THE UNIVERSITY OF MANITOBA

The diet and foraging behaviour of House Wrens (*Troglodytes aedon*) and the abundance of the invertebrate prey

by

DANIEL M. GUINAN

A thesis
submitted to the Faculty of Graduate Studies
in partial fulfillment of the requirements for the
degree of Master of Science

Department of Zoology
Winnipeg, Manitoba

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ABSTRACT

Observations of foraging House Wrens (Troglodytes aedon) and the determination of their diet from gut contents were carried out on the forested dune ridge near Delta, Manitoba, in 1981 and 1982. Despite a large preponderance of midges (Diptera: Chironomidae) in the food resources available, wren diets included most of the invertebrate taxa captured by sweep-net sampling. The ranked importance of 13 taxa in wren diets was most closely correlated with the ranks of their biomass available. When larger individuals within a taxa were available they were consumed in greater proportion by wrens. Chironomids were an exception; small individuals were usually eaten in greater proportion than expected from their abundance in sweep-net samples. The percentage of small chironomids eaten, however, decreased as their abundance increased. Prey selection apparently depended on abundance, size, and ease of capture. House Wrens were less selective when suitable prey were abundant (contrary to the short-term goals of optimal foraging theory). Foraging behaviour varied greatly between the nests studied which suggests that either individuals used different foraging maneuvers and substrates, or that local differences in habitat or prey resources dictated behavioural responses. The latter was supported by a close correlation between the plant spec-

ies used as foraging substrates and the availability of those substrates in the habitat surrounding each nest.

ACKNOWLEDGEMENTS

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INTRODUCTION

A central question in the study of foraging behaviour is how animals select prey items from the food resources in their environment. The results of many laboratory studies suggest that predators select items that maximize their rate of energy intake while foraging (e.g., Pyke et al. 1977; Krebs 1978). Field studies of optimal foraging behaviour have produced ambiguous results partly because it is difficult to measure the complex array of food items that are potentially available to each predator (Schluter 1981). The diets of insectivorous birds in particular often reflect the wide range of prey types available to them because they exploit these ephemeral resources opportunistically (Rotenberry 1980, Sherry 1984).

The ability of predators to respond to diel, seasonal and spatial heterogeneity in resource availability may require more behavioural plasticity than the optimal solutions propose (Sherry 1984). In addition, the deterministic nature of optimal diet models probably oversimplifies the selection mechanism in light of the stochastic distribution of prey and their energetic and nutritional rewards (Oaten 1977; Durell and Goss-Custard 1984). Optimal foraging theory may best be used as a guide to "intuition" (Oaten 1977) or a

baseline of study (Grubb 1979) rather than as a realistic predictor of foraging in natural situations. Field studies of avian foraging have helped define the conditions and limitations under which the optimal selection of prey could provide a mechanism to maximize energy while foraging over a short-term. Long-term foraging goals may influence prey selection if constraints such as nutrient balance (Pulliam 1975; Krebs and Avery 1984), water balance (Tinbergen 1981), digestive assimilation time (Jaeger and Barnard 1981) or the risks of food scarcity (Craig et al. 1979) or predation (Grubb and Greenwald 1982) affect the ultimate goal of maximizing inclusive fitness.

In the present study the prey selection process was examined by determining both the abundance of prey and the diet and foraging behaviour of House Wrens (Troglodytes aedon) on the forested dune ridge, Delta Marsh, Manitoba. At this site several species of foliage-gleaning insectivorous birds breed in high densities (MacKenzie et al. 1982), apparently in response to the abundant supply of ephemeral insects, particularly midges (Diptera: Chironomidae). It was not known to what extent House Wrens used this food resource since anecdotal evidence from other parts of their range indicated a preference for ground- and bark-dwelling invertebrates (Beal et al. 1916, Bent 1948, McAtee 1940). The purpose of this study was to document the diet and foraging behaviour of House Wrens and determine if prey were eaten selectively or in proportion to their availability.

METHODS

I studied wrens nesting in the dune-ridge forest which separates the southern shore of Lake Manitoba from Delta Marsh, Manitoba (50°11'N, 98°19'W). Quantification of wren foraging behaviour and invertebrate populations were made on 3-km of the dune-ridge forest from the Assiniboine River Diversion to Cram Creek (see map in Sealy 1980a). The overstory vegetation was described previously by MacKenzie (1982), and the food resources used by some of the other insectivorous passerines in the study area have been documented (Busby and Sealy 1979, Sealy 1980b, Biermann and Sealy 1982). I determined the abundance and distribution of invertebrates in the dune-ridge forest in 1981, wren foraging behaviour largely in 1982, and examined wren diets in both years. The seasonal influence on these factors was studied by dividing the study periods of both years into seven 12-day sampling periods beginning May 12, May 24, June 6, June 18, June 30, July 12, July 24, 1981; and May 15, May 28, June 9, June 21, July 3, July 15, July 27, 1982.

Diet

House Wrens were collected (by shotgun or in mist-nets) in each sampling period in the dune-ridge forest 8-15 km east of the main study area (on the Bell Estate). Ethanol was injected into the esophagus of each individual to inhibit post-mortem digestion of gut contents. In the laboratory, the upper digestive tract (hereafter 'stomach') including the esophagus, proventriculus and gizzard was removed and preserved in 95% ethanol. Some stomachs were removed immediately in the field. All specimens were weighed (to the nearest 0.1 g) and sexed, and most were prepared as study skins and deposited in the University of Manitoba Zoology Museum (numbers 1663-1683, 2322-2369).

Stomach contents were examined under a dissecting microscope and whole prey items and identifiable body parts were removed. These were measured and counted to determine the minimum number of individual prey in each stomach. Most items were identified to order although chironomids and other Nematocera were identified to family. Some chitinous head capsules, probably of Coleoptera and Hymenoptera, could not be distinguished and were assigned to the 'other adults' category.

Regression equations (Appendix A) were calculated to describe the relationship between total length and the length of body parts often recovered in wren stomachs (Cal-

ver and Wooler 1982). Invertebrates collected in the determination of prey abundance were measured such that the species and sizes within each taxon were included in proportion to the number collected. Invertebrates from wren stomachs were divided by body length into 3-mm size classes. The lengths of damaged prey were estimated conservatively and items represented by fragments were assigned to the modal size class for each taxon and sampling period.

Invertebrates in each category and size class were oven-dried at 100° for five days and weighed (to the nearest 0.1 mg) to produce estimates of dry weight for each size class of each prey category (Appendix B). The mean dry weight of each category was estimated, and compared with a general equation for estimating the dry weight from the length of insects (Rogers et al. 1976). Although the drying method used in this study probably underestimated the weights of invertebrates through excessive heat (see Rogers et al. 1976), rounded and oval-shaped taxa (Araneida, Phalangida, Gastropoda) weighed more than expected from the general equation while elongate groups weighed somewhat less. As this appeared to be a biologically relevant trend, I used the estimates produced from samples collected on the study area rather than the published equation which included insects from around the world.

Bryant (1973) estimated the caloric value of taxonomic categories of the prey of House Martins (Delichon urbica)

using bomb calorimetry and determined that the nearly linear relationship with dry weight made it a good estimator of caloric content. Some variation is expected in the proportion of digestible protein in different taxonomic categories (Calver and Wooller 1982). Biermann and Sealy (1982) reported that the protein component of the dry weight was 59.8 % in chironomids and 62.6 % in larvae collected on this study area.

Comparison between years. The diets of House Wrens collected in 1981 and 1982 were compared by examination of the taxa included in the stomach contents and the size distribution of the prey. Spearman's correlation coefficient was calculated using the number eaten in each of 12 prey categories for each sampling period to determine if prey categories with large values in 1981 were equally important in 1982. The distribution of prey items in four size classes was compared between the diets of birds in 1981 and 1982. The frequency distributions of the sizes of chironomids found in wren stomachs were similarly analyzed using the G statistic (Sokal and Rohlf 1969).

Seasonal variation. Changes in the diet over the breeding season were examined by comparing the mean proportion of all items and the mean proportion of the biomass contributed by each of the five main prey categories. Seasonal prey use was quantified for each prey category by analyzing the variation between sampling periods while considering the varia-

tion between individuals within a sampling period. In this way, a result showing no significance could indicate that either the average proportion of the total stomach contents made up of a particular prey category did not vary seasonally, or that there was a high variability within sampling periods. The proportional data were analyzed after square-root transformation (Sokal and Rohlf 1969) which produced nearly normal distributions in most categories. Data in prey categories with no significant variation between years (determined by analysis of variance with interaction) were grouped together for the examination of seasonal variation.

Age and gender effects. The diets of male and female wrens in the 1982 sample were compared using Spearman's method of rank correlation on the number of prey items in 12 categories. The proportion of the diet contributed by five taxa and five size classes of invertebrates was compared between the sexes using the G statistic. One wren of each gender was omitted in these comparisons because of labeling errors.

Fledgling wrens (defined as young birds which had left the nest but were not yet independent of their parents) made up part of the collection in the last three sampling periods in 1982. The invertebrates eaten by adult and fledgling House Wrens in these sampling periods were compared using Spearman's coefficient of rank correlation. The G-test of independence was used to determine the influence of age on the proportion of five taxa and five size classes of in-

vertebrates in wren diets. The sample size of fledgling wrens was small and complicated by a seasonal component, therefore statistical results were interpreted cautiously.

Invertebrate Abundance

Invertebrates were sampled in a 2-km portion of the dune-ridge forest west of the Assiniboine River Diversion. One sampling site was selected randomly in each of 20 divisions or 'cells' of the study area, 100 m across and (on average) 80 m from the lake to the marsh. Pairs of adjacent cells were combined to produce 10 blocks. Two of these blocks (including four sampling sites) were sampled every second day, weather permitting, in a stratified systematic sampling design. In this way invertebrates were collected in each cell once during each of the seven sampling periods: invertebrates from litter samples were sorted by hand; foliage invertebrates were sweep netted at three heights; and sticky traps placed on live and dead trunks and branches sampled potential prey items on those substrates. This sampling scheme was designed to compare prey abundance on the four categories of foraging station in which foraging wrens were observed.

A 20*20 cm quadrat was placed randomly for each sample of ground invertebrates. Leaf litter and other organic debris and humus from the top 2 cm of the ground were returned to the laboratory and sorted using screens with two differ-

ent sizes of mesh. Invertebrates were preserved in ethanol and later identified under a variable-power microscope, and sorted according to size and taxon.

Invertebrates were collected from foliage with five 180°-sweeps of a standard 38-cm diameter net using approximately constant speed and force. Samples were taken with the lower rim of the net just above the ground and at one and two m above the ground at each sampling site, from 0900 to 1100 hrs. Although the volume of space sampled by sweep netting was nearly constant, the amount of foliage varied between sampling periods. In addition, the plant species composition and presence of alternative substrates (such as infloresences) may have changed. Large proportions of the invertebrate fauna were short-lived adult insects which immigrate from the surrounding aquatic habitats, and therefore populations were unlikely to have been depleted by repeated sampling of individual stations. Since each station was sampled approximately every 12 days the depletion of more sedentary invertebrates was assumed to be minimal.

Sticky traps consisted of 20*20 cm plates of plexiglass coated with a thin layer of insect entrapment paste (Tanglefoot®). I sampled trunks of living trees, trunks and limbs of dead trees, and fallen logs nearest the randomly selected sampling site. Traps were placed on the ground and at 1 m and 2 m above the ground, facing east where possible to minimize and standardize the effects of wind on invertebrate

capture. All traps were exposed for approximately 10 hours, beginning between 0800 and 0900 hrs.

Comparison of methods. The invertebrates captured using the three sampling methods were compared to determine how these methods affected prey capture, and to evaluate their use in estimating the availability of invertebrates to wrens in the four foraging stations. Sweep-net and sticky-trap captures were compared quantitatively using the rank abundance of 13 taxa.

Since wrens and invertebrates were sampled in similar habitat several kilometers apart I used unpublished data (G.B. Pohajdak, pers. comm.) to examine the invertebrate populations of the two areas. Invertebrates were collected in 1982 and 1984 with 8 sweeps at 1m and 3m above the ground in a linear transect of tree foliage. The numbers captured in 9 taxonomic categories were compared with Spearman's coefficient of rank correlation. In 1982 samples from the two areas were taken two days apart while 1984 samples represent consecutive days.

Description of seasonal abundance. Since invertebrate resources were monitored primarily to estimate the availability of prey to House Wrens, detailed analyses of seasonal abundance are not presented. A general description permits a more comprehensive understanding of the resource than the ranked data used to compare with the prey selected. In par-

ticular the relationship of major hatches of ephemeral adults, such as midges, to overall seasonal abundance are outlined in a graphical presentation of these data.

Analysis of temporal and spatial variation. Analysis of variance was used in some major taxa to separate the spatial and temporal variation in capture rates within sampling periods. Some spatial variation was expected as a result of the habitat preferences of the invertebrates but the clumped nature of swarming chironomids, ephemeropterans and other ephemeral adults made quantification of between-cell and between-block captures informative. The separation of spatial effects from possible diel effects was done by analysis of variance with variation between adjacent cells (within blocks) used as the error term and the between-blocks (within days) and between-days (within sampling periods) variation as factors. The total number captured were combined for the three heights and the data were log transformed.

Prey Selection

Spearman's coefficient of rank correlation was calculated to determine whether the invertebrate taxa in wren diets were selected according to their abundance in the habitat. Rank comparisons were preferred because of the limited confidence in sampling invertebrates as an estimate of their availability to wrens. Thirteen taxonomic categories of invertebrates were used regardless of their suitability

as prey. Total sweep-net captures in each sampling period in 1981 were compared to the total number of each taxon in all wren stomachs in the same periods in 1981. In addition, the biomass represented by each taxon in sweep-net samples and wren diets was estimated using the values in Appendix B.

To determine if wrens selected items according to their weight, Ivlev's electivity index was calculated for each taxon in each sampling period (Ivlev 1961, Lechowicz 1982). The proportion of the total biomass of prey in sweep-net samples was subtracted from the proportion of the total biomass in wren stomachs that was contributed by each taxonomic group. This difference, divided by the sum of the two values, produces a ratio with possible values between plus and minus one, and zero indicating random foraging. Positive values therefore indicate selection by wrens while negative values refer to prey items avoided or undetected by foraging wrens. The sizes of prey eaten by House Wrens in 1981 were compared with those captured in sweep-nets using the G statistic for frequency tables.

Foraging Behaviour

Foraging House Wrens were observed near their nest sites since the low number of nesting pairs and their inconspicuous foraging habits made observations in other areas difficult. An observation post was selected within 20 m of each nest so that wren activity at the nest and the sur-

rounding area could be monitored using 9X binoculars or a 25X telescope. The location and behaviour of both members of a pair were recorded for approximately 30-min periods about once per day throughout the nesting period on the study area (19 May - 27 July, 1982). Observations were conducted at 22 of the 24 nest sites found but 92 percent of all foraging data were collected at 10 sites where the paths of foraging birds could be followed and where the nests remained active at least into the incubation stage.

Most observations were made throughout the mornings and evenings; occasional observations in the afternoon showed long periods of wren inactivity. Since wren nests were up to 2 km apart, visits were not completely randomized but the sequence of visitation and starting point were varied such that most pairs were observed in all time-of-day periods. Observations of foraging wrens were divided into four time-of-day divisions for analysis: early morning (<0800 hrs), late morning (0800-1200), afternoon (1201-1700) and evening (>1700 hrs).

Gender was determined where one or both members of a pair were colour banded and subsequently sexed by behaviour, primarily singing. Most males sang frequently and consistently through most of the breeding cycle, thus the gender of members of unbanded pairs could also be determined for many of the observations.

The status of each nest through the nesting season was divided into four stages for analysis: establishment, laying, incubation, and nestling. Laying included the day the first egg of a clutch was laid. All observations before egg laying were included in the establishment category. The incubation period started the day the last egg of a clutch was laid, and the nestling stage began when the first chick hatched.

Foraging was described primarily by the substrates used since attempts to capture prey usually could not be seen unless particularly large prey items were involved or the birds' movements were obvious. An 'observation' therefore represents a particular combination of perch type, foraging station, plant species and the other variables describing how and where the bird was foraging. Each perch used by actively foraging wrens was recorded as one of five types: ground, trunk (primary stem), limb (secondary stem with diameter greater than a wren body length), branch (diameter less than a body length), or twig (diameter less than a wren bill length). Each perch or series of perches used was also characterized by the four major microhabitats corresponding to the invertebrate sampling scheme: ground, dead vegetation, live unfoliated vegetation, and live foliated vegetation.

The heights at which wrens foraged, the plant species they used and the heights of the plant were recorded for

each perch. Visual estimations of heights were recorded to the nearest 0.5m and later assigned to classes. Each attempt to capture prey was recorded in association with the previous perch and classified as glean (bird and prey on substrate), hover (bird in air, prey on substrate), snap (bird on substrate, prey in air), or hawk (bird and prey in air).

The G-test of heterogeneity was used to quantify differences in the proportions of each category of a foraging variable between the categories of five foraging factors (time of season, stage in nesting cycle, time of day, nest location, and gender of bird). The seasonal factor, determined by comparing foraging in 5 different sampling periods with sufficient data, may reveal the effects of prey abundance and plant phenology. Since foraging may be affected by other behaviours that are linked with the stages of the nesting cycle, foraging behaviour was compared in the establishment, laying, incubation and nestling stages.

Diel changes in prey activity and the concomitant response by the avian predators were examined by comparing the foraging that occurred in the four time-of-day categories. The possibility of habitat-mediated differences in prey abundance and substrate availability was studied by testing the heterogeneity of the foraging variables between individual nest sites (labelled A to J for comparitive purposes) .Finally, gender effects such as morphologically based dif-

ferences in substrate use and behavioural partitioning of resources were examined in the foraging observation data.

Substrate Selection

To determine the availability of plant substrates around the nests where foraging was recorded, the number of trees (DBH > 7 cm) within a 10-m radius of the nest tree were counted. Plant species used in prey-capture attempts, as recorded in foraging observations, were used to estimate plant substrate use by wrens. The proportion of foraging attempts made within the area for which substrate availability was known could be estimated from data on the distance birds foraged from their nest sites.

