: 13/01/2012 13:53

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## Food Habits of the Jamaican Lizard *Anolis opalinus*: Resource Partitioning and Seasonal Effects Examined

HENRY B. FLOYD AND THOMAS A. JENSSEN

A stomach analysis of 340 lizards collected in 33 samples over a 12 month period showed that *Anolis opalinus* eats arthropods, primarily ants by number (70%). By volume, however, ants comprised only 12% of the food bulk, with lepidopteran larvae and orthopterans being the main food items (46%). The lizards fed predominantly on soft bodied prey, except for ants.

We found almost no evidence for food niche partitioning in the size dimorphic *A. opalinus*. All age and sex classes of lizards had eaten similar sized prey and prey taxa. When a significant difference was detected among classes, it was frequently the smaller lizards which had eaten the larger prey. In fact, season had more effect on diversifying the diet than did size of the lizards' trophic structures (i.e., mouths) or any possible feeding preferences. Niche overlap indices for prey length (0.86-0.94) and prey taxa (0.82-0.93) among all age-sex classes ran higher than those reported for a mainland anole with almost no sexual size dimorphism.

Comparison of variables between the seasons (dry—Nov.—Mar., wet—April—Oct.) showed that lizards tended to ingest about the same volume of food (approx. 17 mm<sup>3</sup> of food/g of lizard body wt). However, lizards ate more, but smaller prey in the dry season and fewer, but larger prey in the wet season. Relative fat body and liver weights were highest in the dry season and lowest in the wet season. Adult males and especially adult females experienced the greatest weight loss in these energy reserve organs; this was attributed in part to breeding activities. Coefficient of condition calculations (body wt/SVL) showed no body weight loss between seasons for any age-sex class of lizards. For the population, the volume of food taken across seasons appeared sufficient to increase energy reserves during the dry season and maintain body weight during the wet season.

**B**ECAUSE of their high visibility, abundance and extensive ecological radiation, *Anolis* lizards have attracted much attention from ecologists. From a plethora of anoline studies has emerged a body of commonly accepted ecological generalizations. However, there still remains some question as to how widely these generalizations apply outside the specific conditions in which they were originally conceived. A primary goal of our investigation was to test some of the current hypotheses regarding food resource utilization.

Most of the documentation of food niche partitioning has come from studies of anoles on the relatively small Lesser Antillean islands (Andrews, 1979; Schoener, 1967; Schoener and Gorman, 1968). These islands are characterized by high density, simple anole communities (1 or 2 species) and depauperate faunas of potential anoline competitors and predators (Andrews, 1979; Schoener and Schoener, 1978; Wright,

1981). On such islands, the competition experienced by anoles is perceived as intense and largely intrageneric, with the lizards being food limited. In contrast, studies of food habits of anoles on the Central American mainland have not found evidence for food niche partitioning, implying that competition for food is relatively unimportant in these ecologically complex communities (Andrews, 1971, 1976, 1979; Fitch, 1972; Fleming and Hooker, 1975; Sexton et al., 1972). Thus, a strong ecological dichotomy between island and mainland anoles has been suggested based on relatively few studies within a restricted and distinctly divergent set of faunas.

Our study examines *Anolis opalinus*, one of seven species of anoles on the Greater Antillean island of Jamaica. This is an abundant species, with many congeneric competitors, residing in a habitat intermediate between the small island and mainland paradigms. Our data provide the opportunity to: 1) determine the pattern of food

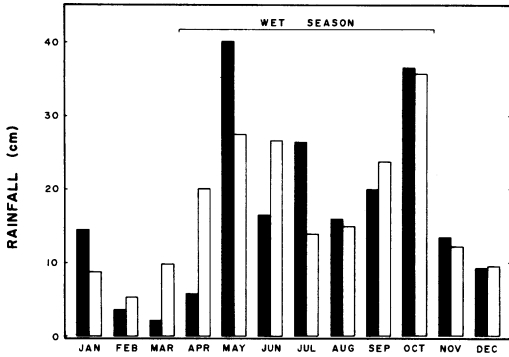


Fig. 1. Annual distribution of rainfall in Mandeville, Jamaica, during year of collection (black bars) and ten year average, 1961-1970 (white bars).

niche partitioning in an intermediate landmass species; 2) examine measured variables for possible food limitation; and 3) look at, for the first time, the effects of seasonality upon the diet of an insular anole.

#### MATERIALS AND METHODS

*Subject.*—*Anolis opalinus* is the smallest and most widely distributed of the seven *Anolis* species on Jamaica. It occurs over the entire island from sea level to elevations above 1,525 m (Underwood and Williams, 1959), and is found in a wide variety of microhabitats. Working near Kingston, Rand (1967a) and Schoener and Schoener (1971a) found *A. opalinus* to be a "trunk-crown" species which occurs in the shaded portions of bushy or forested areas, infrequently perching below 1.5 m. At other localities on the island, *A. opalinus* occupies more open sites (Schoener and Schoener, 1971a), and frequently perches below 1.5 m (Jenssen, 1973). Even in the Kingston area, *A. opalinus* shows significant habitat flexibility by perching high in the presence of a competitor, *Anolis lineatopus*, and low in its absence (Jenssen, 1973).

*Site.*—Mandeville, Manchester Parish, Jamaica was the collection site. The town is located on a plateau (elev. 690 m) in the central part of the island, and is characterized by relatively constant daylength, temperature and humidity, and a seasonally defined rainfall pattern (Fig. 1). With the exception of daylength, weather data were recorded daily during the year of collection (April, 1970–March, 1971) by the junior author and Robert Sutton (a Mandeville

resident), using rain gauges and max-min thermometers at two localities in Mandeville and a hygrothermograph at a single Mandeville site. Daylength varied only about two hours throughout the annual cycle (Licht and Gorman, 1970); maximum monthly temperatures varied about 4.5 C (27.5–32 C), with monthly minima ranging from 11 C to 17 C; and the mean monthly humidity fluctuated between 62% RH in April to 80% RH in Sept.

Of the recorded climatic variables, only rainfall showed noteworthy seasonal differences. Rainfall in Jamaica divides the year into dry and wet seasons (Fig. 1). Mann-Whitney U tests (Siegel, 1956) showed that rainfall was significantly higher ( $P < 0.01$ ) in the described wet season than in the dry season, and that rainfall in May and Oct. was significantly higher ( $P < 0.05$ ) than the remainder of the wet season. These same trends were true of a 10 year (1961–1970) Mandeville record (Robert Sutton, pers. comm.). The monthly rainfall in the year of collection correlated well with the average monthly rainfall measured over Sutton's 10 year record ( $r = 0.74$ ), with the total annual rainfall on the collection site (203.5 cm) being very similar to the annual ten year average (208.8 cm).

*Collections.*—Food habit data were obtained from 340 lizards collected in 33 samples (approx. three samples/month) by the junior author. Lizards were killed within an hour of capture using chloroform. An individual identification number (marked by toe clipping), body weight (to nearest 0.01 g), snout-vent length (SVL), total length, collection site and date of capture were recorded for each animal. The lizards were fixed with 10% formalin, and 24 h later washed in water and stored in 70% ethanol.

Specimens were divided into four age and sex classes: 1) adult males (45–53 mm SVL,  $N = 101$ ,  $\bar{x} = 48.33 \pm SE 0.19$  mm), 2) adult females (37–44 mm SVL,  $N = 148$ ,  $\bar{x} = 40.42 \pm SE 0.16$  mm), 3) subadult males 37–44 mm SVL,  $N = 45$ ,  $\bar{x} = 40.84 \pm SE 0.38$  mm) and 4) juvenile male and females (<37 mm SVL,  $N = 46$ ,  $\bar{x} = 33.11 \pm SE 0.39$  mm). The criteria for establishing these age and sex classes are as follows.

Adult males were determined by physiological and behavioral evidence. Some *A. opalinus* males exhibited spermatogenesis at 36 mm SVL, and at 40 mm SVL about half of the males were producing sperm. It was only when males were 45 mm SVL or larger that they were all reproductively mature and had the body size to de-

TABLE 1. TAXONOMIC DISTRIBUTION OF STOMACH CONTENTS BY PERCENT FREQUENCY OF OCCURRENCE AND PERCENT VOLUME FOR 141 *Anolis opalinus* IN THE DRY SEASON AND 199 IN THE WET SEASON.

Prey type	% Number			Prey type	% Volume		
	Dry*	Wet**	Overall		Dry*	Wet**	Overall
H. Formicidae	71.1	68.0	69.5	Lepidoptera (larvae)	44.5	21.7	32.7
Hemiptera	4.5	3.0	3.7	Orthoptera	5.0	21.5	13.5
Diptera	4.3	3.5	3.9	H. Formicidae	9.4	14.8	12.2
Coleoptera	3.4	4.7	4.1	Lepidoptera	9.0	9.6	9.3
Homoptera	3.4	2.1	2.7	Diptera	6.7	2.8	4.7
Lepidoptera (larvae)	2.8	1.8	2.3	Hemiptera	6.5	8.3	7.5
Araneida	2.5	2.1	2.3	Homoptera	3.8	2.6	3.2
Hymenoptera	2.0	8.4	5.3	Araneida	3.7	6.2	5.0
Homoptera (nymph)	2.0	1.6	1.8	Reptilia	3.2	—	1.5
Acarina	0.8	0.5	0.6	Coleoptera	3.2	6.9	5.1
Lepidoptera	0.7	0.7	0.7	Diptera (larvae)	1.8	0.1	0.9
Coleoptera (larvae)	0.3	0.2	0.3	Isopoda	1.2	1.5	1.3
Collembola	0.3	0.2	0.2	Coleoptera (larvae)	0.5	trace	0.3
Thysanoptera	0.3	0.1	0.2	Hymenoptera	0.5	2.9	1.8
Diptera (larvae)	0.3	0.0	0.1	Gastropoda	0.4	0.3	0.3
Pseudoscorpionidae	0.2	0.5	0.4	Homoptera (nymph)	0.3	0.3	0.3
Gastropoda	0.2	0.2	0.2	Acarina	0.1	0.1	0.1
Orthoptera	0.2	0.5	0.4	Hemiptera (nymph)	0.1	trace	trace
Psocoptera	0.2	1.2	0.7	Pseudoscorpionidae	trace	0.1	0.1
Hemiptera (nymph)	0.2	trace	0.1	Psocoptera	trace	0.2	0.1
Isopoda	0.2	0.4	0.3	Thysanoptera	trace	trace	trace
Insect eggs	trace	0.2	0.1	Collembola	trace	trace	trace
Reptilia	trace	trace	trace	Insect eggs	trace	trace	trace
Total	99.9	99.9	99.9		99.9	99.9	99.9

\* Based on 2,777 prey items.

\*\* Based on 2,924 prey items.

fend territories in order to participate in reproduction (Jenssen, unpubl. data).

Adult females were determined by presence of oviductal eggs. Only 7% of females smaller than 37 mm SVL were gravid. For size classes of 37 mm SVL and larger, the percentage of gravid females ranged from 61–85%.

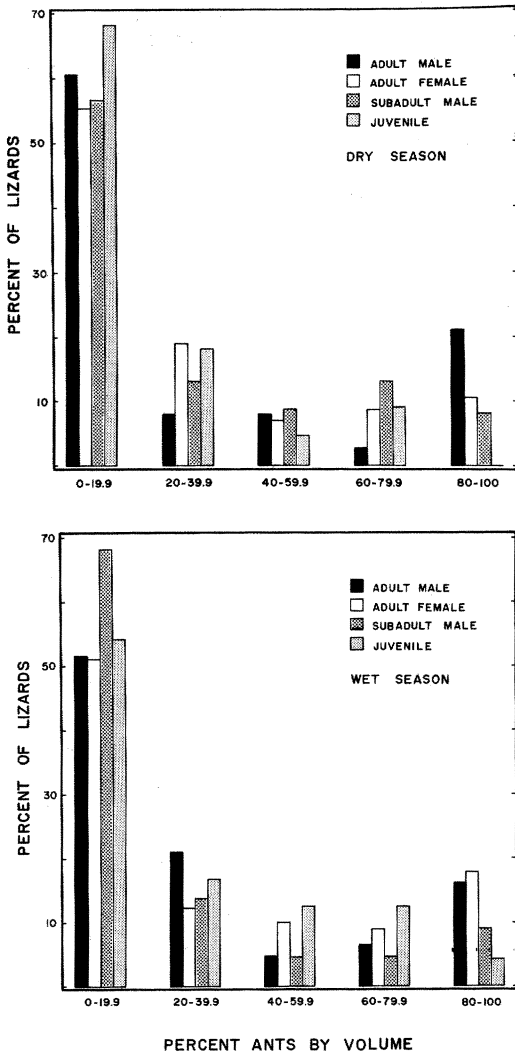
Subadult males matched the SVL range of the adult female class (37–44 mm). These subadult males were in varying states of sexual maturity, whereas no males smaller than 37 mm SVL exhibited spermatogenesis.