RESULTS

Diet

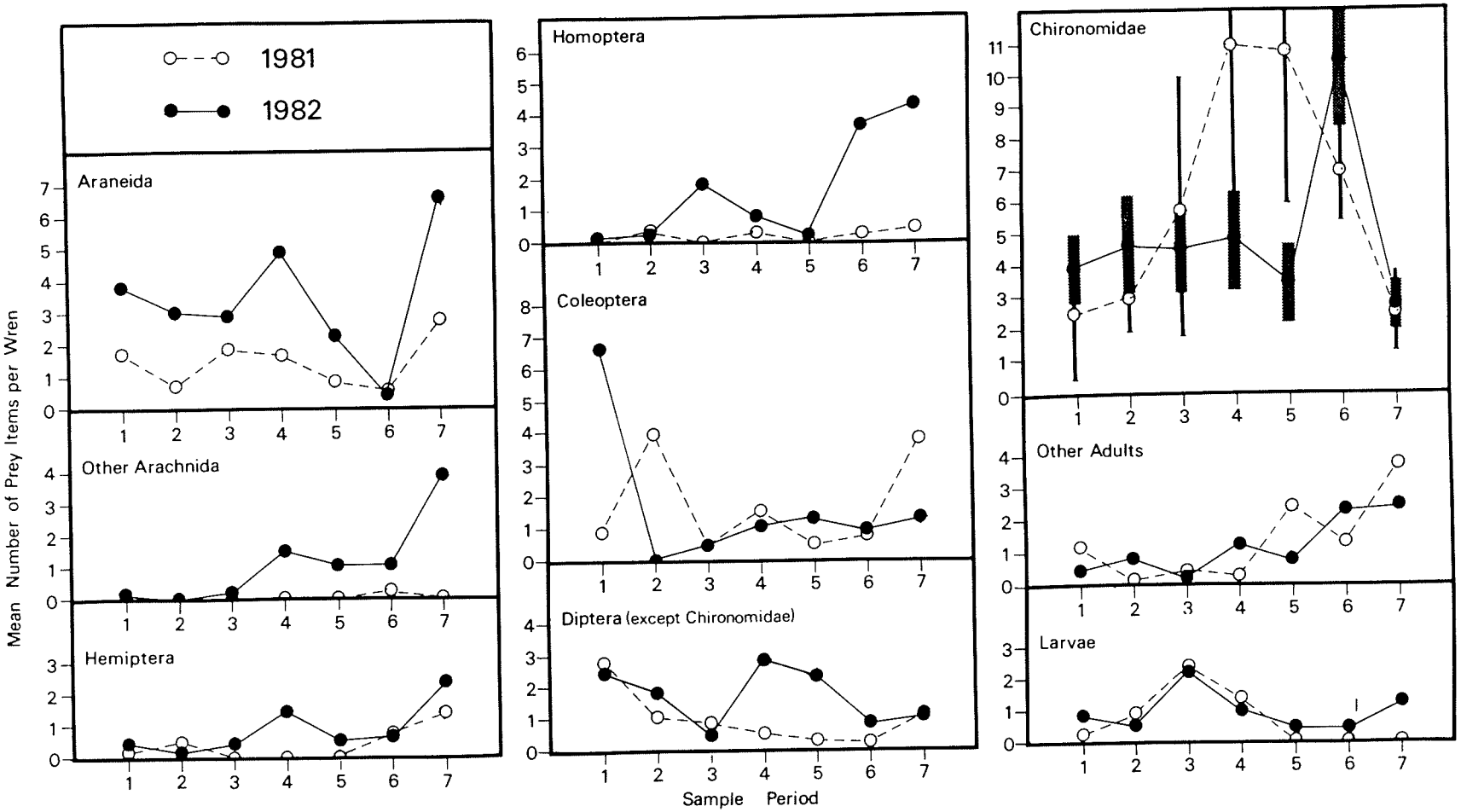
In 1981, 29 adult male, 3 adult female and 6 fledgling male House Wrens were collected for stomach content analysis. In 1982, 25 adult males, 16 adult females, 5 fledgling males and 4 fledgling females were collected. The numbers of wrens collected in each sampling period were 6,6,5,5,7,6,3 and 8,7,7,7,8,8,5 for 1981 and 1982, respectively. The collection dates of 1981 were not repeated exactly in 1982, primarily because of inclement weather. Since the phenologies of the vegetation, invertebrates and House Wrens are unlikely to have been consistent between years, stomach contents from corresponding sampling periods were compared directly despite differences of several calender days in some periods.

House Wren stomachs contained fragments of several orders of insects and arachnids, as well as gastropods and, in a few instances, seeds. The total number of items retrieved from wren stomachs was 468 in 1981 and 849 in 1982. Chironomids were used most frequently with representation in 84.2 % and 82.0 % of wren stomachs and accounting for 51.9% and 29.45% of all prey items in 1981 and 1982, respectively.

Chironomid use peaked earlier in 1981 than 1982, but the standard errors indicate that this may have been related to the small sample sizes (Figure 1). Beetles and Diptera other than Chironomidae were taken early in the season and the 'other adults' category (primarily Lepidoptera and Hymenoptera) and hemipterans were used by wrens in late July and early August. Larvae, which were primarily lepidopteran, peaked in wren stomachs during mid-June of both years. Spiders were taken consistently, but their importance decreased during the chironomid peaks.

Comparison of years. Spearman's test of rank correlation indicated no significant correlation between the number of prey items in twelve taxa in 1981 and 1982 ($r = 0.3828$, $P > 0.05$). The largest differences in rank importance include a higher use of nematoceran Diptera other than Chironomidae and Culicidae and Hymenoptera in 1981, and other Arachnids and Homoptera in 1982. There was a significant difference ($t = -2.44$, $df = 86$, $P < 0.05$) in the overall mean number of items from all categories identified in wren stomachs in 1981 ($\bar{X} = 12.34$, $SD = 8.54$) and 1982 ($\bar{X} = 16.98$, $SD = 9.06$). When the dry weight of prey in wren stomachs was estimated using the length-weight regression equations calculated from the invertebrate reference collections, the overall difference between 1981 ($\bar{X} = 34.6$ mg, $SD = 24.48$) and 1982 ($\bar{X} = 43.2$ mg, $SD = 28.47$) was not significant ($t = -1.49$, $df = 86$, $P > 0.05$). Estimates of prey size relied on placement in

Figure 1. Mean number of prey items ($\bar{X} \pm$ SE shown for Chironomidae) of nine taxonomic groups eaten by House Wrens in seven sampling periods beginning May 12, May 24, June 6, June 18, June 30, July 12 and July 24 in 1981 and beginning May 15, May 28, June 9, June 21, July 3, July 15 and July 27 in 1982.


1981
1982
Araneida
Other Arachnida
Hemiptera
Homoptera
Coleoptera
Diptera (except Chironomidae)
Chironomidae
Other Adults
Larvae
Mean Number of Prey Items per Wren
Sample Period

the modal size class for 23.6% and 28.7% of items in 1981 and 1982, respectively. A majority of these were fragments of chironomid eyes which were clearly identifiable but of unknown size.

The size distribution of all prey taken by wrens did not differ significantly between the two years ($G = 4.86$, $df = 3$, $P > 0.05$), although there were significantly different proportions of the size classes represented in the two years for four of the sampling periods (Figure 2). Chironomids were frequent enough in wren diets to be compared similarly. The wrens sampled in 1981 ate more small (3 - 5.9 mm) and fewer large ($\geq$ 9 mm) chironomids. The size distribution was significantly different from that found in 1982 ($G = 34.30$, $df = 2$, $P < 0.005$) with five sampling periods showing size classes that varied independently of year (Figure 3).

Seasonal variation. The proportion of the total number of prey items identified to the five major categories of prey in each stomach showed significant seasonal variation for larvae in both years but no significant seasonal pattern in chironomids or the 'other adults' category in either year (Table 1). Spiders and beetles showed significant overall seasonal patterns in 1982 but not in 1981. In this analysis, non-significant seasonal variation may indicate no statistically relevant fluctuation in the average proportion of the total stomach contents made up of a particular prey category or a high variability in the proportions between wrens col-

Figure 2. The proportion of prey items in four size classes eaten by House Wrens in 1981 (n = 56, 62, 58, 80, 102, 64, 46 for the seven sample periods respectively) and 1982 (n = 154, 80, 91, 135, 97, 165, 127) and the degree of heterogeneity estimated by the G statistic.

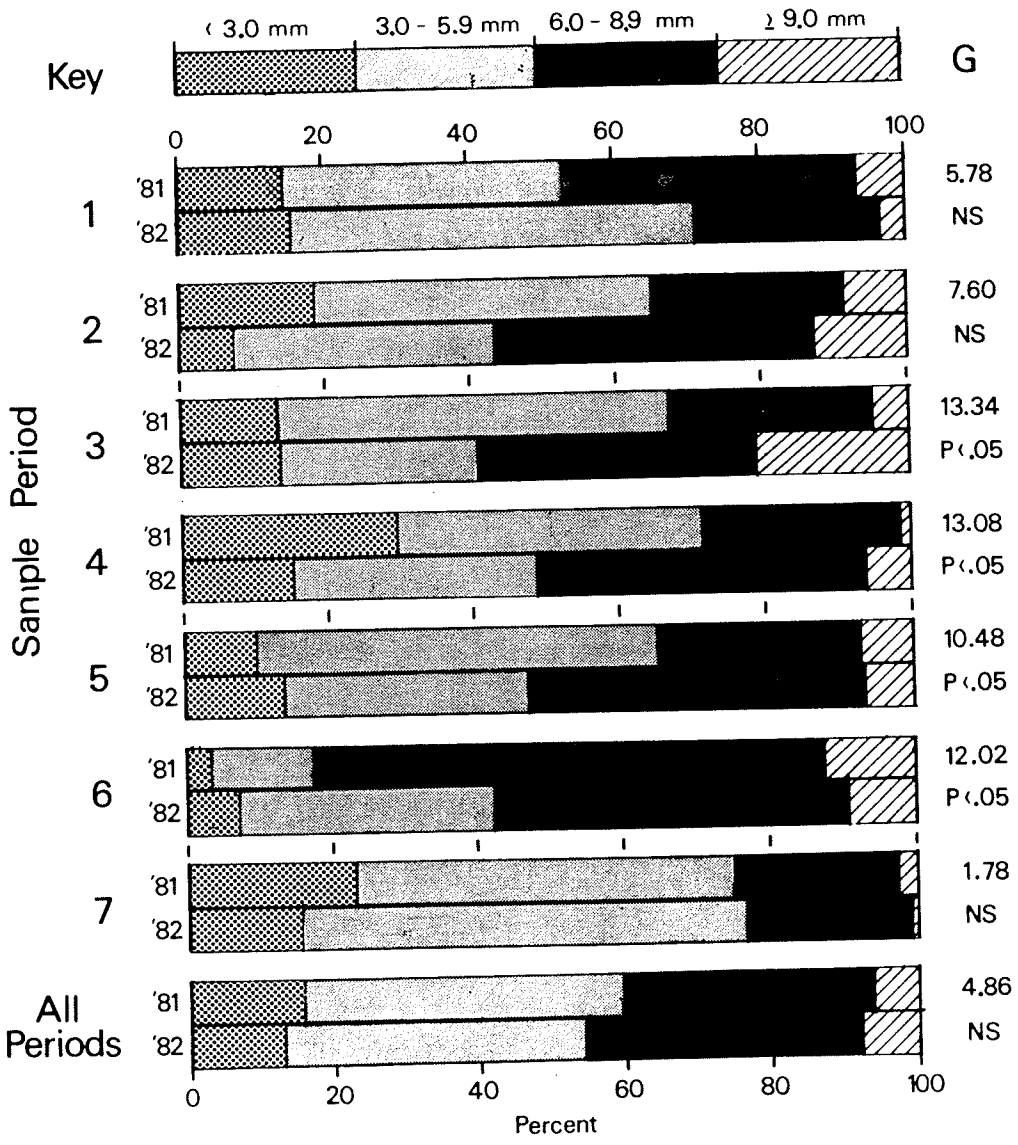

Key
< 3.0 mm
3.0 - 5.9 mm
6.0 - 8.9 mm
≥ 9.0 mm
G
0
20
40
60
80
100
Sample Period
1
2
3
4
5
6
7
All Periods
'81
'82
5.78
NS
7.60
NS
13.34
P<.05
13.08
P<.05
10.48
P<.05
12.02
P<.05
1.78
NS
4.86
NS
Percent

Figure 3. The proportion of chironomids in three size classes eaten by House Wrens in 1981 (n = 15, 18, 29, 55, 76, 42, 8 in the seven sampling periods respectively) and 1982 (n = 31, 32, 31, 33, 27, 83, 13) and the degree of heterogeneity estimated by the G statistic.

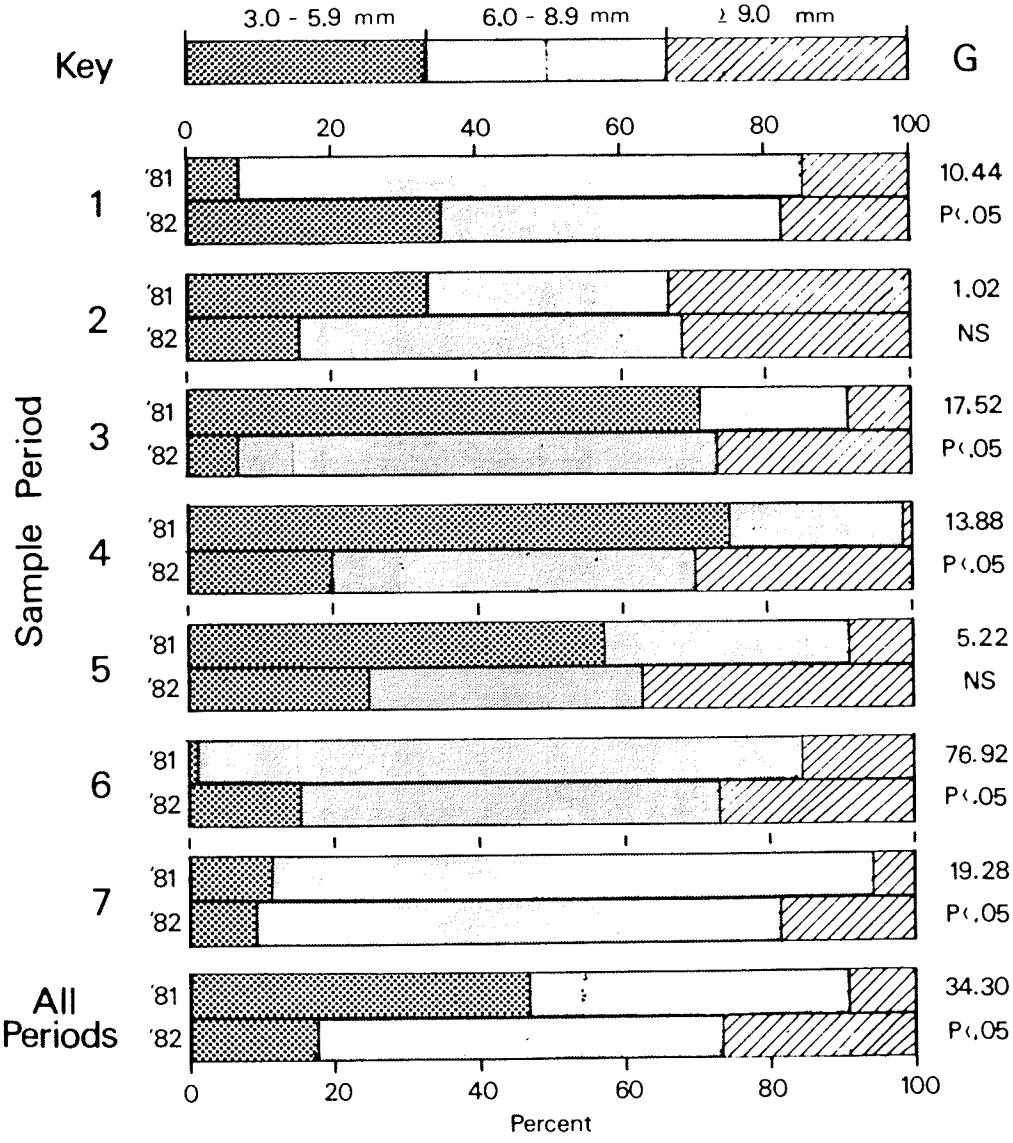

Key
3.0 - 5.9 mm
6.0 - 8.9 mm
≥ 9.0 mm
G
0
20
40
60
80
100
Sample Period
1
2
3
4
5
6
7
All Periods
'81
'82
10.44
P<.05
1.02
NS
17.52
P<.05
13.88
P<.05
5.22
NS
76.92
P<.05
19.28
P<.05
34.30
P<.05
Percent

Table 1. Percentage ($\bar{X} \pm SE$) of the total number of prey items in House Wren stomachs contributed by five categories in 1981 and 1982; and for both years combined where differences between years were not significant (ANOVA with interaction).

1981	PERCENT OF DIET				
SAMPLE PERIOD	Araneida	Coleoptera	Chironomidae	Other Adults	Larvae
1	23.87± 6.14	9.07± 6.61	21.90±12.88	41.04±12.48	4.20± 4.16
2	4.58± 3.50	35.45±15.40	34.00±15.93	14.13± 6.03	11.92± 5.34
3	27.02±14.17	4.52± 2.78	32.30±13.94	11.24± 5.08	24.98± 9.26
4	15.32± 4.67	14.02±11.65	53.58±14.73	8.88± 5.96	8.26± 2.36
5	10.13± 5.49	4.31± 2.19	65.17±11.72	20.45± 9.31	0.04± 0.00
6	4.27± 1.98	8.92± 6.58	61.87± 9.95	25.00± 9.56	0.04± 0.00
7	21.56± 8.31	22.65± 9.28	16.02± 3.90	39.76± 6.73	0.04± 0.00
P	>.05	>.05	>.05	>.05	.0002

1982	PERCENT OF DIET				
SAMPLE PERIOD	Araneida	Coleoptera	Chironomidae	Other Adults	Larvae
1	22.66± 4.25	29.79± 6.65	21.15± 6.08	21.70± 3.46	4.72± 2.28
2	26.65± 9.06	0.04± 0.00	48.13±14.90	22.31± 7.27	2.98± 1.91
3	24.74± 5.81	3.30± 1.60	25.94± 7.91	26.11± 4.88	19.94± 3.39
4	24.32± 3.65	5.51± 1.22	22.39± 4.70	42.20± 6.94	5.60± 1.74
5	24.16±11.71	10.15± 3.82	26.40± 9.58	34.79± 7.36	4.57± 2.62
6	2.70± 1.32	4.79± 1.93	51.76± 8.65	37.78± 9.12	3.04± 1.55
7	28.97± 2.90	4.83± 4.79	12.46± 4.90	53.23± 9.65	0.57± 0.53
P	.0040	.0001	>.05	>.05	.0003

1981-1982 COMBINED	PERCENT OF DIET				
SAMPLE PERIOD	Araneida*	Coleoptera**	Chironomidae	Other Adults***	Larvae
1			21.47± 6.22		4.50± 2.11
2			41.61±10.62		7.11± 2.85
3			28.59± 7.09		22.04± 4.15
4			35.38± 7.84		6.71± 1.40
5			44.49± 8.87		2.46± 1.48
6			56.09± 6.42		1.76± 0.95
7			13.80± 3.26		0.37± 0.33
P			.0194		.0001

* Significant differences between 1981 and 1982 (P=.0308).