Juveniles were composed solely of nonreproductive males and females, all being smaller than 37 mm SVL.

*Data collection and analysis.*—The head length and head width of 12 lizards from each class (whose SVL's were within a millimeter of their class mean) were measured according to the procedure of Schoener (1968) to compare trophic structure size with body size (SVL) and lengths of ingested prey.

The entire digestive tract, fat bodies, liver, kidneys and reproductive tract were removed from each lizard and placed in vials of 70% ethanol along with the lizard's identification number. The liver and fat bodies were blotted of excess ethanol and weighed to the nearest 0.1 mg on a Mettler balance; these weights are relative because some fats are alcohol soluble. The gastrointestinal tract was divided into four sections: stomach, first and second halves of the small intestine, and the large intestine. Each section was separately analyzed for its food contents. However, only the stomach contents formed the basis for the dietary analysis.

Individual prey items (almost exclusively arthropods) were identified to order using Borror and DeLong (1954), their length, width and depth were measured with an ocular micrometer, and their volumes were estimated by multiplying prey length × width × depth. Each prey item was separated according to its outward appearance ("morpho-species"), and then isolated in a separate vial for future reference. When the



Figs. 2, 3. Comparison of dry season data, relating percent of lizards within an age-sex class to percent volume of their stomach contents composed of ants. Sample sizes are: (2) adult male, 38; adult female, 58; subadult male, 23; and juvenile, 22; (3) adult male, 62; adult female, 90; subadult male, 22; and juvenile, 24.

same morph-species was encountered again, measurements of the previously isolated individual were used. Different castes of the same species of ant were considered separate morpho-species.

Prey items were assigned to one of eight size classes. Since most food items of *A. opalinus* were less than 5 mm in length, prey size categories were established in 1 mm increments up to 5

mm; categories for prey items 6 mm and larger were established in 5 mm increments (e.g., 6-10, 11-15 and 16-20 mm).

All data were keypunched on IBM cards and then transcribed to the direct access discs of an IBM 370 computer. Programmed packages of the Statistical Analysis System (Barr et al., 1976, 1979) and of Biomedical Computer Programs (Dixon, 1975) were used for much of the analysis. Parametric tests (Sokal and Rohlf, 1969) were applied to normally distributed data and nonparametric tests (Siegel, 1956) were employed when the data were not normally distributed.

#### GENERAL DIET

Ninety-nine percent of the food items found in the stomachs of 340 lizards were arthropods, with over 90% being from one of six orders (Hymenoptera, Coleoptera, Diptera, Hemiptera, Lepidoptera and Araneida) (Table 1). Besides invertebrates, cast skins of the lizards (eaten during shedding) were the next most common item, appearing in 6% of the stomachs. Of rare appearance were items apparently ingested accidentally (dirt, pebbles, fecal pellets and bits of vegetation). Only 6% of the lizards had empty stomachs, and only two lizards had empty digestive tracts. The only vertebrate prey item found was a hatchling *Anolis valencienni* in the stomach of an adult male, indicating that *A. opalinus* is a potential predator on young anoles.

Ants (Formicidae) comprised about 70% of all captured food items in both the wet and dry seasons (Table 1). If the prey taxa are ranked according to frequency of appearance, *A. opalinus* might appear to be myrmecophagous. However, this is not reflected by a volumetric comparison of these taxonomic categories as ants only accounted for approximately 12% of the diet (Table 1).

*Formicidae*.—Ants occurred at high frequency in the *opalinus* diet. All but two lizards had fed on ants. The dry season lizards averaged 14 ants/stomach, while those from the wet season averaged 10/stomach. Approximately 80% of the captured ants were of the Myrmicinae; the most common was *Wasmannia auropunctata* (Roger), a small (1.3 mm) species which comprised 46% of the ants found in the stomachs. Ants, therefore, represented small individual food items, 98% of which were  $\leq 3$  mm in length.

Even though ants were numerically dominant

to all other taxa, they constituted less than 20% of the diet biomass in more than half the lizards sampled in either season (Figs. 2, 3). Those lizards (45) in which ants composed 80% or more of their stomach content volumes had eaten significantly less than other lizards (295) (mean prey volumes = 10.6 mm<sup>3</sup> vs 31.4 mm<sup>3</sup>; Mann-Whitney U test,  $P < 0.001$ ). Thus, lizards feeding solely on ants were not filling their stomachs with this prey.

Another way of evaluating the importance of ants as a food source is to calculate the volume of prey acquired per prey capture. Ants averaged only 0.28 mm<sup>3</sup>/item; 17 of the 23 taxonomic categories yielded greater mean volumes per capture than ants (Table 2). In terms of volume, 200 ants were equivalent to one adult orthopteran, and 86 ants were equal to one lepidopteran larva. Because each ant provides such a small volume intake for a lizard, it appears that high availability and ease of capture are primary factors influencing the lizards' choice of food.

*Prey quality.*—Although no direct study was made of prey digestibility, the condition of intestinal contents indicated that some food items were more readily digested than others. For example, only the head capsules of lepidopteran larvae remained intact after passing into the small intestine. In contrast, whole exoskeletons of ants and coleopteran adults were commonly found in the large intestine. Those prey orpho-species which appeared to have a high proportion of indigestible material to volume (e.g., coleopterans, hymenopterans, hemipterans, acarines and gastropods) were designated hard bodied. Conversely, those morpho-species with a small proportion of indigestible body parts (e.g., lepidopterans, orthopterans, dipterans, araneids and homopterans) were designated soft bodied.

By volume, lizards tended to eat soft bodied prey; this food comprised 57–81% of the diet, depending on season and lizard class (Table 3). The large number of ingested ants, however, skewed the numbers of prey taken by all lizard classes toward hard bodied food (60–85%). If the ants are excluded, soft bodied prey predominated numerically as well as volumetrically.

#### FOOD RESOURCE PARTITIONING

*Trophic structure and prey length.*—*Anolis opalinus* exhibits size dimorphism for mean head length,

TABLE 2. MEAN VOLUME OF INGESTED PREY TAXA AND THEIR VOLUMETRIC RELATIONSHIP TO MEAN ANT VOLUME, EXPRESSED AS A RATIO OF MEAN ANT VOLUME/MEAN PREY VOLUME (MAV/MPV).

Prey type	Mean prey volume (mm <sup>3</sup> )	MAV/MPV
Lepidoptera (larvae)	22.85	0.012
Orthoptera	55.98	0.005
H. Formicidae	0.28	
Lepidoptera	21.79	0.013
Hemiptera	3.20	0.087
Coleoptera	2.01	0.139
Araneida	3.53	0.079
Diptera	1.91	0.146
Homoptera	2.82	0.099
Hymenoptera	0.53	0.527
Reptilia	140.88	0.002
Isopoda	6.74	0.041
Diptera (larvae)	10.57	0.026
Gastropoda	2.36	0.119
Homoptera (nymph)	0.25	1.142
Coleoptera (larvae)	1.59	0.176
Psocoptera	0.22	1.258
Acarina	0.22	1.266
Pseudoscorpionidae	0.28	0.997
Insect eggs	0.37	0.753
Hemiptera (nymph)	0.37	0.763
Collembola	0.09	3.278
Thysanoptera	0.07	3.732

head width and snout-vent length. These measurements were approximately 1.2 times greater for adult males than for adult females and subadult males, and 1.2 times greater for the last two classes than for juveniles (Fig. 4). Thus, larger lizards had larger trophic structures (i.e., mouths). This condition predicts that the large-mouthed lizards should take large-size prey.

Comparisons of prey size distributions, however, did not indicate substantial resource partitioning during either season (Figs. 5, 6). Kolmogorov-Smirnov two-tailed tests showed that during the wet season adult females ate significantly larger prey than did either adult males ( $P < 0.001$ ) or subadult males ( $P < 0.05$ ); even juveniles ate significantly larger prey than adult males ( $P < 0.025$ ) during this period. The only other significant comparisons showed juveniles eating smaller food items in the dry season than any other age-sex class ( $P_s < 0.05$ ). The exclusion of ants from the analysis did not change the above results.

*Niche overlap.*—Evidence of resource partition-

TABLE 3. PERCENTAGES OF PREY CAPTURES AND PREY VOLUMES FOR HARD- AND SOFT-BODIED PREY TAKEN DURING THE DRY AND WET SEASONS BY LIZARDS OF AN AGE-SEX CLASS.

Data set	Class	Prey kind	% Number		% Volume	
			Dry	Wet	Dry	Wet
Stomach contents with ants	Adult males	Soft	14.96	16.73	74.96	69.49
		Hard	85.04	83.27	25.04	30.51
	Adult females	Soft	21.54	25.91	78.98	66.33
		Hard	78.46	74.09	21.02	33.67
	Subadult males	Soft	16.48	25.89	78.80	81.04
		Hard	83.52	74.11	21.20	18.96
	Juveniles	Soft	27.16	37.44	75.32	57.54
		Hard	72.84	62.56	24.68	42.46
Stomach contents without ants	Adult males	Soft	70.92	67.06	81.16	79.36
		Hard	29.08	32.94	18.84	20.64
	Adult females	Soft	70.37	76.42	89.58	83.19
		Hard	29.63	23.58	10.42	16.81
	Subadult males	Soft	54.74	68.23	86.98	85.64
		Hard	45.26	31.77	13.02	14.36
	Juveniles	Soft	76.39	82.52	82.12	74.87
		Hard	23.61	17.48	17.88	25.13

ing can be demonstrated from the amount of overlap for a niche dimension shared by two or more groups. The less the overlap, the greater is the degree of partitioning. Overlap was calculated from an index used by Schoener (1968),

$$D = 1 - \frac{1}{2} \sum_{i=1}^n |P_{x,i} - P_{y,i}|,$$

where  $P_{x,i}$  and  $P_{y,i}$  are frequencies for classes  $x$  and  $y$ , respectively, for the  $i$ th category. The index,  $D$ , ranges from zero (no overlap) to one (complete overlap). Two data sets were used: frequencies of occurrence for prey "size" (length) and frequencies of occurrence for prey "taxa" (morpho-species). These two data sets were also analyzed with ants deleted.

The overlap indices were all greater than 0.7 for the various age-sex class comparisons, with most being over 0.85 (Table 4). All overlap values for prey size were extremely high, with the greatest overlaps for the year being between adult males and adult females (0.94), between adult males and subadult males (0.94), and between subadult males and juveniles (0.94). The lizards were not only eating prey of about the same size, but they were also eating nearly the same food taxa; the smallest seasonal overlap values for prey taxa were found among adult males and juveniles (0.81—dry season, 0.73—wet season).

Because ants were consistently small and numerically dominant in both data sets, the resulting overlap indices were somewhat biased toward high overlap values. When ants were deleted, corresponding  $D$  values dropped 0.02–0.20 in magnitude across prey size and taxa comparisons (Table 4). The lowest seasonal overlap values were generally between adult males and juveniles for both prey size (0.68—dry season, 0.70—wet season) and taxa (0.62—dry season, 0.59—wet season).

A fact to be emphasized is that overlap indices derived across seasons within lizard classes tended to be smaller than those resulting from comparisons among lizard classes within any season (Table 5). Therefore, season had more apparent influence upon diversifying the diet than did size of trophic structure or any possible feeding preferences.

*Ant utilization.*—Although ants were the most frequently eaten taxon for all classes of lizards, both adult classes ate significantly more ants ( $2 \times 2$ :  $\chi^2$  contingency tables,  $P < 0.05$ ) than did juveniles in the wet season, and adult males ate significantly more ants ( $P < 0.05$ ) than all other classes during both seasons. The largest lizards most heavily utilized some of the smallest morpho-species food items.