** Significant year*sample period interaction (P=.0002).

*** Significant differences between 1981 and 1982 (P=.0027).

lected in the same sampling periods. Since the within-sample variation is sensitive to sample size, the 1981 and 1982 samples were combined in those categories where no significant between-year variation existed, thus improving the estimates of variability. Larvae maintained a significant seasonal pattern in their appearance in wren diets and chironomids showed a significant seasonal pattern in wren diets although none was found in either year alone. Coleoptera interact significantly between year and sampling period, possibly because of differing phenologies in the two years, and the combined analysis of seasonal variation was therefore not valid. Spiders and the 'other adults' category could not be examined because of significant differences between the years.

Analysis of the variation in the proportion of the biomass which the five major categories of prey contributed to the total dry weight estimated for each stomach (Table 2) showed significant seasonal patterns of consumption in all categories in at least one of the two years of sampling. When the two years were considered together only beetles did not vary significantly between sampling periods. This is again apparently a factor of the highly significant interaction between sampling period and year.

These analyses show that, despite differences in the diets of individual wrens, significant seasonal patterns exist in the composition of the diet. The estimation of biom-

Table 2. Percentage ($\bar{X} \pm$ SE) of the total biomass of prey in House Wren stomachs contributed by five categories in 1981 and 1982; and for both years combined where differences between years were not significant (ANOVA with interaction).

1981	PERCENT OF BIOMASS EATEN				
SAMPLE PERIOD	Araneida	Coleoptera	Chironomidae	Other Adults	Larvae
1	44.81± 5.44	1.86± 1.77	15.30±11.56	32.21± 7.55	5.90± 5.86
2	15.08± 9.52	29.67±15.56	33.91±16.29	8.94± 4.93	12.49± 9.68
3	26.77±11.17	1.41± 0.89	14.36± 9.73	6.30± 4.73	51.23±11.08
4	24.11±10.98	3.87± 2.85	32.95± 9.44	2.07± 1.51	37.07± 9.97
5	27.23±11.73	2.74± 1.40	61.53±13.52	8.56± 4.43	0.04± 0.00
6	6.88± 5.42	4.07± 3.21	55.94±11.60	33.17±12.57	0.04± 0.00
7	35.27± 7.85	11.86± 7.67	16.06± 3.87	36.81± 3.49	0.04± 0.00
P	>.05	>.05	.0394	.0046	.0001

1982	PERCENT OF BIOMASS EATEN				
SAMPLE PERIOD	Araneida	Coleoptera	Chironomidae	Other Adults	Larvae
1	40.84± 7.34	11.54± 5.33	17.73± 7.55	14.33± 3.53	15.61± 8.44
2	39.92±12.21	0.04± 0.00	43.66±15.80	7.86± 3.08	8.61± 7.79
3	25.59± 6.05	0.68± 0.43	15.08± 5.81	4.50± 2.43	54.19± 6.74
4	46.10±10.23	0.62± 0.18	13.92± 4.28	24.26± 6.71	15.19± 7.25
5	33.12±12.73	3.02± 1.56	29.43±13.31	19.71± 6.99	14.78±10.21
6	2.77± 1.42	1.86± 0.71	57.67±11.40	24.36± 8.42	13.41± 6.82
7	40.19±10.41	1.53± 1.49	14.70± 8.62	38.79±12.11	4.85± 3.34
P	.0022	.0005	>.05	.0197	.0048

1981-1982 COMBINED	PERCENT OF BIOMASS EATEN				
SAMPLE PERIOD	Araneida	Coleoptera*	Chironomidae	Other Adults	Larvae
1	42.54± 4.66		16.69± 6.30	21.99± 4.39	11.45± 5.42
2	28.46± 8.39		39.16±10.96	8.36± 2.69	10.40± 5.89
3	26.08± 5.53		14.78± 5.01	5.25± 2.31	52.96± 5.77
4	36.94± 7.89		21.85± 5.23	15.01± 5.06	24.26± 6.51
5	30.37± 8.45		44.41±10.10	14.51± 4.38	7.90± 5.62
6	4.53± 2.40		56.93± 7.89	28.13± 7.02	7.68± 4.21
7	38.34± 6.79		15.21± 5.31	38.05± 7.34	3.05± 2.18
P	.0002		.0024	.0003	.0001

* Significant differences between 1981 and 1982 (P = .0344) and year * sample period interaction (P = .0002).

ass revealed further significant patterns apparently by equalizing the effects of fewer large and more small items, especially spiders, chironomids and 'other adults', eaten by different individual wrens within the same sampling periods. Beetles were not eaten in a significant seasonal pattern in 1981 but 1982 data showed a seasonal trend. Overall, these results provide a background for comparing the food resources that wrens used in 1981 with those available, as measured by invertebrate sampling.

Gender effects. Examination of the wrens collected in 1982, in which male and female birds were represented in all sampling periods, revealed a significant correlation in the rank number of twelve prey categories in wren stomachs ($r = 0.8042$, $P < 0.01$). The number of invertebrates of the five main categories eaten by male and female wrens (Figure 4a) show that choice of taxa was independent of sex ($G = 4.24$, $n = 838$, $P > 0.05$). Male and female House Wrens ate similar proportions ($G = 2.12$, $n = 838$, $P > 0.05$) of prey items in five categories of length (Figure 5a).

Age effects. Diets of nine fledgling wrens were significantly correlated ($r = 0.6399$, $P < 0.025$) with the ranked importance of 12 prey categories in the diets of 12 adults collected during the same periods (July 14, July 25, August 6, 1982). The proportions of the five main categories of prey items in the stomachs of adult and fledgling wrens (Figure 4b) were not significantly different ($G = 5.95$, $n =$

Figure 4. The proportion of the total number of prey items in five taxonomic categories eaten by a) 29 male and 19 female and b) 9 fledgling and 12 adult House Wrens in 1982.

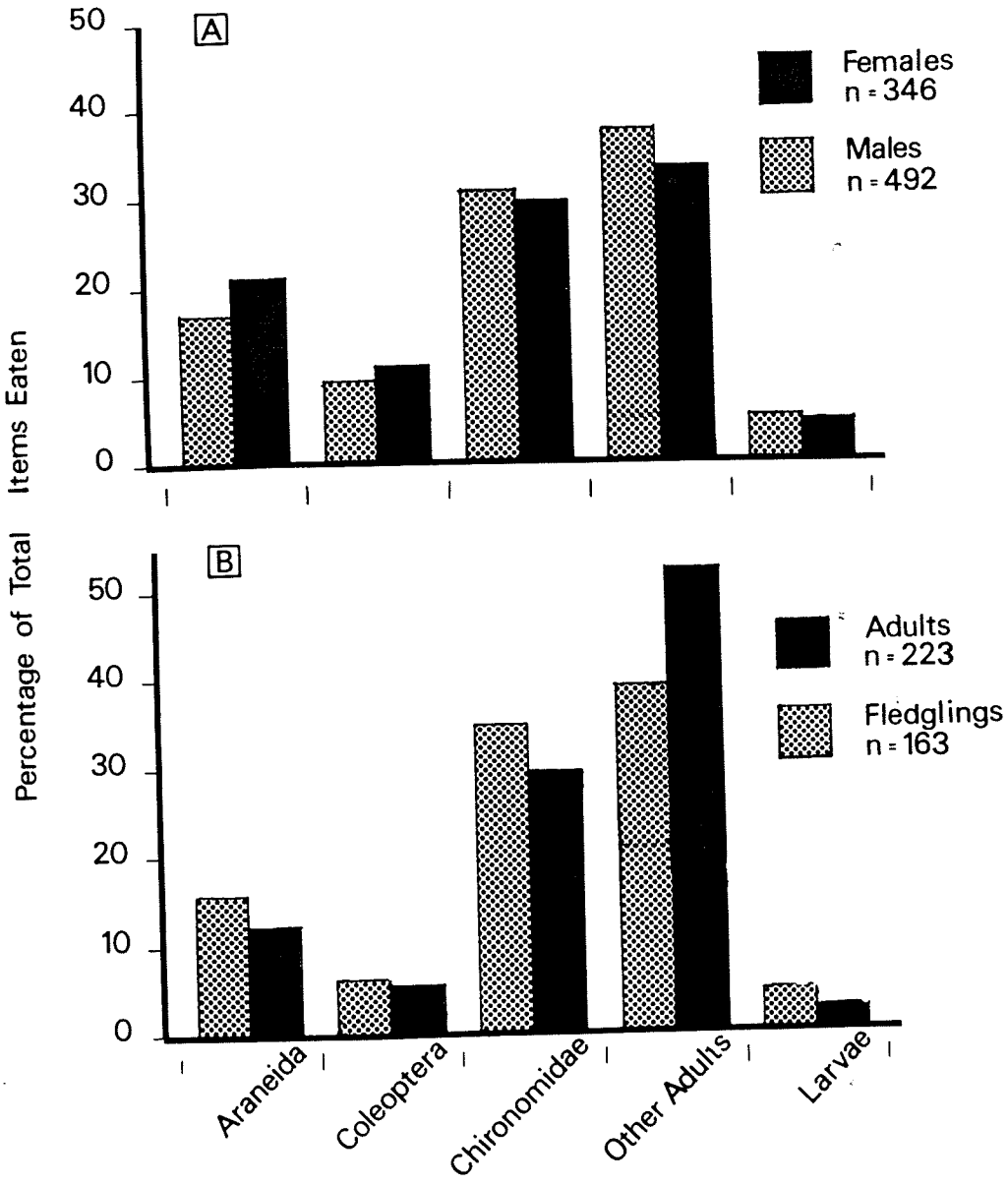
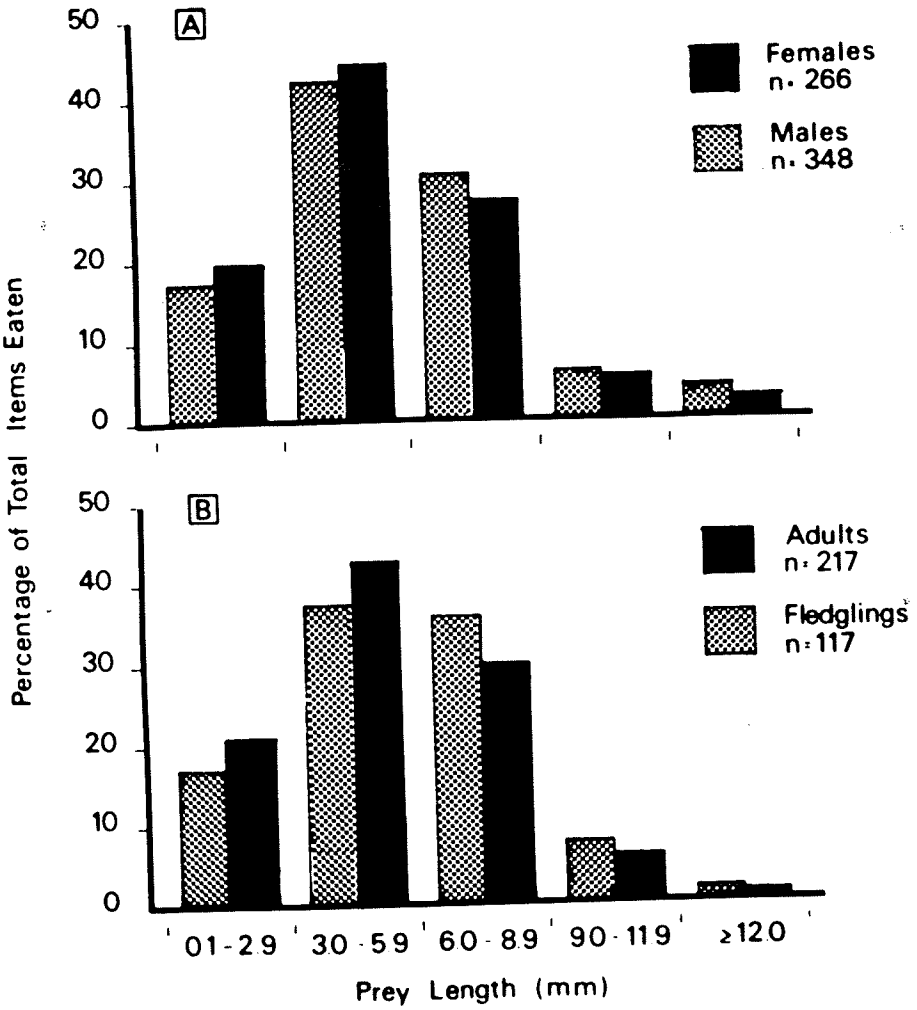

A
B
Females
n = 346
Males
n = 492
Adults
n = 223
Fledglings
n = 163
Items Eaten
Percentage of Total
50
40
30
20
10
0
Araneida
Coleoptera
Chironomidae
Other Adults
Larvae

Figure 5. The proportion of the total number of prey items in five size classes eaten by a) 29 male and 19 female and b) 9 fledgling and 12 adult House Wrens in 1982.


A
B
Females
n. 266
Males
n. 348
Adults
n. 217
Fledglings
n. 117
Percentage of Total Items Eaten
0
10
20
30
40
50
01-29
30-59
60-89
90-119
≥120
Prey Length (mm)

383, $P > 0.05$). The sizes of prey items (Figure 5b) revealed no significant age-related differences in diet ($G = 2.49$, $n = 386$, $P > 0.05$).

Invertebrate Abundance

While sweep nets and sticky traps caught similar types of invertebrates, at least at the taxonomic level used in the present analysis, there were qualitative differences in taxa collected in litter samples. A total of 4177 invertebrates was collected during the study period in 1981 from approximately 5.6 m^2 of ground area. A large proportion of invertebrates on the ground were annelids (20.4 %) which were not found in wren stomachs, and gastropods (7.8 %) and non-lepidopterous insect larvae (33.4 %) which were rarely eaten by wrens. Lepidoptera larvae (1.2 %), hemipterans (2.4 %) and 'other adults' (4.2 %) were infrequent and of relatively small absolute abundance. Spiders (8.4 %) and beetles (22.2 %) may have been an available food resource, particularly in the first sampling period when new vegetative growth was sparse. House Wrens seldom foraged on the ground except at two nest sites where they used the ground but gleaned prey primarily from low vegetation (see Figure 12). No wrens probed the ground or disturbed the leaf litter in search of prey, thus I did not use ground invertebrate data for comparison with wren diets.

The taxonomic composition of sweep-net samples was significantly correlated (Spearman's rank correlation) with the composition of sticky trap captures for 86.9% of collections on living substrates and 85.6% on dead substrates (20 cells * 7 sampling periods = 140 collections in 1981). The two microhabitats sampled by sticky traps exhibited the most consistently high level of correlation with no significant difference in the ranked abundance of taxa for 97.1% of collections. Spearman's rank correlations between sweep samples and sticky traps on live unfoliated vegetation were calculated for the total number of invertebrates captured in each sampling period (Table 3). The mean differences in rank showed that beetles and 'advanced' flies (Diptera: Cyclorrhapha, Brachycera) were ranked higher in sticky traps while chironomids, hemipterans and homopterans were consistently sampled more by sweep nets.

Sticky traps apparently captured flying insects rather than those which normally occurred on the substrates on which the traps were placed. Since the rank number of invertebrates captured were significantly correlated and the absolute values from the sweep-net sampling were much larger, only sweep-net data were used to compare prey abundance with diet. In addition, foraging observations indicate that wrens collected most of their food from foliated substrates rather than by hawking airborne prey.

Table 3. Spearman's rank correlation of the number of invertebrates captured in 13 categories on sticky traps (ST) and in sweep nets (SN) in each sampling period and the total for all sampling periods in 1981.

	SAMPLING PERIOD															
	ONE		TWO		THREE		FOUR		FIVE		SIX		SEVEN		TOTAL	
TAXA	ST	SN	ST	SN	ST	SN	ST	SN	ST	SN	ST	SN	ST	SN	ST	SN
Araneida	11	90	26	530	17	393	19	271	5	246	45	1310	38	1330	161	4170
Other Arachnida	404	4	11	196	41	428	6	417	25	536	19	419	13	228	519	2228
Collembola	0	7	12	265	458	1119	78	457	22	180	264	907	96	711	930	3646
Hemiptera	3	35	0	31	5	84	1	265	5	251	9	595	13	463	36	1723
Homoptera	21	54	20	177	4	110	19	320	18	635	30	912	24	603	136	2811
Coleoptera	54	103	85	648	76	508	59	471	50	260	33	386	34	187	391	2563
Culicidae	0	0	0	21	4	141	2	363	4	122	1	57	0	103	11	807
Chironomidae	13	57	805	40506	679	10236	824	3649	336	12021	387	19128	169	2925	3213	88522
Other Nematocera	166	45	683	1966	1547	6053	1355	7968	1310	2444	429	1804	421	1476	5911	21756
Cyclorrhapha and Brachycera	138	14	1112	752	1698	1065	2385	3306	1850	4801	2654	2069	3101	1317	12938	13324
Hymenoptera	9	13	55	619	90	805	169	1261	142	1388	298	2521	446	1258	1209	7865
Other Adults	8	9	1	81	5	80	47	285	44	450	34	1445	16	405	155	2755
Larvae	0	0	0	20	1	46	2	43	1	29	2	32	0	36	6	206
Spearman's r	0.4794		0.9615		0.8819		0.8681		0.8778		0.8681		0.8297		0.8681	
$P < \|r\|$	P>0.05		P<0.001		P<0.001		P<0.001		P<0.001		P<0.001		P<0.001		P<0.001	

The relative abundance of invertebrates in nine taxonomic categories was significantly correlated between the two study areas in all sampling periods (Table 4). Differences in the ranks of individual taxa on the two areas were small and there were no consistent patterns between sample periods or years. For example, in 1982 the largest difference between the two areas was in the rank of Homoptera but this taxa was ranked higher on the main study area in two sampling periods, on the Bell Estate in two periods, and of equal rank in the remaining period.

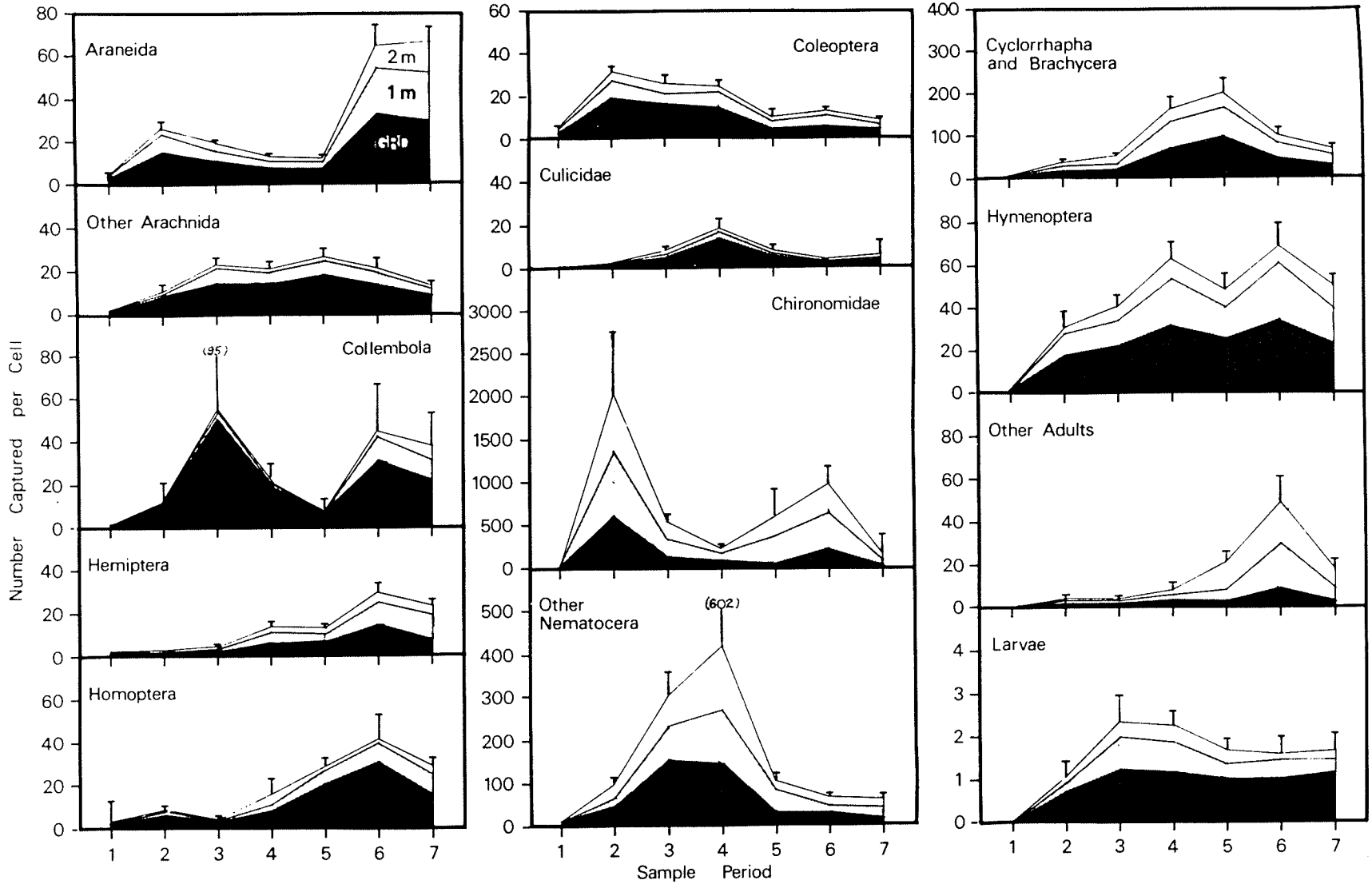
Seasonal abundance patterns. The general pattern of invertebrate abundance is shown by the mean catch for each sampling period averaged over the 20 sampling sites (Figure 6). The standard error therefore represents the variation between cells, including variation between the five days sampled in each period, and the error expected from habitat preferences and other environmental factors. Busby and Sealy (1979) found similar seasonal patterns of invertebrate abundance on this study area with similar numbers per sweep of the net for those categories that are comparable. Geometrid larvae were noticeably more common with as many as 10 individuals collected per sweep during a peak in early June of 1976 (Busby and Sealy 1979). In 1981 all larvae consistently remained well below an average of one individual per sweep.

Table 4. Spearman's rank correlation of 9 categories of invertebrates captured in the same sampling periods on the two study areas in 1982 and 1984 by G.B. Pohajdak (BE = Bell Estate, FS = University Field Station, Delta Marsh).

1982	BE M 26	FS M 24	BE Jn 8	FS Jn10	BE Jn20	FS Jn22	BE Jy 2	FS Jn30	BE Jy14	FS Jy12
ARACHNIDA	11	6	7	8	3	14	17	16	10	7
HEMIPTERA	0	0	0	0	0	0	3	1	3	6
HOMOPTERA	10	1	2	2	3	21	1	17	28	22
COLEOPTERA	73	32	2	6	8	18	4	14	9	4
CHIRONOMIDAE	16	4	535	163	796	403	99	405	118	110
OTHER DIPTERA	10	5	54	47	63	91	95	212	43	29
HYMENOPTERA	3	0	2	1	3	9	6	3	4	6
OTHER ADULTS	0	0	0	0	0	1	3	7	5	0
LARVAE	0	0	2	4	1	1	0	0	0	0
Spearman's r	0.9125		0.9583		0.9375		0.6875		0.8417	
P < |r|	<0.001		<0.001		<0.001		<0.025		<0.005	

1984	BE M 23	FS M 24	BE M 28	FS M 29	BE M 31	FS Jn 1	BE Jn12	FS Jn14	BE Jn18	FS Jn19	BE Jy 6	FS Jy 5
ARACHNIDA	3	4	11	9	7	17	15	8	11	7	31	14
HEMIPTERA	0	0	0	0	0	0	1	0	1	0	2	0
HOMOPTERA	0	0	1	1	0	0	3	7	71	6	5	1
COLEOPTERA	12	5	21	9	16	9	20	13	9	32	0	0
CHIRONOMIDAE	1	1	30	192	112	1432	259	359	86	80	466	478
OTHER DIPTERA	4	5	3	5	22	35	63	22	53	49	30	25
HYMENOPTERA	0	1	6	7	3	0	6	1	0	0	5	3
OTHER ADULTS	0	0	0	0	1	2	0	0	0	1	0	0
LARVAE	1	2	2	0	0	0	1	1	6	3	8	6
Spearman's r	0.9458		0.9500		0.9167		0.9125		0.8458		0.9667	
P < |r|	<0.001		<0.001		<0.001		<0.001		<0.005		<0.001	

Figure 6. Cumulative abundance (± SE of total) of invertebrates in 13 categories captured by sweep nets at three heights in seven sampling periods beginning May 12, May 24, June 6, June 18, June 30, July 12 and July 24 in 1981.


Araneida
2 m
1 m
Other Arachnida
Collembola
(95)
Hemiptera
Homoptera
Coleoptera
Culicidae
Chironomidae
Other Nematocera
(602)
Cyclorrhapha and Brachycera
Hymenoptera
Other Adults
Larvae
Number Captured per Cell
Sample Period

The distribution of invertebrates at the three heights sampled (Figure 6) showed that for most taxa, and in most sampling periods, sweeps collected fewer individuals with increased height above the ground. Chironomids clearly were exceptional, with nearly equal numbers being caught at all heights during the first peak in early June but in the second major peak 1-m sweeps collected 42.5 % and 2-m sweeps collected 34.5 % of the total. Busby and Sealy (1979) reported that most categories of invertebrates were more common at 0.3-3 m than at 7-9 m above the ground with the exception of geometrid larvae which were up to eight times as abundant in the canopy.

Analysis of temporal and spatial variation. Analysis of variance showed that for some of the major taxa much of the variation in captures within each sampling period was caused by daily fluctuations in abundance. This was the case for three of the six sampling periods analyzed for Nematocera (including Chironomidae, Culicidae and other families) and in two sampling periods for the 'advanced' flies (Cyclorrhapha and Brachycera). The other emergent groups, Trichoptera and Ephemeroptera, were lumped into the 'other adults' category and the variation within sampling periods was not compared.

A large proportion of the total variation in Homopteran abundance was between blocks on the same day in three sampling periods. In most taxa the variation between the five

days and between the two blocks of cells was not significant when compared with the degree of variation between adjacent cells. This variation included random differences in invertebrate populations between the two sampling sites within one block as well as differences in habitat and other physical and biological properties of the individual sampling sites.

Prey Selection

Selection of taxa. The ranked importance of invertebrate groups in wren stomachs collected in 1981 did not correlate significantly with their rank abundance as estimated by sweep-net samples in any of the sample periods in 1981 (Table 5). The significant correlation between the numbers eaten and available in the 39 categories of taxa and size classes (Table 5) suggests selective predation on certain size-classes within the original 13 taxonomic groups. When the estimated dry weight of the prey items in wren stomachs and sweep-net samples was used instead of raw abundance the effects of size-selective predation were minimized.

Absolute numbers of prey available were not significantly correlated with the biomass of the prey items in wren stomachs. Biomass eaten compared with biomass available, and number eaten compared with biomass available, were correlated significantly in four and three of the seven sampling periods, respectively. The best overall correlation,

Table 5. Spearman's correlation coefficients, and the probability of a greater correlation, for the comparisons of invertebrate taxa in House Wren stomachs and sweep net samples in the seven sampling periods in 1981, and in all periods when size classes within taxa are considered.

VARIABLES	SAMPLING PERIOD (number of categories)							
	ONE(13)	TWO(13)	THREE(13)	FOUR(13)	FIVE(13)	SIX(13)	SEVEN(13)	ALL PERIODS(36)
Number Eaten	0.4266	0.3525	0.0377	0.1765	0.4098	0.3622	0.3764	0.3627
Number Available	NS*	NS	NS	NS	NS	NS	NS	0.0233
Biomass Eaten	0.2000	0.0739	-0.0838	0.0173	0.4132	0.4764	0.4465	0.0872
Number Available	NS	NS	NS	NS	NS	NS	NS	NS
Biomass Eaten	0.1889	0.4374	0.6040	0.2832	0.6010	0.7494	0.6556	0.2952
Biomass Available	NS	NS	0.0288	NS	0.0298	0.0032	0.0150	NS
Number Eaten	0.3984	0.5559	0.7363	0.4833	0.5056	0.6679	0.3792	0.5332
Biomass Available	NS	0.0485	0.0048	NS	NS	0.0126	NS	0.0005

* $P > 0.05$

especially considering the comparison of the 39 size and taxonomic categories, was the rank of the number of prey items of each taxonomic category in wren stomachs and the ranks of the biomass of those prey items in sweep samples (Table 5).

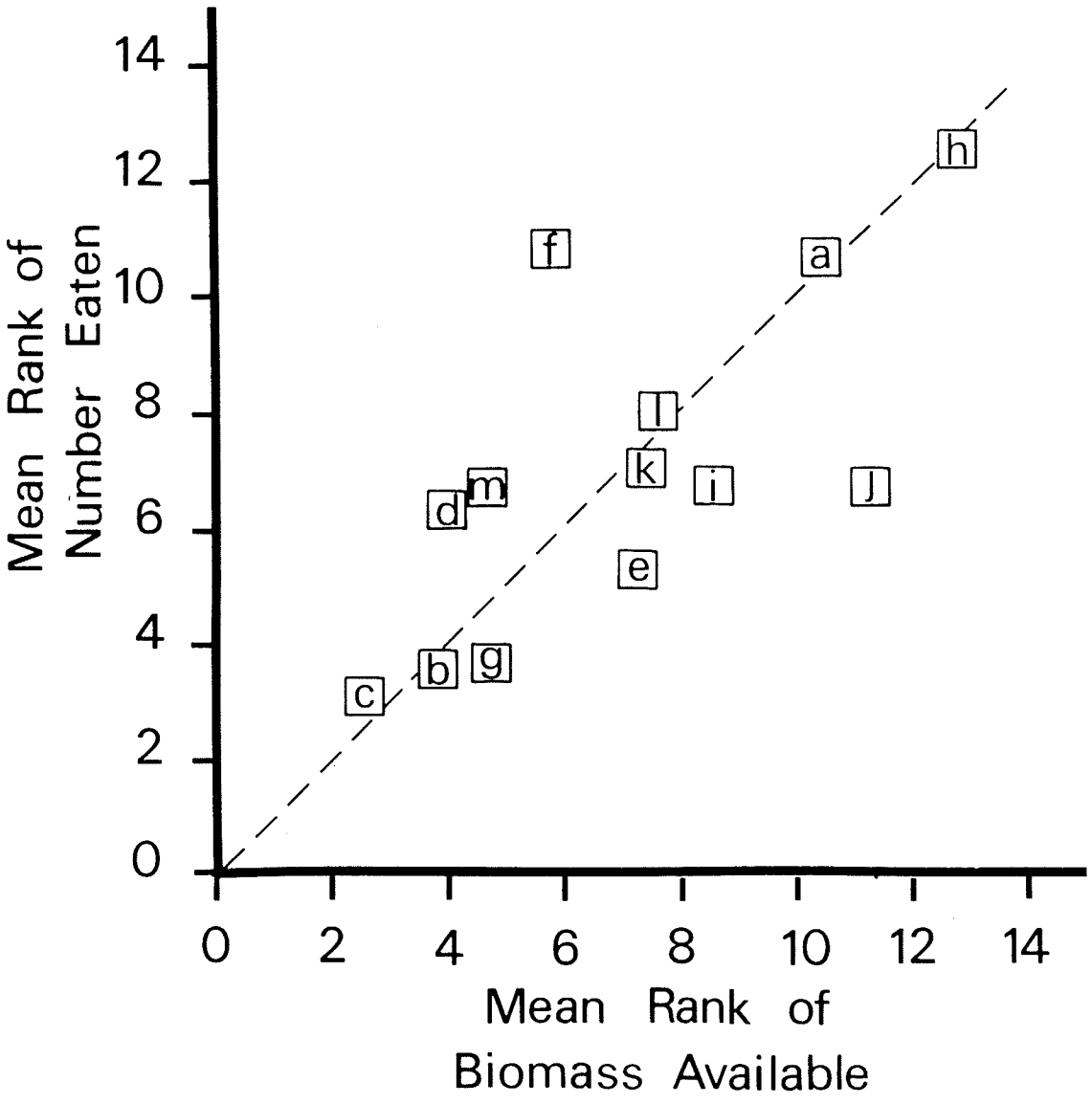
An examination of the ranks of the number of each prey category eaten and the biomass 'available' (Table 6) reveals further information on the relationship between the wren diets and the availability of prey. The large positive overall mean difference of Coleopterans resulting from a consistently higher rank in wren stomachs than in sweep nets suggests active selection by wrens. Another possibility is that sweep-net sampling underestimated the actual abundance or the actual availability of beetles to foraging wrens. For example, if beetles were associated with woody substrates not penetrable by a sweep net. The ranks of the number eaten and the biomass available show an equally consistent rejection of 'advanced' flies leading to similar questions of the availability and suitability of these insects as prey.

The correlation between the mean rank of the number of each category eaten and the mean rank of the biomass of each category available (Figure 7) was significant ($r = 0.59$, $P < 0.05$). The mean rank of the number of each category eaten was not significantly correlated with the rank of the number available (not adjusted for biomass) further supporting the influence of size on prey selection by wrens.

Table 6. The number of each invertebrate category eaten by House Wrens (E) and the biomass (mg) available (A), as estimated by sweep-net samples in the seven sampling periods in 1981.