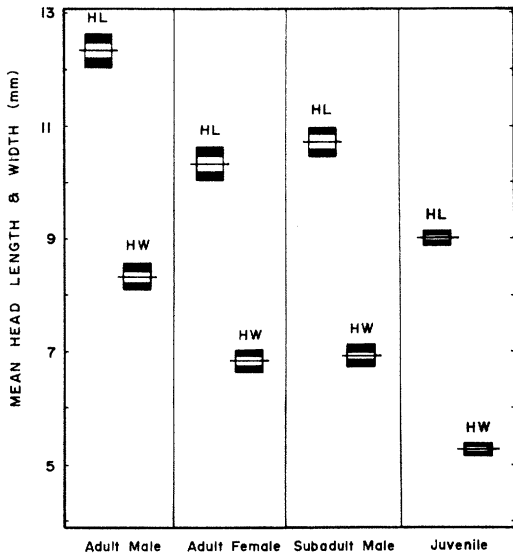


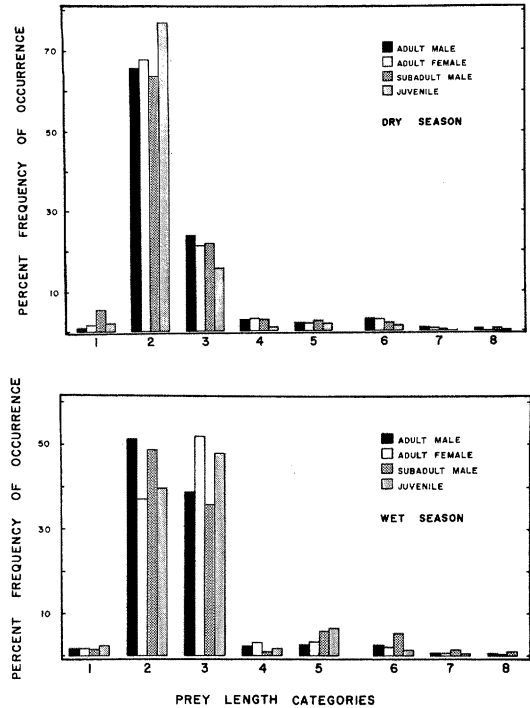
Fig. 4. Mean head length (HL) and head width (HW) for age-sex classes of *Anolis opalinus*. Horizontal line indicates mean value, outer ends of white bars indicate standard error of the mean, and outer ends of black bars are 95% confidence limits of the mean.

SEASONAL EFFECTS

*Prey taxa (frequency and volume).*—Numerically, ants dominated the diets of all classes of lizards during both seasons. Comparisons showed no significant differences ( $2 \times 2$ :  $\chi^2$  contingency table test) in the number of ants eaten between seasons for both adult classes of lizards. However, the subadult males and juveniles ate significantly more ants ( $P < 0.05$ ) in the dry season than in the wet.

Using volumetric data, lepidopteran larvae contributed heavily (44%) to *A. opalinus* diet in the dry season and less so (22%) in the wet season (Table 1). Orthopterans, primarily grasshoppers, made up most of the volumetric difference when the lizards were eating fewer caterpillars in the wet season; orthopteran prey shifted from 5% in the dry season to 22% of volume intake during the wet. Lepidopterans and orthopterans were the principle prey items contributing to the food volume. Ants, the third most important contributor to dietary biomass (9–15%), remained relatively constant between seasons.

*Prey size (frequency and volume).*—Frequency of occurrence comparisons of prey lengths be-



Figs. 5, 6. Percent frequency of occurrence for eight prey length categories (1–5 in 1 mm increments; 6–8 in 5 mm increments) in the dry season. Sample sizes are: (5) adult male, 682; adult female, 1,235; subadult male, 455; and juvenile, 405; (6) adult male, 1,022; adult female, 1,451; subadult male, 224; and juvenile, 227.

tween seasons showed that all classes of lizards ate significantly larger prey items in the wet season when compared with the dry (Kolmogorov-Smirnov two-tailed test,  $P < 0.001$ ) (Figs. 5, 6). This is also reflected in the low overlap values for prey size when comparing within each lizard class among seasons (Table 5).

The seasonal shift to larger prey size in the wet season was offset by a concomitant decrease in the average prey number/stomach. This decrease between the dry and wet seasons, respectively, was 17.9–16.5 for adult males, 21.3–16.1 for adult females, 19.8–10.2 for subadult males, and 18.4–9.5 for juveniles. The actual volume of food taken, however, remained relatively constant across seasons (Figs. 7, 8). The Wilcoxon rank-sums test (SAS, Barr et al., 1979) indicated no significant differences in prey volume intake between seasons for each class of lizards. Even when using the more powerful discriminant analysis (BMDP, Dixon, 1975) on



TABLE 4. OVERLAP INDICES FOR PREY SIZE AND PREY TAXA AMONG THE AGE-SEX CLASSES OF *Anolis opalinus* IN BOTH DRY AND WET SEASONS.

Data set	Overlap pair	Prey size			Prey taxa		
		Dry	Wet	Overall	Dry	Wet	Overall
Stomach contents with ants	Ad. male—Ad. female	0.967	0.850	0.935	0.874	0.867	0.881
	Ad. male—Subad. male	0.946	0.927	0.935	0.882	0.841	0.883
	Ad. male—Juvenile	0.874	0.861	0.914	0.806	0.729	0.818
	Ad. female—Subad. male	0.946	0.812	0.877	0.936	0.893	0.934
	Ad. female—Juvenile	0.904	0.934	0.862	0.879	0.841	0.886
	Subad. male—Juvenile	0.867	0.851	0.943	0.848	0.817	0.845
Stomach contents without ants	Ad. male—Ad. female	0.840	0.829	0.919	0.722	0.720	0.781
	Ad. male—Subad. male	0.820	0.765	0.902	0.737	0.828	0.801
	Ad. male—Juvenile	0.676	0.700	0.849	0.621	0.590	0.693
	Ad. female—Subad. male	0.824	0.873	0.862	0.795	0.772	0.797
	Ad. female—Juvenile	0.835	0.842	0.910	0.725	0.767	0.781
	Subad. male—Juvenile	0.718	0.815	0.807	0.617	0.647	0.645

these comparisons, there were no significant differences between seasons for three lizard classes; only juveniles showed a significant ( $P < 0.01$ ) decrease from 18.6 mm<sup>3</sup> in the dry season to 10.1 mm<sup>3</sup> in the wet season. In addition, the discriminant analysis found no significance when comparing volume intake between lizard classes of any season.