	SAMPLING PERIOD													
	ONE		TWO		THREE		FOUR		FIVE		SIX		SEVEN	
TAXA	E	A	E	A	E	A	E	A	E	A	E	A	E	A
Araneida	10	62.1	4	396.8	9	428.3	8	446.5	5	276.2	3	743.1	8	772.8
Other Arachnida	0	0.4	0	19.7	0	41.1	0	106.5	0	140.1	1	135.6	0	116.4
Collembola	0	0	0	24.4	0	111.8	0	45.7	0	17.7	0	89.8	0	68.9
Hemiptera	1	2.9	3	4.8	0	18.0	0	47.7	0	61.8	4	301.6	4	302.7
Homoptera	0	27.0	2	93.2	0	61.5	1	163.6	0	292.2	1	358.4	1	295.1
Coleoptera	5	18.5	23	209.7	2	260.9	7	246.6	3	79.1	4	31.0	11	31.1
Culicidae	5	0	0	25.6	0	174.8	0	456.6	0	181.6	0	64.8	0	111.8
Chironomidae	15	54.3	18	122567.4	29	22363.4	55	5731.9	76	41617.0	42	66865.3	8	7950.6
Other Nematocera	10	4.8	5	342.3	3	780.9	2	948.5	0	272.6	0	137.2	0	194.2
Cyclorrhapha and Brachycera	1	8.7	1	590.4	1	875.2	1	2554.4	1	3269.2	1	1360.4	3	883.0
Hymenoptera	1	3.2	0	157.6	0	200.3	0	327.9	15	269.2	1	381.1	9	266.5
Other Adults'	7	0.3	1	27.1	2	54.0	0	328.4	2	613.7	7	1412.3	2	515.6
Larvae	1	0	5	116.6	12	261.2	6	223.6	0	107.2	0	70.7	0	77.7
Spearman's r	0.3984		0.5559		0.7363		0.4833		0.5056		0.6679		0.3792	
P< |r|	P>0.05		0.0485		0.0048		P>0.05		P>0.05		0.0126		P>0.05	

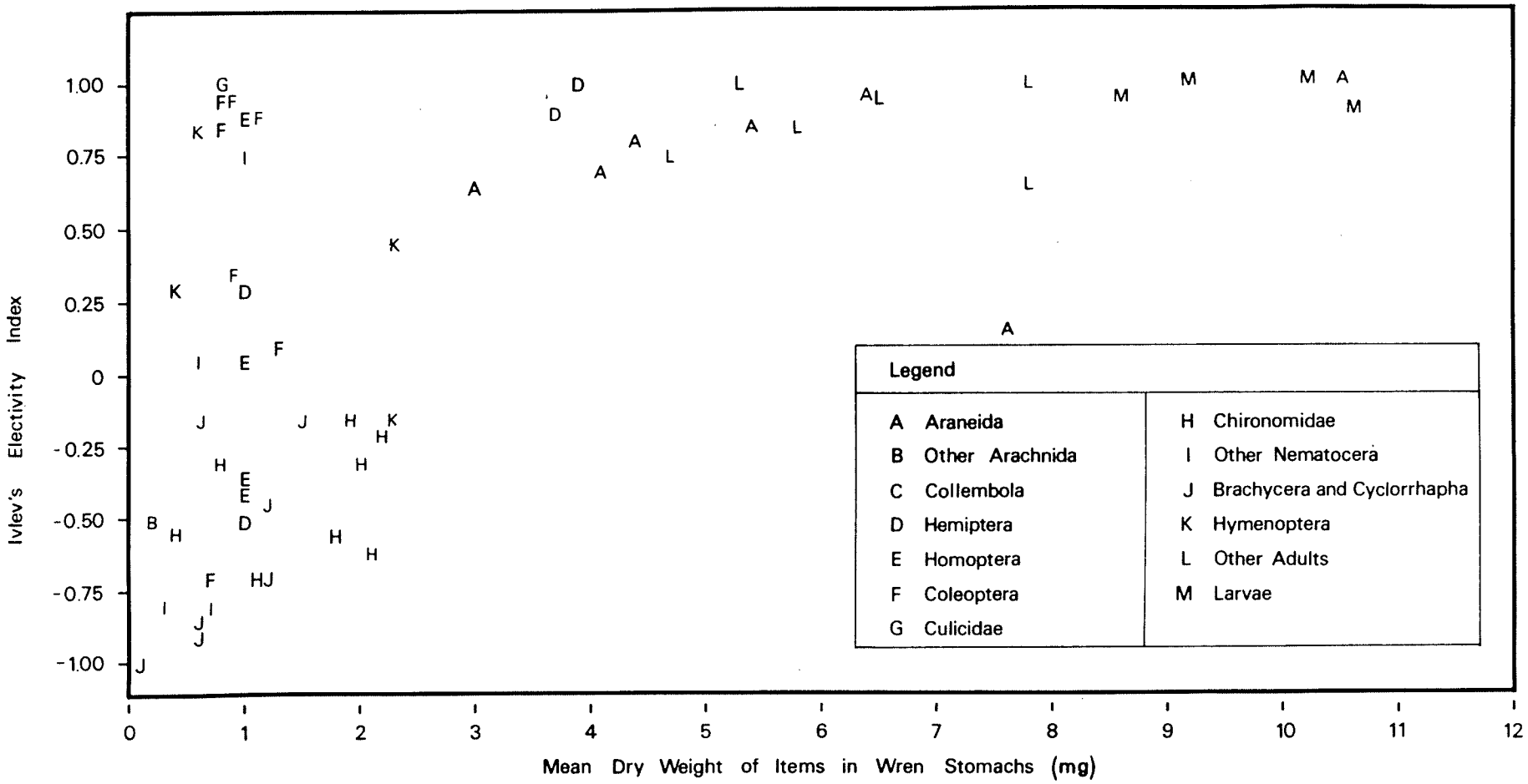
Figure 7. The rank of each invertebrate category in House Wren stomachs averaged over 7 sampling periods in 1981 and the mean rank of invertebrate biomass available in sweep-net samples in 1981 (higher ranks denote higher values; key to taxa: a = Araneida, b = Other Arachnida, c = Collembola, d = Hemiptera, e = Homoptera, f = Coleoptera, g = Culicidae, h = Chironomidae, i = Other Nematocera, j = Brachycera and Cyclorrhapha, k = Hymenoptera, l = Other Adults, m = Larvae).


Mean Rank of Number Eaten
14
12
10
8
6
4
2
0
0
2
4
6
8
10
12
14
Mean Rank of Biomass Available
a
b
c
d
e
f
g
h
i
J
k
l
m

Since chironomids were of great importance in the diet, comparisons of the selection of them by wrens with other diet variables are illuminating. Dietary diversity (Brillouin diversity index, Sherry 1984) showed a non-significant negative relationship with the mean number of chironomids eaten per bird in the seven sampling periods of 1981 ($r = -0.51$, $P > 0.05$). Similarly, the Spearman's coefficient for the correlation between number of each taxa eaten and rank of the biomass available increased when the abundance of chironomids increased ($r = 0.62$, $n = 7$, $P > 0.05$).

Size selection. The mean dry weight of prey items in each taxonomic category was positively correlated with the mean dry weight of the same taxa in sweep-net samples ($r = 0.47$, $df = 89$, $P < 0.001$). In general, when more of the large sizes of a taxon were available, larger individuals were also consumed more by wrens. Only larvae showed a significant correlation by themselves ($r = 0.93$, $df = 5$, $P < 0.001$) and some taxa, including chironomids, had a non-significant negative relationship between the mean biomass available and eaten. In addition, in sample periods when the mean dry weight of a prey taxon increased, that taxon was also selected in greater proportion than expected on the basis of its availability as measured by Ivlev's electivity index. This relationship was significant ($r = 0.58$, $df = 54$, $P < 0.001$) when all prey categories and sample periods were considered (Figure 8).

Figure 8. The electivity index values and the mean dry weight of invertebrates eaten by House Wrens in seven sampling periods in 1981 (excluding periods when no prey of a given taxon were eaten, n = 56).


Ivlev's Electivity Index
1.00
0.75
0.50
0.25
0
-0.25
-0.50
-0.75
-1.00
0
1
2
3
4
5
6
7
8
9
10
11
12
Mean Dry Weight of Items in Wren Stomachs (mg)
Legend
A Araneida
B Other Arachnida
C Collembola
D Hemiptera
E Homoptera
F Coleoptera
G Culicidae
H Chironomidae
I Other Nematocera
J Brachycera and Cyclorrhapha
K Hymenoptera
L Other Adults
M Larvae

The sizes of chironomids in wren stomachs compared with those collected in sweep-net samples (Figure 9) showed that chironomids $\geq$ 9 mm in length were eaten more than available only in one sampling period, while smaller sizes were often selected more than their abundance would predict. The proportion of chironomids in three size classes eaten by House Wrens was independent of the proportion available in six sampling periods (SP1: $G = 22.36$, $P < 0.001$; SP2: $G = 4.66$, $P > 0.05$; SP3: $G = 12.76$, $P < 0.005$; SP4: $G = 14.35$, $P < 0.001$; SP5: $G = 157.50$, $P < 0.001$; SP6: $G = 56.98$, $P < 0.001$; SP7: $G = 12.81$, $P < 0.005$; $df = 2$ in all cases). These comparisons, however, are based on the number of chironomids of known size in wren stomachs and all require cautious interpretation because of small cell totals.

The contribution of small chironomids (3.0 - 8.9 mm) to House Wren diets in 1981 decreased as their contribution to the available food resources, estimated by sweep-net sampling, increased (Figure 10). This relationship was significant only when the datum from sampling period 1 was omitted ($r = -0.9493$, $n = 6$, $P < 0.01$). Selection of chironomids in period 1 was probably limited by their low absolute abundance (less than 4% of the next lowest sampling period total).

Figure 9. Percentage of chironomids in each size class eaten by House Wrens and available in sweep samples for each sampling period in 1981, and all periods combined (size class B = 3.0 - 5.9 mm, C = 6.0 - 8.9 mm, D $\geq$ 9.0 mm).

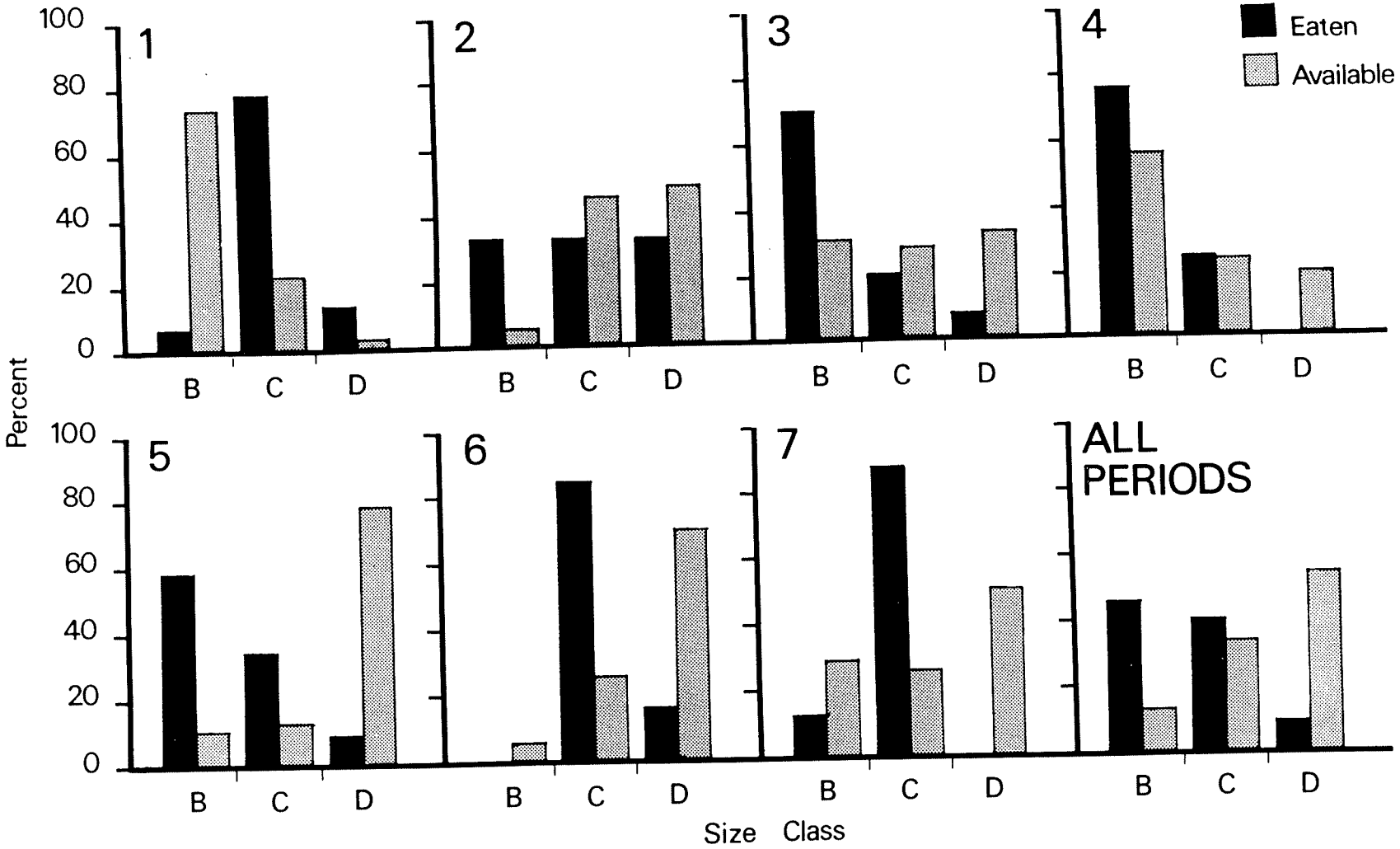
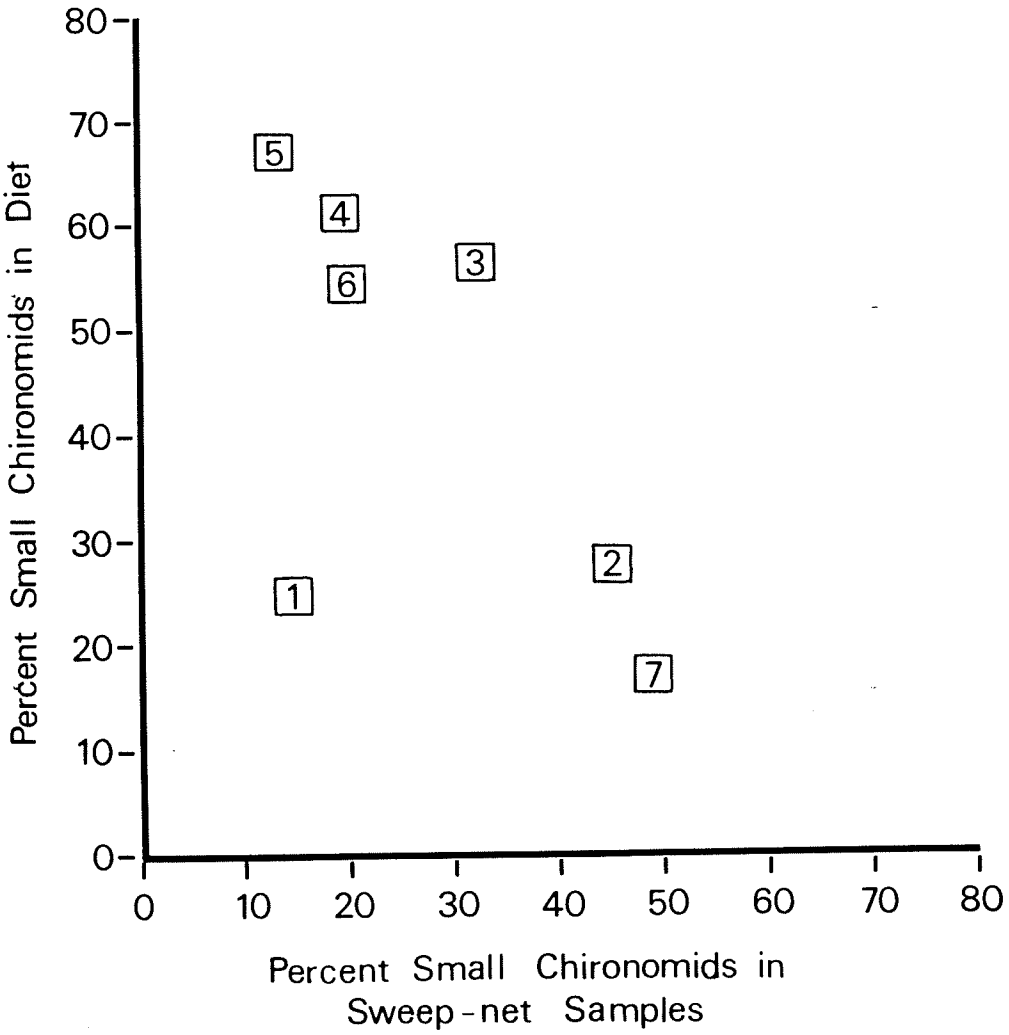

Eaten
Available
Percent
100
80
60
40
20
0
1
2
3
4
5
6
7
ALL PERIODS
B
C
D
Size Class

Figure 10. Contribution of small chironomids to House Wren diets (% of all prey items) and their proportion in sweep-net samples in seven sampling periods in 1981.


Percent Small Chironomids in Diet
80
70
60
50
40
30
20
10
0
5
4
6
3
2
1
7
0
10
20
30
40
50
60
70
80
Percent Small Chironomids in Sweep-net Samples

Foraging Behaviour

Five major factors that were tested for their effects on House Wren foraging (time of season, stage in nesting cycle, time of day, nest location, and gender) interacted significantly (Table 7). For example, the limited number of nesting pairs available for observation and their asynchrony in breeding activity made it difficult to distinguish the effects of sample period and nest location. There was no significant difference in the proportion of each gender observed in each stage of the nesting cycle (Table 7). The sex of the birds observed foraging varied significantly between sampling periods but this was influenced by a shift from a high proportion of males observed in sampling periods 3 and 4 (70.4% and 63.6%, respectively) to more equal proportions of the sexes in sampling periods 5, 6, and 7 (46.5%, 50.9%, and 54.6%, respectively).

The interaction of gender with nest location (Table 7) may have been influenced by the difficulty of determining the sex of foraging birds at certain nests. At four nests where more than 20% of the observations were on birds of unknown sex, the average percentage of males seen foraging was 63.2 while at four nests where sex was determined for at least 80% of the observations, 56.0% of foraging observations were by male wrens. Within this latter group there was no significant interaction of sex and nest ($G = 6.16$, $df = 3$, $P > 0.05$), while the former group was marginally significant ($G = 8.28$, $df = 3$, $P < 0.05$).

Table 7. The degree of heterogeneity (G statistic) in the interactions of the five variables used to examine House Wren foraging behaviour (number of observations = 449, except comparisons involving nest stage = 415).

	N	SAMPLE PERIOD	GENDER	NEST STAGE	NEST SITE	TIME OF DAY
SAMPLE PERIOD	5	—	11.26 **	549.74 ***	548.74 ***	100.40 ***
GENDER	2	—	—	6.89 NS	27.86 ***	164.11 ***
NEST STAGE	4	—	—	—	558.22 ***	68.28 ***
NEST SITE	11	—	—	—	—	202.09 ***
TIME OF DAY	4	—	—	—	—	—

** 0.025, *** 0.010.

Prey capture methods. Wrens foraged primarily by gleaning; birds hovered in 12.8% of recorded attempts, and other maneuvers accounted for only 4.7% of all observations. For statistical validity the proportion of gleans was compared with the combined frequency of all other foraging methods, ensuring adequate cell frequencies (Figure 11). There was no significant difference in the frequency of foraging methods used by wrens in the four time-of-day categories ($G = 5.18$, $n = 364$, $df = 3$, $P > 0.05$). The proportion of gleans used in prey capture attempts did not change significantly as the breeding cycle progressed ($G = 4.21$, $n = 159$, $df = 3$, $P > 0.05$). Female House Wrens used significantly fewer alternate foraging maneuvers than males ($G = 11.56$, $n = 288$, $df = 1$, $P < 0.01$). The proportion of gleans varied significantly ($G = 32.60$, $n = 324$, $df = 9$, $P < 0.001$) between the 10 observation nests with no apparent pattern relating to the interaction of seasonal or gender effects. The method of capture was significantly dependent on the sampling period ($G = 14.59$, $n = 360$, $df = 4$, $P < 0.01$) though the effect of nest probably contributes to this variation.

Foraging station. There was a significant difference in the proportion of the four stations at which wrens were observed foraging in the four time-of-day periods ($G = 47.28$, $n = 639$, $df = 9$, $P < 0.001$). The greatest shift in the use of foraging stations involved an increased use of dead and live unfoliated vegetation in the evening (Figure 12). The use

Figure 11. The percentage of gleans and other prey capture maneuvers within each category of the five foraging variables (EM = early morning, LM = late morning, A = afternoon, E = evening; E = establishment, L = laying, I = incubation, N = nestling; M = male, F = female).

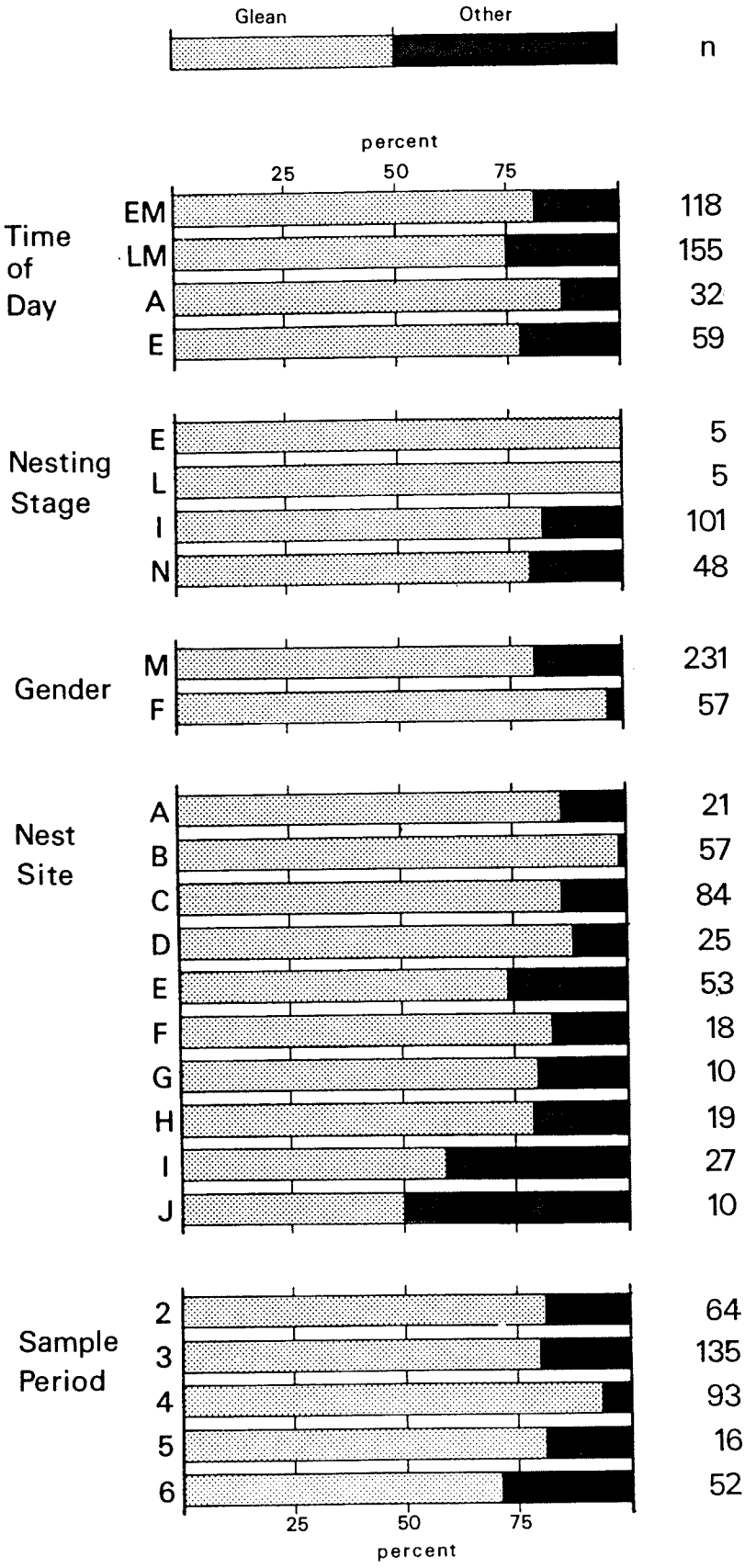
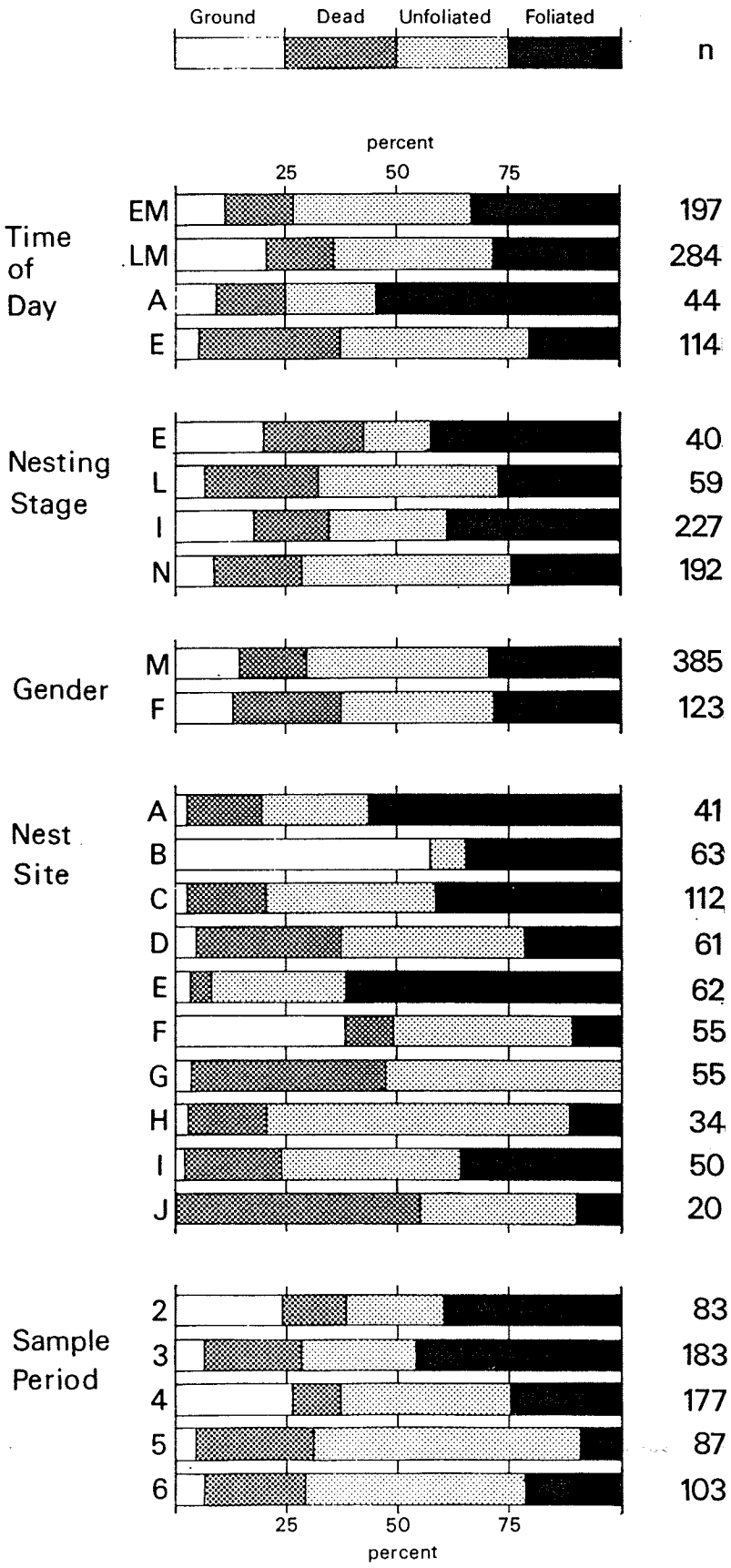

Glean
Other
n
percent
25
50
75
Time of Day
EM
LM
A
E
118
155
32
59
Nesting Stage
E
L
I
N
5
5
101
48
Gender
M
F
231
57
Nest Site
A
B
C
D
E
F
G
H
I
J
21
57
84
25
53
18
10
19
27
10
Sample Period
2
3
4
5
6
64
135
93
16
52
25
50
75
percent

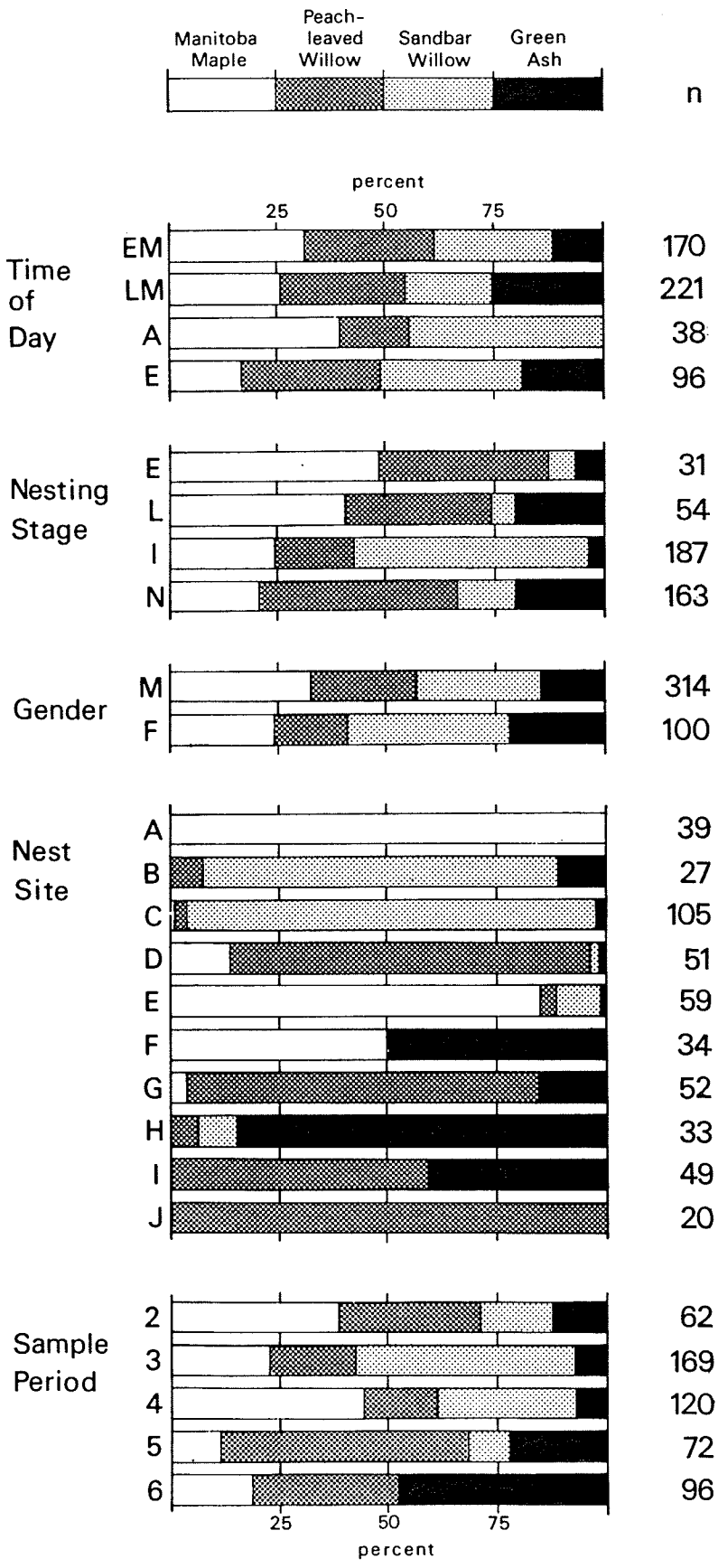
Figure 12. The percentage use of the four categories of foraging station within each division of the five foraging variables.


Ground
Dead
Unfoliated
Foliated
n
percent
25
50
75
Time of Day
EM
LM
A
E
197
284
44
114
Nesting Stage
E
L
I
N
40
59
227
192
Gender
M
F
385
123
Nest Site
A
B
C
D
E
F
G
H
I
J
41
63
112
61
62
55
55
34
50
20
Sample Period
2
3
4
5
6
83
183
177
87
103
25
50
75
percent

of foraging stations differed significantly with the stages of the nesting cycle ($G = 38.35$, $n = 518$, $df = 9$, $P < 0.001$), the sampling period ($G = 118.84$, $n = 633$, $df = 12$, $P < 0.001$), and the nest site ($G = 305.15$, $n = 627$, $df = 30$, $P < 0.001$). Male and female wrens used similar proportions of the four foraging stations ($G = 4.89$, $n = 508$, $df = 3$, $P > 0.05$).

Plant species. The plant species in which House Wrens foraged varied significantly between the four time-of-day periods ($G = 43.33$, $n = 525$, $df = 9$, $P < 0.001$). The use of substrates in the four recognized stages in the breeding cycle also differed significantly ($G = 128.10$, $n = 435$, $df = 9$, $P < 0.001$). Manitoba maple (Acer negundo) and peach-leaved willow (Salix amygdaloides) remained important throughout, but the wrens' use of green ash (Fraxinus pennsylvanica) and sandbar willow (S. interior) varied (Figure 13). There was a great deal of heterogeneity in the proportion of each plant species used in different sampling periods ($G = 202.29$, $n = 519$, $df = 12$, $P < 0.001$). This seasonal variation was probably related to the more influential effect of nest location on tree species use ($G = 848.78$, $n = 469$, $df = 27$, $P < 0.001$). Males foraged slightly more in maples and peach-leaved willows while females used sandbar willows and ashes more often ($G = 7.93$, $n = 414$, $df = 3$, $P < 0.05$).

Figure 13. The percentage of each plant species upon which House Wrens foraged within each division of the five foraging variables.


Manitoba Maple
Peach-leaved Willow
Sandbar Willow
Green Ash
n
percent
25
50
75
Time of Day
EM
LM
A
E
170
221
38
96
Nesting Stage
E
L
I
N
31
54
187
163
Gender
M
F
314
100
Nest Site
A
B
C
D
E
F
G
H
I
J
39
27
105
51
59
34
52
33
49
20
Sample Period
2
3
4
5
6
62
169
120
72
96
25
50
75
percent

Perch type. There was no significant difference ($G = 5.18$, $n = 507$, $df = 4$, $P > 0.05$) in the proportion of each perch type used by male and female wrens (Figure 14). Perch use varied considerably with time of day but when the ground foraging observations were excluded, and the afternoon and evening periods are combined to increase cell frequencies, there is no significant difference in perches used by time-of-day category ($G = 12.21$, $n = 549$, $df = 6$, $P > 0.05$). In examining the types of perches used in the different stages of the nesting cycle there was significant heterogeneity ($G = 60.66$, $n = 452$, $df = 6$, $P < 0.001$) even when ground foraging was excluded and the pre-incubation stages were grouped to increase low cell frequencies. Wrens initiated more capture attempts from trunks and fewer from branches as the season progressed, and twig use peaked in sampling periods 3 and 6. The seasonal use of perches was highly variable ($G = 134.40$, $n = 632$, $df = 16$, $P < 0.001$). The perch types used by pairs of wrens at each nest were too variable to allow statistical comparison. Frequently only two or three perch types were used at each nest.

Plant height. House Wrens foraged on plants of different heights in the four daytime periods ($G = 54.51$, $n = 318$, $df = 8$, $P < 0.01$). Wrens foraged in taller plants in the late morning, possibly reflecting the nest sites that were visited most frequently in each daytime period (Figure 15). The interaction that nest location exerts was also apparent when

Figure 14. The percentage use of the five categories of perch within each division of the five foraging variables.