In summary, lizards were eating more but smaller prey in the dry season, and fewer but larger prey in the wet season. These two counter-balancing trends produced a constant volume of food intake that was independent of season, age-sex class, and body size.

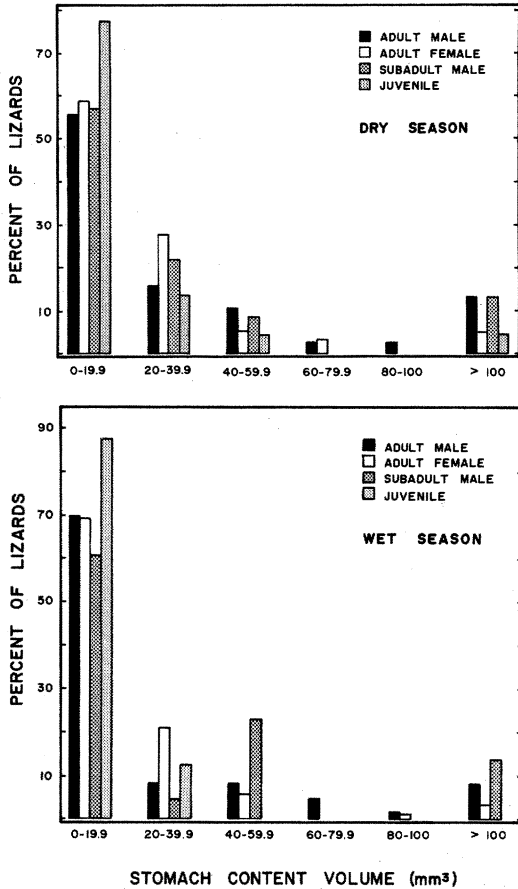
*Organ weight cycling.*—The fat bodies and liver are recognized organs of lipid and glycogen storage. After adjusting for each lizard's size (organ weight/body weight), relative fat body and liver weights were compared across seasons by class of lizard. The resulting fat body and liver ratios were largest in the dry season for all classes of lizards (Fig. 9).

Discriminant analysis (BMDP, Dixon, 1975) disclosed significantly greater dry season fat body ratios ( $P < 0.01$ ) for both adult sexes than their corresponding wet season values. For adult males, this dry season value was 2.9 times as great as that from the wet, and for adult females there was an even more dramatic seasonal differential, with the mean fat body ratio being 9.3 times as large in the dry as in the wet season. In contrast, subadult male and juvenile values did not fluctuate significantly between seasons (Fig. 9).

The adult females withdrew a larger percentage (89%) of their lipid reserves during the wet season than any of the lizard classes. In fact, 90% of adult females from the wet season sample had negligible to no fat bodies. Since all wet season females were gravid, this seasonal effect was expected in light of lipid demand for egg production (Gorman and Licht, 1974; Hahn and Tinkle, 1965; Licht and Gorman, 1970). To reinforce this interpretation, the reproductive conditions of adult females from the dry season

TABLE 5. OVERLAP INDICES FOR PREY SIZE AND PREY TAXA AMONG SEASONS FOR EACH AGE-SEX CLASS OF *Anolis opalinus*.

Data set	Overlap pair	Adult male		Adult female		Subadult male		Juvenile		All lizards	
		Prey size	Prey taxa	Prey size	Prey taxa	Prey size	Prey taxa	Prey size	Prey taxa	Prey size	Prey taxa
Stomach contents with ants	Dry—wet	0.839	0.918	0.680	0.881	0.788	0.887	0.624	0.755	0.741	0.904
Stomach contents without ants	Dry—wet	0.882	0.749	0.794	0.684	0.686	0.755	0.565	0.540	0.817	0.721



Figs. 7, 8. Comparison of dry season data, relating percent of lizards within an age-sex class to stomach content volume. Sample sizes are the same as Figs. 2 and 3.

were also examined; 62% contained oviductal eggs. These gravid females had significantly smaller ( $P < 0.05$ ) fat body ratios than non-gravid adult females (1.76 vs 4.25), indicating lipid utilization correlated with egg production and not with season alone.

The liver ratios followed the same seasonal trend as the fat body ratios. Discriminant analysis found adult males ( $P < 0.01$ ), adult females ( $P < 0.01$ ), and subadult males ( $P < 0.05$ ) had significantly lower liver ratios in the wet season as compared with their corresponding class values from the dry season.

COEFFICIENT OF CONDITION

Lipid and glycogen reserves were apparently reduced to the greatest extent during the wet

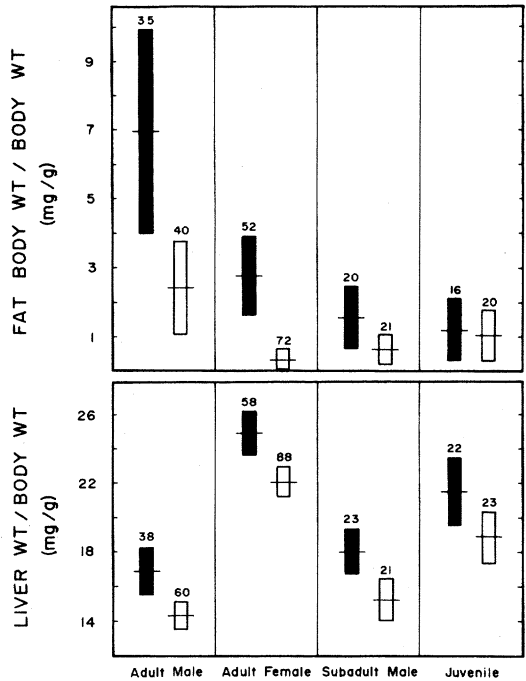


Fig. 9. Mean fat body weight/body weight and liver weight/body weight ratios for lizards of an age-sex class during the dry season (black bars) and the wet season (white bars). Horizontal line indicates mean ratio and outer ends of bars are 95% confidence limits of the mean. Sample sizes are shown above bars.

season, earmarking this as a period of high energetic demand. Should food intake not meet the energetic output of this season, the lizards could experience general protein catabolism and weight loss. To check for this, we calculated the coefficient of condition (body weight/SVL) for each lizard. The results showed no seasonal effect on relative stoutness for any class of lizard (Fig. 10). Given the relatively constant volume of food intake across seasons, the population reflected no severe food limitation for any particular season. These and other factors examined for seasonality are summarized in Table 6.