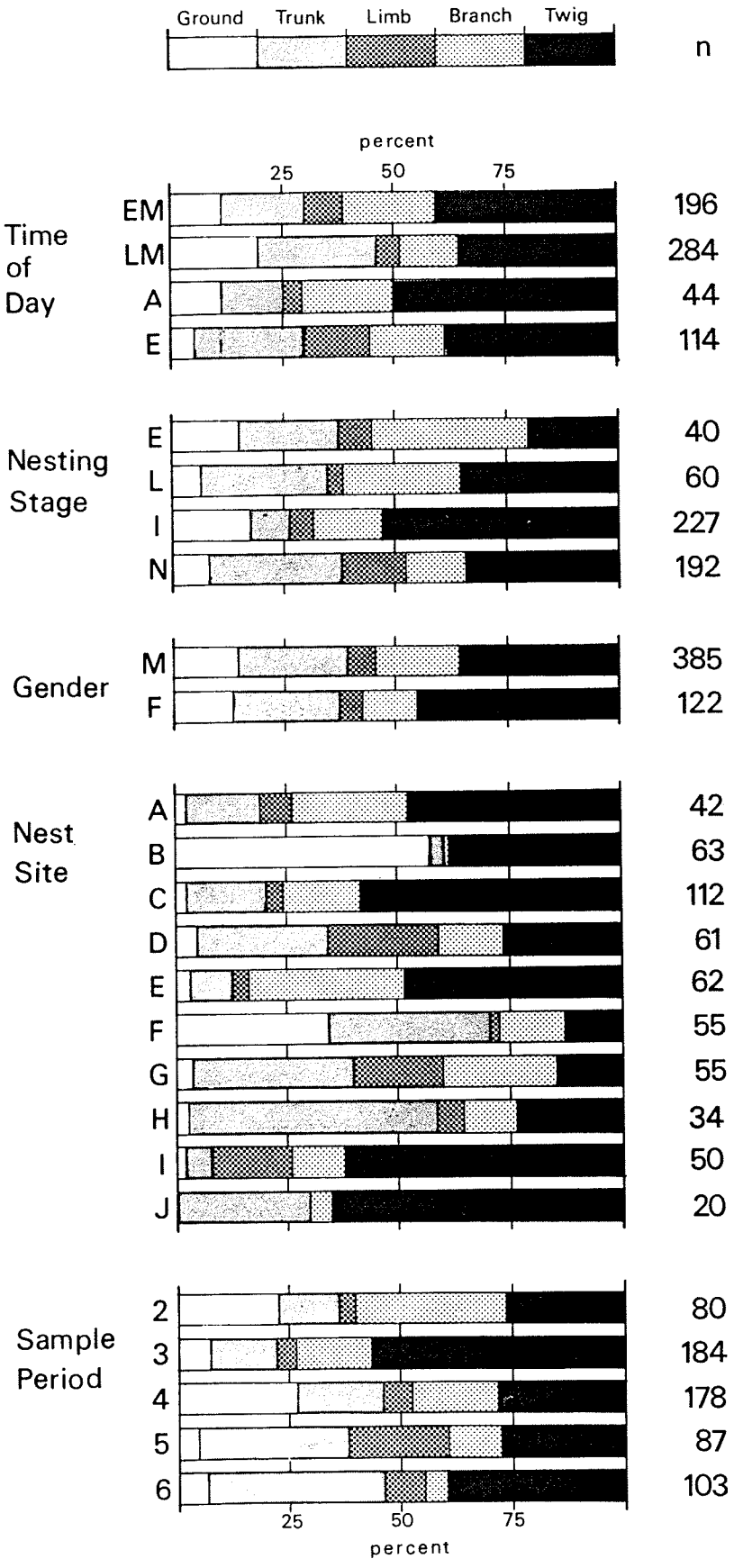
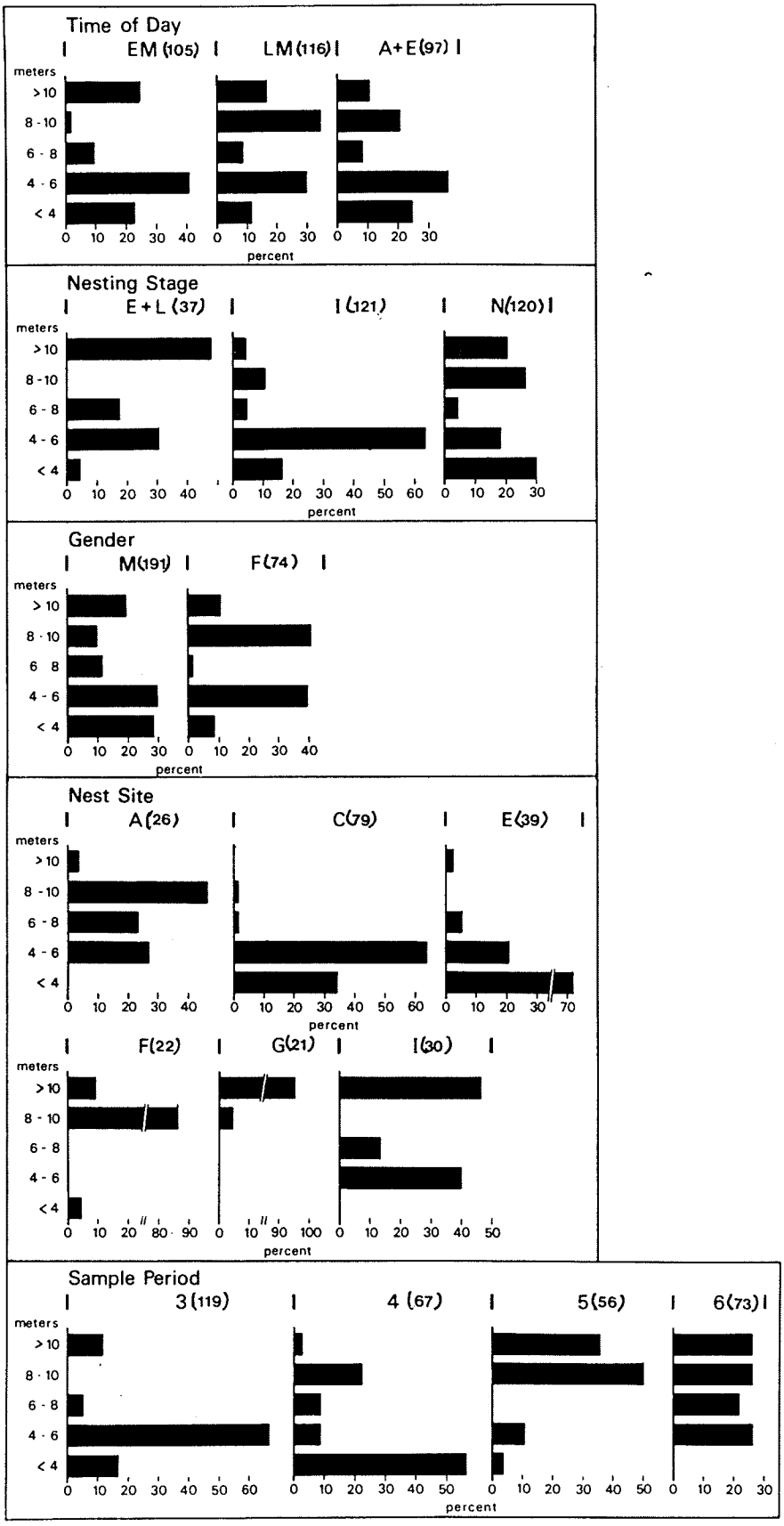

Ground
Trunk
Limb
Branch
Twig
n
percent
25
50
75
Time of Day
EM
LM
A
E
196
284
44
114
Nesting Stage
E
L
I
N
40
60
227
192
Gender
M
F
385
122
Nest Site
A
B
C
D
E
F
G
H
I
J
42
63
112
61
62
55
55
34
50
20
Sample Period
2
3
4
5
6
80
184
178
87
103
25
50
75
percent

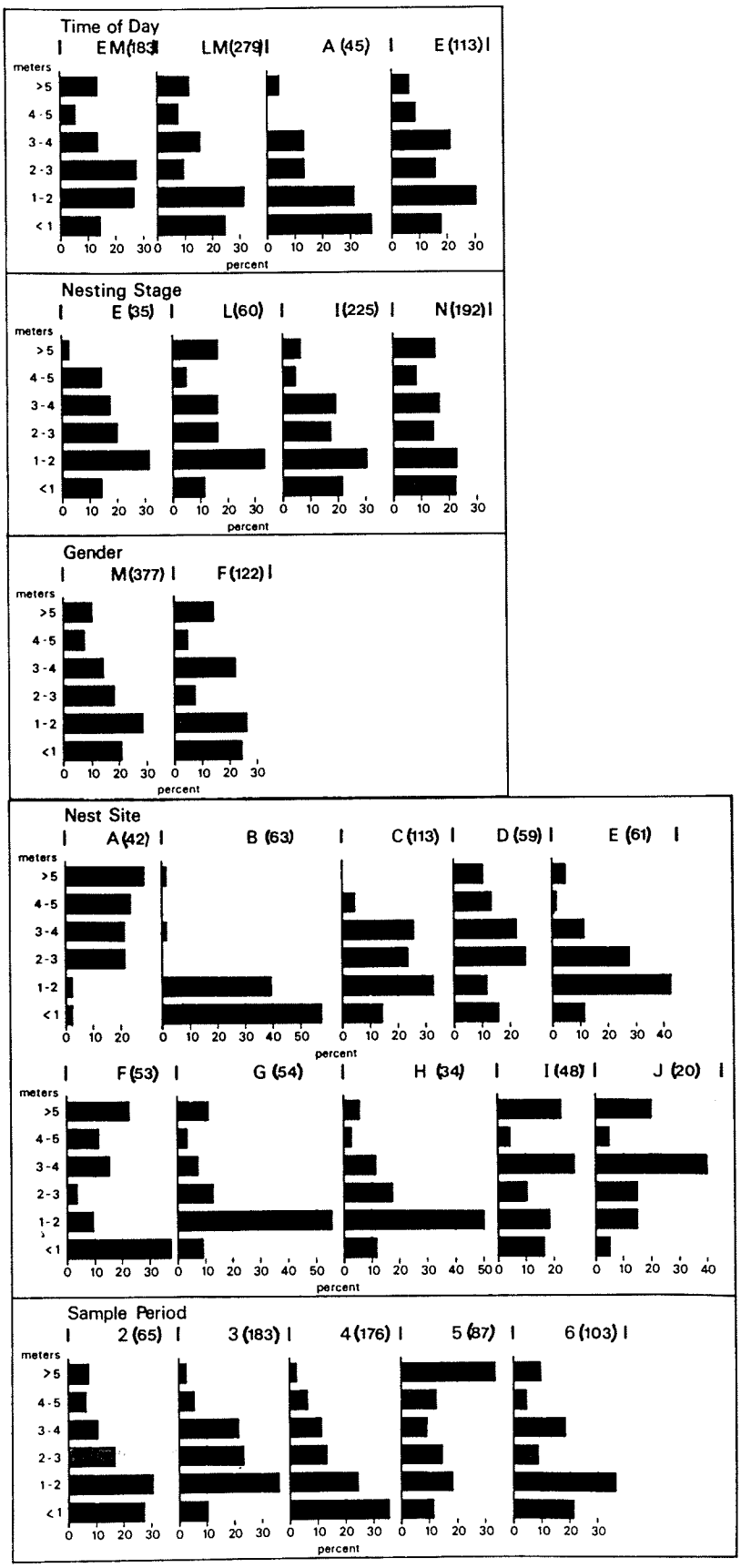
Figure 15. The heights of the plants used by foraging House Wrens within each division of the five foraging variables.


Time of Day
EM (105)
LM (116)
A+E (97)
meters
> 10
8 - 10
6 - 8
4 - 6
< 4
0 10 20 30 40
0 10 20 30
0 10 20 30
percent
Nesting Stage
E + L (37)
I (121)
N (120)
meters
> 10
8 - 10
6 - 8
4 - 6
< 4
0 10 20 30 40
0 10 20 30 40 50 60
0 10 20 30
percent
Gender
M (191)
F (74)
meters
> 10
8 - 10
6 8
4 - 6
< 4
0 10 20 30
0 10 20 30 40
percent
Nest Site
A (26)
C (79)
E (39)
meters
> 10
8 - 10
6 - 8
4 - 6
< 4
0 10 20 30 40
0 10 20 30 40 50 60
0 10 20 30 70
percent
F (22)
G (21)
I (30)
meters
> 10
8 - 10
6 - 8
4 - 6
< 4
0 10 20 80 90
0 10 90 100
0 10 20 30 40 50
percent
Sample Period
3 (119)
4 (67)
5 (56)
6 (73)
meters
> 10
8 - 10
6 - 8
4 - 6
< 4
0 10 20 30 40 50 60
0 10 20 30 40 50
0 10 20 30 40 50
0 10 20 30
percent

the stage of the nesting cycle ($G = 59.92$, $n = 241$, $df = 4$, $P < 0.01$) and sampling period ($G = 212.62$, $n = 315$, $df = 6$, $P < 0.001$) were compared to the height of plants on which wrens foraged. The proportion of all observations over 6 m at each nest was bimodally distributed with four nests ranging from 0-25% of observations and six nests ranging from 60-100% of observations in plants more than 6 m tall. There was also significant heterogeneity in the heights of the plants in which male and female wrens foraged ($G = 45.49$, $n = 265$, $df = 4$, $P < 0.01$).

Height of foraging wrens. Wrens foraged at significantly different heights during the four daytime periods ($G = 48.96$, $n = 620$, $df = 15$, $P < 0.01$). They shifted to heights less than 1 m during the late morning and afternoon with a greater proportion of observations at moderate heights (2-4 m) in the early morning and evening (Figure 16). There was a marginally significant difference in the heights of foraging in the four stages of the nesting cycle ($G = 17.24$, $n = 512$, $df = 10$, $P > 0.05$) which becomes significantly more distinct if the establishment and laying stages are grouped to increase sample size and cell frequencies. The height at which wrens foraged did not vary independently of the time of season ($G = 112.27$, $n = 614$, $df = 20$, $P < 0.01$). If foraging heights are grouped so that the proportion of observations at each nest above and below 3 m are compared, there was a highly significant difference between nests ($G =$

Figure 16. The heights at which House Wrens were seen foraging within each division of the five foraging variables.


Time of Day
EM(183)
LM(279)
A (45)
E (113)
Nesting Stage
E (35)
L(60)
I(225)
N(192)
Gender
M(377)
F(122)
Nest Site
A(42)
B (63)
C(113)
D(59)
E (61)
F(53)
G (54)
H (34)
I(48)
J (20)
Sample Period
2 (65)
3 (183)
4(176)
5 (87)
6 (103)
meters
>5
4-5
3-4
2-3
1-2
<1
percent

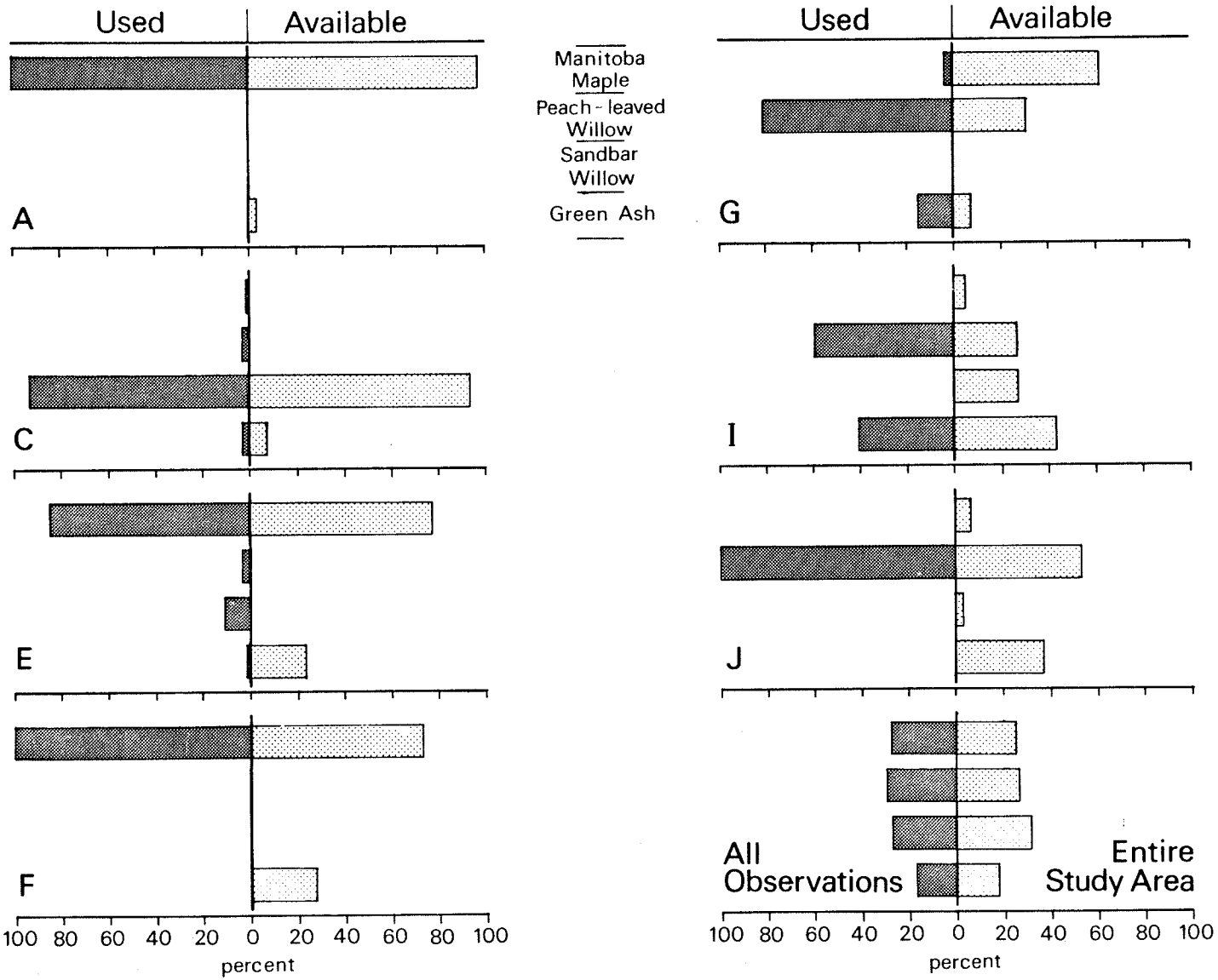
115.78, n = 608, df = 10, $P < 0.01$). The effect of gender was also significant ($G = 15.01$, n = 499, df = 5, $P < 0.05$), but the pattern suggests an effect of nest location rather than a biologically relevant segregation.

Substrate Selection

House Wren foraging was influenced by the availability of the four major tree species at seven nests where the availability of plant substrates was measured (Figure 17). Observations at six nests were largely within 10 m of the nest ($\bar{X} = 79.88$ %, SD = 11.65, n = 312). Only 27.9 % of observations of foraging wrens at site 'E' were within the radius for which substrate availability was measured but substrates were still used in approximate proportion to their availability. Only three nest sites had peach-leaved willow available within 10 m and at each of these sites this species was used in greater proportion than expected. Wrens at six of the seven nests with green ash available as a foraging substrate used it less than expected.

The proportion of those plant species used by foraging wrens at all nests did not differ significantly ($X^2 = 4.98$, n = 518, $P > 0.05$) from their availability as determined by MacKenzie (1982) for the entire study area (Figure 17). This implies that foraging wrens did not consistently select or avoid certain tree species or that they were unable to select nest sites so as to increase the proportion of preferred substrates in the habitat surrounding their nests.

Figure 17. The availability (% of tree stems within 10m) and usage (% of observations) of plant substrates for foraging by House Wrens at seven nest sites (A _ J), and for the study area as a whole.


Used
Available
A
C
E
F
Manitoba Maple
Peach-leaved Willow
Sandbar Willow
Green Ash
G
I
J
All Observations
Entire Study Area
100 80 60 40 20 0 20 40 60 80 100
percent

DISCUSSION

Although House Wren foraging strategies have not been well documented, the birds in this study appear to have been highly opportunistic in foraging behaviour and diet. Wrens used foliage gleaning and included chironomids in their diets more than would be expected from previous descriptions of their foraging behaviour (Beal et al. 1916, Bent 1948, McAtee 1940). This opportunism was apparent in the variation in foraging maneuvers and substrates used by wrens at different nest sites. The prey items eaten by individual wrens also varied greatly and seasonal patterns in the use of major invertebrate categories were described.

Several factors could account for the large variation in foraging behaviour exhibited by House Wrens at different nest sites. Individual preferences, probably related to the developmental history of the individuals, have been described in several species of birds for their choice of microhabitats (Goss-Custard and Durell 1983), prey types (Durell and Goss-Custard 1984) and foraging maneuvers (Partridge 1976). The distribution of prey could also affect the foraging behaviour observed at each nest. If prey were distributed in patches then the exploitation of particular patches could lead to large differences in behaviour between

nests. The selection of substrates by House Wrens, however, indicates that tree species were used in proportion to their availability at each nest suggesting that prey were randomly or (considering the abundance of invertebrates) evenly distributed around each nest. Large inter-nest variation in the foraging parameters measured seems best explained by the random use of substrates and foraging maneuvers according to the local conditions near each nest.

Evidence suggests that House Wrens did not eat items directly in proportion to their abundance. The ranks of prey categories in the diets were not significantly correlated with the ranks of the same taxa captured in sweep-net samples during the same period. Even in sampling periods where some correlation existed in the comparisons using the estimated biomass of prey available (Table 4) the raw data often indicated selection by foraging wrens. In sample period two, for example, chironomids represented 88.7 % of the invertebrates caught in sweep nets but more beetles than chironomids were eaten.

While the proportions of the major prey categories in the diet varied seasonally, the relative contribution of each taxon was not correlated with its abundance. Within taxonomic groups different size classes were not included in the diet in proportion to their abundance. Small chironomids were eaten more than expected considering their abundance, yet all sizes were apparently acceptable food items

because they were often eaten by the same individuals. When all taxa were considered, selection by wrens increased when larger items were consumed (Figure 8) indicating that size is probably a criterion used by wrens in prey selection.

Two possible scenarios exist that might explain the differences between the invertebrates that wrens consumed and those sampled in sweep nets. First, the wrens may not have encountered the same types or proportions of prey items 'available' as determined by the sampling methods. Second, they may have rejected some of the prey that they encountered. In the first case, some taxa or certain groups may not be available to House Wrens. A food resource may be unavailable if it cannot be detected by the sensory apparatus of the predator or if the predator is not morphologically or behaviourally equipped to exploit it. Fitzpatrick (1981), for example, believed that species of tyrant flycatchers that hawk distant aerial prey probably have retinal or neuromuscular adaptations that differ from species which glean in dense vegetation. Similarly, bill size and tarsal length affect the foraging behaviours and diets of insectivorous passerines (Selander 1966, Hespenheide 1971, Greenberg 1981).

Johnson (1980) detailed how the subjective determination of what resources are available or suitable for a particular consumer can affect the evaluation of food selection. However, it is difficult to assess invertebrate

abundance without excluding some types which might be available to a predator. Sweep nets are widely used to sample insects in terrestrial foliage but probably underestimate the abundance of taxa which can avoid them (Southwood 1978) or are not easily dislodged from the substrate (Martin 1977). A major assumption of the examination of prey selection in this study was that sweep-netting provided a reasonably accurate sample of invertebrate abundance and that most of the invertebrates captured were actually available to foraging wrens.

Most of the food resources commonly encountered in the sweep net samples of foliage in this study were represented in the diets of the House Wrens sampled. Collembola were the only abundant taxa which were totally absent from stomach samples. This insect group may be too small to be detected or handled by House Wrens although Acari and Psocoptera, which were occasionally eaten, are about the same size. Alternatively, Collembola may be unsuitable because of nutritional constraints or their jumping escape behaviour.

The largest insects that were commonly encountered in sweep sampling were also represented in House Wren stomachs. These included large Ephemeroptera and both adult and larval Lepidoptera which probably approach the upper prey size limit for House Wrens. Dragonflies (Odonata: Anisoptera), which were not taken by the wrens examined, were rarely sampled by the methods used in this study but may have been

more abundant in localized areas. Annelids were common in the leaf litter and were within the maximum size of prey eaten but were apparently not consumed by wrens. They may not have been encountered with the search paths and foraging maneuvers commonly used by wrens on this study area.

The selection of feeding sites and maneuvers could affect the types or proportions of prey encountered by foraging wrens. Davies (1977) described how Spotted Flycathers (Muscicapa striata) actively searched for small prey in the canopy but hawked large prey from low perches in response to diel patterns of abundance of the preferred large prey. Tinbergen (1981), studying Starlings (Sturnus vulgaris) feeding on two prey species in two distinct microhabitats, found that the choice of prey type dictated which microhabitat was visited.

The wrens in this study used a broad range of microhabitats as indicated by their selection of foraging stations, heights and substrates. Much of the variation, at least for the plant species selected, was influenced by the availability of substrates near the nest. In this way variations in the habitats from which wrens were collected could alter the observed composition of the diet. Busby and Sealy (1979) found fewer arthropods on ashes than on maples and willows but gave no indication of compositional differences. Although differences relating to plant species and form are expected (Southwood et al. 1982), the ranked abundance may

not differ significantly as was found between the sticky traps and sweep net samples in this study.

Since the diet was determined from a small number of birds, and stomach contents probably reflect a limited amount of foraging prior to collection (Custer and Pitelka 1975), individual variation in foraging habits or random variation in habitat could affect the comparison of prey types eaten and available. This is especially so for taxa that fluctuated from day to day because of immigration from surrounding habitats and those with clumped distributions. For the most part, however, the ranks of prey types were not affected by random or directed variation as much as the raw data. In addition, the significant seasonal pattern of the wren diets indicates that the small number of stomachs sampled suitably estimated the diet of the wren population as a whole.

The observed differences in prey eaten and present in the habitat may be the result of active selection by the wrens or their rejection of some of the prey encountered. The profitability of prey as a criterion for selecting an optimal diet continues to be a major focus of interest in the foraging literature (Pyke 1984). Laboratory studies strongly suggest that prey are rejected and selected by predators on the basis of the profitability of different prey sizes (Krebs et al. 1977) and prey taxa (Zach and Falls 1978).

Optimal foraging theory predicts that the available prey categories will be ranked according to their profitability, defined as the net energy intake (gross energy less the amount needed to process the item) per unit of handling time (Krebs 1978). As less profitable items are included in the diet both the net food intake and the time needed to find the next acceptable item decrease. The optimal diet includes the most highly ranked items above the point at which the net food intake per unit time would decrease because of increased time spent handling less profitable items. The major advantage of this method of prey selection is in deciding which taxa to reject when items are encountered sequentially.

Three predictions of optimal diet models are generally used to test for evidence of optimal foraging (Pyke et al. 1977, Krebs 1978). The first holds that since prey are included in the diet according to their profitability, the probability that an item will be eaten does not depend directly on its abundance but only on the abundance of higher-ranked items. Several workers have examined the relationship between the abundance of large items and the proportion of small items in the diet. Turner (1982) found no correlation between these variables; the proportion of small items in the diet was related only to the relative abundance of small items. Goss-Custard (1977a) found that small prey were taken at a rate inversely proportional to the density of the large prey but not in direct proportion to their own density.

These studies examined the first prediction of optimal foraging theory assuming that the size of a prey item approximates its profitability. Goss-Custard (1977b) calculated profitability by measuring the net energy and handling time of prey items. He found that Redshanks (Tringa totanus) ate amphipods in proportion to their abundance and not relative to the abundance of more profitable polychaete prey. Size and profitability of prey differed in a laboratory study of Ovenbird (Seiurus aurocapillus) foraging (Zach and Falls 1978). Naive birds offered 12 prey types at first selected the types in proportion to their dry weight, but in later trials in proportion to the profitability of the prey items as calculated from their dry weight (less the weight of chitin), divided by the handling time.

In the present study, none of the prey categories were represented in the diet in proportion to their abundance over the seven sampling periods. Profitability, however, was not measured directly and the selection of small chironomids indicates that length or dry weight may not reliably estimate profitability. Furthermore, the sizes and species of prey available within the taxonomic categories probably changed between sampling periods making seasonal comparisons difficult. Thus, if small chironomids are assumed to have been the most profitable items, the first prediction of the optimal foraging model does not hold. The contribution small chironomids made to the wrens' diet decreased as the rela-

tive abundance of chironomids increased (although the correlation was significant only with the removal of one data point).

The second prediction of optimal diet models states that as the abundance of high-ranking prey increases (and therefore search time for the next acceptable prey item decreases) the predator becomes more specialized. There was a negative (though non-significant) relationship between dietary diversity and the mean number of chironomids per wren in the seven sampling periods of 1981. According to the second prediction this suggests that chironomids were profitable food items but, as previously noted, their proportion in the diet did not increase in correlation with their proportion in sweep-net samples. Apparently either chironomids were not highly profitable food items (although they were the most frequently eaten) or wrens did not specialize as the theory predicts.

The third prediction of optimal diet selection predicts that items are completely included or completely excluded from the diet on the basis of their profitability rank. Since actual encounters with prey were not recorded in this study and the invertebrates available to individual wrens probably varied greatly I could not determine if high-ranking prey were always selected and low-ranking prey always rejected. If chironomids were the most highly ranked prey it is doubtful that they were always eaten since they were ex-

tremely abundant during the second sampling period when wrens ate more beetles than chironomids.

Although selection of prey on the basis of profitability has been documented, most predators do not exclude prey of low profitability. In fact, most predators take a wide range of food even when the availability of profitable types is high (Schluter 1981). This is often considered to be the result of sampling available items to monitor their profitability (Krebs 1978) or mistaken identification in distinguishing prey types (Krebs et al. 1977, Rechten et al. 1983).

A third possible explanation is that selection for particular constituents of food items in an attempt to obtain a balanced diet leads to 'partial preferences' for most items (Pulliam 1975). Krebs and Avery (1984) found that the mixed diet of two prey types which European Bee-eaters (Merops apiaster) commonly feed to their nestlings resulted in a higher growth efficiency than pure diets of either prey type. Caloric assimilation did not differ in the three diets but chicks fed a mixed diet gained more weight per gram of food delivered to the nest apparently because of qualitative differences in prey composition.

Optimal diet selection models often ambiguously predict the diet patterns of predators in field studies (Schluter 1981) but some of the observations in this study seem best

explained by the use of profitability by wrens. The selection of small chironomids is difficult to explain on the basis of a different availability to wrens of large and small chironomids. Net energy content is often assumed to increase with increasing size within the same taxonomic group because the surface-area-to-volume ratio should decrease, giving a higher proportion of digestible protein (Jaeger and Barnard 1981). The assumption that exoskeletal thickness increases in proportion to total size may be false in some taxa. Small size classes of a particular prey group may also be more profitable than large size classes if the handling time increases dramatically with size.

The increase in the correlation between the prey categories eaten and available when the prey were ranked by the biomass available (Table 5) suggests that wrens selected prey on the basis of both abundance and size. Furthermore, a biologically relevant trend is apparent in the deviation of taxa from the expected selection pattern (Figure 7). Those groups that were eaten more than expected from the biomass available (Coleoptera, Hemiptera and larvae) are relatively sedentary and rely on crypsis or hardened exoskeletons for predator defence. The taxonomic groups that were selected less than expected from their biomass in the habitat ('advanced' flies, Homoptera and small nematocerous Diptera) use flying and jumping predator escape behaviours.

Sherry (1984) found that the factors distinguishing the diets of a behaviourally diverse group of neotropical flycatchers reflected differences in how the prey responded to the predators. Whereas differences in prey handling times related to the preparation of prey for ingestion are usually related to size, the time needed to pursue and subdue a prey item once it has been encountered is probably affected by the predator avoidance mechanisms of the prey. Laboratory studies of optimal diet selection have generally not considered this aspect of handling time since different sizes of the same prey type (Jaeger and Barnard 1981; Krebs et al. 1977, Werner and Hall 1974) or dead prey of different taxa (Zach and Falls 1978) are typically used in the measurement of handling times.

The observation in the present study which is most inconsistent with the theory of optimal foraging is the decreased importance of chironomids in wren diets with increasing relative abundance of chironomids. One explanation is that other prey such as beetles and larvae, which were selected consistently more than expected from their biomass available, were within the set of profitable items but were rarely eaten because of their low abundance. The contribution of these taxa to wren diets, however, did not increase in proportion to their abundance as would be expected from theory.

Another explanation is consistent with the observed relationship between dietary diversity and chironomid abundance. As the abundance of chironomids increased the correlation between the taxa eaten and their biomass available became significant. This implies that wrens became less selective when the probability of encountering profitable prey was high. Although this contradicts the second prediction of optimal diet selection models, Schluter (1981) found that eight of 15 field studies of foraging for which he could calculate or estimate seasonal food abundance also showed that predators were more specialized when the abundances of their prey was lowest.

Bryant (1973) found a pattern of prey selection in House Martins similar to that described here. When large and profitable prey became abundant martins specialized less on those taxa and their diet correlated significantly with the proportion of each taxon available. When the probability of encountering profitable prey was high martins could be less selective in their choice of prey and still obtain a diet similar to that which would result from selective foraging. Bryant believed that foraging randomly was less costly than foraging selectively because search path tortuosity was decreased.

Schluter (1982) pointed out that optimal diet selection models, which assume a limited time available for foraging, may not hold when food resources are abundant and a fixed

amount of time spent foraging can ensure an 'adequate' rather than optimal diet. As an indication of the magnitude of changes in food abundance over the seven sampling periods of this study, mean chironomid numbers ranged from 0.19 to 135.02 individuals per sweep of the net (with 300 individual sweeps taken during each sampling period). House Wrens selected prey categories at or near their rank of biomass available at densities greater than about 27 chironomids per sweep.

Observations by Freed (1981) and those in the present study provide qualitative evidence that wrens spend considerable time at rest, even when feeding nestlings. Like hummingbirds, which spend a large proportion of their time perched, wrens may reduce the number of foraging trips per day at the expense of energy and time efficiency within each foraging bout (see Montgomerie et al. 1984). If departure from the theoretical optimal solution does not decrease the fitness of a predator then an 'adequate' diet, or one which accommodates the long-term foraging goals, may be an efficient strategy for selecting prey from a complex array of food resources.

The House Wrens in this study apparently were able to select prey items from the invertebrate resources available to them. The importance of prey taxa in wren diets was more closely correlated with the biomass of those groups in the habitat than with their numerical abundance. When larger in-

dividuals within a taxa were eaten they were generally selected in greater proportion than available. While diet selection models based on optimality theory did not adequately explain the patterns of selection of prey taxa and sizes observed in this study there was some indication that the abundance of the food resources on this study area led to an opportunistic foraging strategy. Similarly, the large variation in foraging behaviours between the nests studied may have been in response to an abundant food supply. Tree species use at each nest indicated that foraging substrates were selected randomly; again reflecting an opportunistic foraging strategy.

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Appendix A. Estimation of invertebrate lengths from measurements of body parts often found in House Wren stomachs.

TAXA	N	REGRESSION EQUATION	R^2
O.Opiliones	15	Length = 1.62 + 2.78(chelicera length)	0.59
		L = 2.12 + 6.75('finger' length)	0.63
		L = 2.05 + 0.29(chelicera length) + 6.09('finger')	0.62
O.Araneida	40	L = 0.30 + 4.62(chelicera length)	0.86
		L = 0.76 + 9.54(fang length)	0.86
		L = 0.46 + 2.41(chelicera length) + 4.77(fang length)	0.88
O Hemiptera	31	L = 0.76 + 3.38(head width)	0.73
		L = -0.08 + 5.05(head length)	0.81
		L = 0.01 + 0.88(head width) + 3.94(head length)	0.82
F.Reduvidae	20	L = -1.31 + 8.73(head width)	0.86
O.Homoptera	30	L = 1.06 + 2.28(head width)	0.74
O.Coleoptera	28	L = 0.12 + 5.27(head width)	0.79
		L = -0.10 + 8.39(head width) - 0.67(elytra length) - 0.50(elytra width)	0.85
O.Diptera			
SO.Nematocera			
F.Culicidae	15	L = 0.01 + 6.53(head width)	0.43
F.Chironomidae	61	L = -0.28 + 7.57(head width)	0.79
SO.Cyclorrhapha and Brachycera	20	L = 0.69 + 2.94(head width)	0.90
O.Hymenoptera	37	L = -0.76 + 5.66(head width)	0.95
O.Trichoptera	15	L = 1.88 + 3.53(head width)	0.47
O.Lepidoptera(larvae)	36	L = 2.59 + 7.87(head length)	0.55

Appendix B. Weight of size classes within invertebrate taxa.

TAXA	SIZE CLASS	N	LENGTH (mm)($\bar{X}$±SD)	DRY WEIGHT (mg)($\bar{X}$)	DRY * WEIGHT (mg
O.Gastropoda	A	15	1.60±0.35	0.7	0.10
O.Opiliones	All	15	5.47±1.39	7.3	2.62
O.Araneida	A	15	2.12±0.60	0.5	0.22
	B	15	4.15±0.83	2.1	1.27
	C	10	6.72±0.42	10.4	4.49
O.Psocoptera	A	10	1.84±0.37	0.1	0.15
O.Thysanoptera	A	10	1.76±0.21	0.1	0.13
O.Hemiptera	A	15	2.32±0.40	0.1	0.28
F.Miridae	B	15	3.76±0.45	0.8	0.98
	C	1	6.35	6.0	3.87
F.Reduvidae	B	10	5.10±0.51	0.9	2.18
	C	10	6.82±0.41	2.6	4.66
F.Pentatomidae	C	2	7.82±0.32	6.5	6.68
O.Homoptera	A	15	2.58±0.27	0.5	0.36
	B	15	3.84±0.82	0.1	1.05
O.Neuroptera	All	6	7.47±2.16	1.5	5.92
O.Coleoptera	A	15	2.12±0.47	0.1	0.22
	B	9	4.28±0.93	0.7	1.38
	C	4	6.55±0.42	1.2	4.20

Appendix B (continued). . .

O.Trichoptera	All	15	6.59±0.72	1.5	4.26
O.Lepidoptera(adt.)	A	5	7.79±4.76	6.4	6.61
O.Lepidoptera(lar.)	C	5	7.42±0.82	1.8	5.82
	D	8	10.24±0.68	7.9	13.53
	E	6	13.64±0.82	10.5	28.68
	F	8	16.57±0.76	14.6	47.74
	G	4	19.26±0.45	21.0	70.81
	H	2	22.18±1.45	22.0	102.50
	I	1	24.05	12.0	126.71
O.Diptera					
SO.Nematocera	A	15	2.19±0.49	0.1	0.24
F.Tipulidae	All	5	15.18±1.66	8.8	37.95
F.Culicidae	B	15	5.14±0.53	1.0	2.22
	C	15	6.64±0.44	1.4	4.35
F.Chironomidae	B	15	4.41±0.91	0.5	1.49
	C	15	7.68±1.01	1.9	6.37
	D	15	9.94±0.91	4.3	12.52
F.Sciaridae	B	6	3.33±0.28	0.5	0.71
SO.Cyclorrhapha	A	15	2.27±0.40	0.5	0.26
and Brachycera	B	15	4.54±0.77	1.1	1.61
	C	15	7.09±0.70	3.7	5.16
	D	5	10.23±0.75	6.8	13.50
O.Hymenoptera(adt.)	A	16	2.25±0.47	0.2	0.26
	B	16	4.09±0.84	0.5	1.22
	C	5	7.79±0.70	2.2	6.61
O.Hymenoptera(lar.)	All	6	8.88±1.73	2.7	9.10

* Estimated using equation $W = 0.0305\ L^2$ (Rogers et al. 1976).