DISCUSSION

*General diet.*—The *A. opalinus* food habits data generally agreed with the findings of studies on other comparably sized anoles. Insular congeners typically take small prey, particularly ants (Andrews, 1979). Island anoles, however, can be divided into two groups on the basis of ant

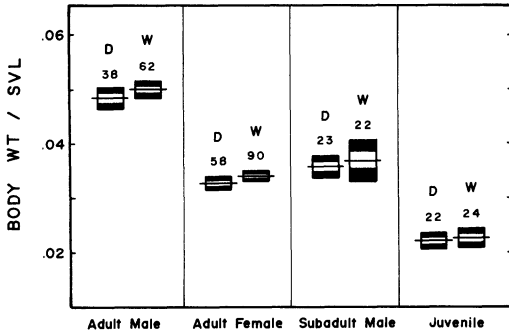


Fig. 10. Coefficients of condition (body weight / SVL) for lizards of an age-sex class during the dry season (D) and the wet season (W). Horizontal line indicates mean coefficient, outer ends of white bars indicate standard error of the mean, and outer ends of black bars are 95% confidence limits of the mean. Sample sizes are shown above bars.

utilization. One group, composed of *A. distichus* (Schoener, 1968), *A. roquet* (Schoener and Gorman, 1968), and *A. oculatus* (Andrews, 1976, 1979), appears to be myrmecophagous because ants comprise the majority of their food by both frequency of occurrence and volume. For the second group, *A. opalinus* (present study), *A. conspersus* (Schoener, 1967), *A. sagrei* (Schoener, 1968) and *A. aeneus* (Schoener and Gorman, 1968), ants are not a large proportion of their prey biomass even though ants are frequently eaten. This last group of anoles seems to be facultative ant eaters. *A. opalinus* appears to use ants as a readily available food substitute in the temporary absence of larger soft bodied arthropods.

*Food niche partitioning.*—Current theory (Schoe-

ner, 1974) predicts that insular anoles are likely to decrease intraspecific competition for food in two ways. First, intraspecific age and sex classes have been shown to partition their structural habitat by choosing perches of different height and thickness (Rand, 1964; Schoener, 1967, 1968; Schoener and Schoener, 1971a, b). This provides each class of lizard with a somewhat different microhabitat within which to forage. Second, it is hypothesized that sexual dimorphism in body size has evolved to decrease overlap in prey size utilization among intraspecific age and sex classes (Andrews, 1979; Rand, 1967b; Schoener, 1967, 1968; Schoener and Gorman, 1968; but also see Trivers, 1976). Evidence for these partitioning methods by *A. opalinus* are examined below.

In Mandeville, *A. opalinus* rarely perched above 2 m and there was no significant difference in perch height and perch diameter between the sexes, although adult males did tend to occupy the higher and larger diameter perches (Jenssen, 1973). Any spatial separation which might occur among lizard classes is further minimized if Andrews' (1971) observations of *A. polylepis* can be extrapolated to *A. opalinus*. She found that the points at which prey captures were made overlapped more among intraspecific classes than their corresponding perch height data. Therefore, the available information on *A. opalinus* does not indicate that structural habitat partitioning is a significant factor promoting decreased intraspecific competition for food.

The moderate sexual dimorphism in size exhibited by *A. opalinus* suggests that this may be morphological evidence that the species is partitioning food resources by prey size. However, the food habit data do not support this theo-

TABLE 6. SUMMARY OF SEASONAL EFFECTS ON NINE VARIABLES RELATED TO THE FOOD HABITS OF *Anolis opalinus*.

Variable	Dry season	Wet season
Principle food by volume	Lepidopteran larvae	Orthopterans
Ant utilization	Constant	Constant
Prey number	High	Low
Prey size	Small	Large
Prey volume	Constant	Constant
Fat body weight/body weight	High	Low
Liver weight/body weight	High	Low
Reproductive activity	Low	High
Body weight/SVL	Constant	Constant

retical construct. Adult males, adult females, and subadult males ate similar sized prey in the dry season, and adult females and juveniles ate larger prey than adult males in the wet season (Figs. 5, 6). Measurements of overlap (D) for prey length and prey taxa indicated a high degree of dietary similarity for all age and sex classes (Table 4). In fact, there was more diet diversity within a class when comparing across seasons than between classes within a season (Table 5). Our data showed little relationship between prey size and predator size within *A. opalinus*.

Prey length overlap values for the adult *A. opalinus* sexes were compared with similar data taken by Fleming and Hooker (1975) for the mainland *Anolis cupreus*. This latter anole has a low sexual dimorphism ratio for body size (1.07), with no evidence of food niche partitioning among its age and sex classes (Fleming and Hooker, 1975). Overlap values for prey length among the adult sexes were evaluated as high (0.70—dry season, 0.81—wet season). Analogous overlap values for *A. opalinus* were even greater, being 0.97 and 0.85 for the dry and wet seasons, respectively. Deleting ants from the *A. opalinus* data to make a very conservative comparison still produced greater prey length overlap for *A. opalinus* (0.84—dry season, 0.83—wet season) than for *A. cupreus*. For *A. opalinus*, then, our data do not support the hypothesis that sexual dimorphism in body size is functioning to reduce intraspecific competition for food.

A comparison of *A. opalinus* adult males with conspecific juveniles further emphasizes the absence of apparent food resource partitioning. These two classes had the most divergent perch habits (Jenssen, 1973; Schoener and Schoener, 1971a) and trophic structure dimensions. The adult male: juvenile head width and head length ratios were 1.57 and 1.37, respectively; the head length ratio approaches the median head length ratios for adult sexes of solitary species on small islands (Schoener, 1977). Nevertheless, adult male and juvenile *A. opalinus* overlapped extensively in size of prey and taxa (0.91 and 0.82, respectively). In fact, juveniles took significantly larger prey than adult males in the wet season (Fig. 6).

One might speculate that the lack of food niche partitioning by *A. opalinus* is an artifact of a restricted distribution of available prey sizes. We have no estimate on prey availability to directly refute this possibility, but there are strong

inferential data. First, all *A. opalinus* age and sex classes took prey over the same relatively wide prey-length spectrum (1–20 mm). Second, the same range of prey sizes was taken by opalinus-sized anoles in Bimini (*A. sagrei* and *A. distichus*), where these species were found to partition by prey length (Schoener, 1968).

*Seasonal effects.*—Fat body and liver weights varied with season. Several factors might affect these organ weight cycles, one being seasonal fluctuations in prey availability. Though arthropod abundance was not measured, the lizards' food volume intake did not change significantly between seasons; if there were large fluctuations in available food, the lizards appeared to compensate. In fact, if ants are being used as a substitute when more preferred food is less available, there were few seasonal data indicating such a shift toward ants. Only subadult males and juveniles ate more ants in the dry season, a period when prey availability may be low (Stamps and Tanaka, 1981).

A more likely factor for seasonal organ weight fluctuations is that there were increased energetic demands in the wet season associated with reproduction (e.g., egg production and territorial defense). A correlation between increased reproductive activity and reduced fat body weights supports this contention. Relative fat body and liver weights were lowest for *A. opalinus* in the wet season, the period of maximum reproductive activity (Fig. 9). Even in the dry season, gravid females had significantly smaller ( $P < 0.05$ ) fat body ratios than nongravid females (1.76 vs 4.25). The absence of marked organ weight cycling in the nonreproductive subadult male and juvenile classes (Fig. 9) also indicated that organ weight cycles were the result of lipid utilization for sex-related activities. This was not unexpected, as fat body and liver weights have been shown to cycle inversely with reproduction in both insular and mainland anoles (Fleming and Hooker, 1975; Gorman and Licht, 1974; Licht and Gorman, 1970; Sexton et al., 1971).

We found no evidence from our data that *A. opalinus* experienced a seasonal bottleneck in feeding. The lizards took about the same volume of prey across seasons. In conjunction with a relatively constant food intake, coefficients of condition did not change seasonally (Fig. 10), implying that there was no extended period of energetic stress that might have forced the lizards to catabolize body mass. *A. opalinus* built

up their fat bodies in the dry season and, with the exception of some reproductively active adult females, continued to have these lipid reserves present through the wet season. These data suggest that food resources are adequate for this species throughout the year. Furthermore, the absence of apparent food niche partitioning among the age and sex classes suggests that intraspecific food competition may not be a significant factor for *A. opalinus* as it appears to be for previously studied congeners on small islands.

In summary, *A. opalinus* shares certain characteristics with other insular anoles, being sexually dimorphic in size and feeding on many ants. However, this species more closely resembles mainland anoles in its conspicuous lack of food niche partitioning.

#### ACKNOWLEDGMENTS

We are indebted to R. M. Andrews, J. A. Cranford and W. H. Robinson for critiquing the manuscript. W. H. Robinson and Howard Frank also assisted with some insect identifications. Costs associated with collections and field data were supported by a postdoctoral NIMH fellowship (GF 02M4 33485-01A1) to T. A. Jenssen.

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*Copeia*, 1983(2), pp. 331–338

## Overlap and Pollution-induced Variability in the Feeding Habits of Filefish (Pisces: Monacanthidae) from Apalachee Bay, Florida

WILLIAM H. CLEMENTS AND ROBERT J. LIVINGSTON

**The distribution and feeding habits of two species of filefish, *Monacanthus ciliatus* and *Stephanolepis hispidus*, were examined. Spatial and temporal distribution and feeding habits of the two species overlapped broadly. The apparent similarity in diet was reduced when prey were identified to species. Analysis of ontogenetic variation of each species indicated a tendency toward herbivory with increasing standard length.**

**The feeding habits of *M. ciliatus* taken from areas affected by pulp mill effluents were compared to those from a nearby unpolluted estuary. Cluster analysis of stations within the two systems, based on feeding habits of *M. ciliatus*, were similar to those based on numbers of fishes and macrophyte biomass. Differences in the feeding habits between the two systems may be due to pollution-induced habitat modifications and resulting changes in prey distribution.**

RELATIVELY few studies have assessed spatial, temporal and ontogenetic variability in feeding habits (Grossman, 1980; Stoner, 1980a; Livingston 1980). Many are limited by small sample sizes, thus making it difficult to distinguish among potential sources of variability. Failure to account for the effects of location, season, and growth can bias results. For example, seasonal changes in the diet may be complicated by ontogenetic changes that occur simultaneously (Ross, 1978; Grossman, 1980; Stoner, 1980a). Ontogenetic variation in feeding habits has been observed for numerous species, but has only recently been emphasized in trophic studies (Carr and Adams, 1973; Grossman, 1980; Stoner, 1980a; Livingston, 1980). Results of these studies indicate that the use of a species as a trophic unit in feeding studies without regard for ontogenetic variability can lead to erroneous conclusions. The

division of the species into smaller units based on feeding habits as a function of standard length may provide a realistic alternative in trophic studies (Stoner, 1980a; Livingston, 1980).

The effects of pulp mill effluents on estuarine organisms are well documented (Livingston, 1975; Heck, 1976; Zimmerman and Livingston, 1976). The impact of pollution on feeding habits and trophic structure is, however, uncertain. Changes in the distribution and abundance of prey resulting from disturbances will often be reflected in a predator's diet (Keenleyside, 1967; Klarberg and Benson, 1975; Stoner, 1980a; Livingston, 1980; Jefree and Williams, 1980).

The purpose of this study was to compare feeding habits of juvenile *Monacanthus ciliatus* and *Stephanolepis hispidus* taken from Apalachee Bay seagrass meadows, accounting for seasonal and ontogenetic variability. Also, the feeding habits of *M. ciliatus* collected from a disturbed