

SPATIAL AND DIEL AVAILABILITY OF FLYING INSECTS AS POTENTIAL DUCKLING FOOD IN PRAIRIE WETLANDS

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Abstract: We examined spatial and diel availability of flying insects that are a critical food resource to young ducklings. We sampled insects in three native prairie wetlands on the Woodworth Study Area of south-central North Dakota. Insects were sampled with floating sticky traps within emergent macrophyte, edge, and open water microhabitat zones. Sampling took place from 12 June to 4 July 1995, a period that coincided with peak dabbling duck (*Anas* spp.) hatching in this region. Our sticky traps collected 28,527 insects and spiders totaling at least 32 families and 150 species. Chironomidae (Diptera) was the most abundant group, constituting 60% of the total insect count and 32.9% of the biomass (mg dry weight). Mixed-model ANOVA showed that a population of similar undisturbed wetlands may show differences in insect availability when considering both time and space, primarily due to differences in community structure among sites. In spite of these significant random effects, interactions between or among the fixed date, zone, and trap-height effects significantly influenced insect availability. Insects stratified near the water surface in open water areas on all dates except during cool, rainy weather (28 June); on this date, insects were virtually absent from open water. Vertical stratification of insects was less prevalent within and at the edge of stands of emergent vegetation, although most insects were present in the emergent zone near the water surface during inclement weather. ANOVA models from our diel study showed that a significant diel pattern in insect availability existed among zones, but this interaction also depended upon trap-height (chironomid biomass) or date (chironomid counts and biomass). Generally, more insect numbers and biomass were captured in and along stands of emergent macrophytes during the day but chiefly in open water near the surface at night. This diel-zone effect was especially apparent for large chironomids, which were essentially absent during daylight but abundant in open water and edge zones during night. Daytime chironomids were small and predominantly trapped in stands of emergent vegetation. Our results are consistent with previously documented brood foraging behavior and may indicate a trade-off between low energy foraging in the open at night and potentially safer but less productive foraging in stands of emergent vegetation during the day.

Key Words: Chironomidae, dabbling duck, ducklings, food availability, insects, North Dakota, prairie wetlands, sticky trap, waterfowl management, Woodworth Study Area

INTRODUCTION

Wetland insects are an important food resource for many different birds and their young (Murkin and Batt 1987, Swanson and Duebbert 1989, Krapu and Reinecke 1992). Insects play an especially significant role

in the development of pre fledging waterfowl (Chura 1961, Collias and Collias 1963, Sugden 1973, Sedinger 1992). Very young dabbling ducks (*Anas* spp.) feed primarily at and above the water surface and hence rely heavily upon flying insects present near the air-water interface (e.g., Sugden 1973, Pehrsson 1979).

Also, unproductive wetlands negatively influence growth and survivorship (Street 1977, Hunter et al. 1984), and wetland invertebrate availability may dictate the use of wetlands by broods (Bélanger and Couture 1988, Sedinger 1992). Therefore, knowledge of factors affecting insect abundance is important for quantifying and managing wetland productivity as well as assigning values to wetlands (Crow and McDonald 1978, Weller 1978).

While the significance of wetlands as sources of animal foods to migratory waterfowl has been well-documented, most studies have quantified benthic and nektonic invertebrates (e.g., Krull 1970, Whitman 1974, Voigts 1976, Murkin and Kadlec 1986, Cox and Kadlec 1995) or emerging insects (e.g., Danell and Sjöberg 1977, Driver 1977, Wiederholm et al. 1977, Wrubleski and Rosenberg 1990). Cooper and Anderson (1996) recently studied the relationship between brood densities and aquatic invertebrate abundance, but they did not consider food above the water surface. Very little information is available on spatial distribution of flying insects among wetland microhabitats (Chura 1961, Todd and Foote 1987) or similar wetlands. Similarly, diel patterns of insect availability have not been well-investigated (Sjöberg and Danell 1982, Wrubleski and Ross 1989, Jacobsen 1991). These spatial and temporal factors may be important in understanding brood movements and feeding behavior (Swanson 1977, Talent et al. 1982, Mauser et al. 1994), survival (Krapu and Luna 1991), and selection of particular wetlands as breeding sites (Stewart and Kantrud 1973).

Here, we describe flying insect availability as potential food for young waterfowl in prairie wetlands. The objective of this research was to estimate numbers and biomass of flying insects, particularly Chironomidae (Diptera), in foraging habitats of young ducklings. We addressed variability between or among several factors that may influence insect availability to ducklings: (1) similar wetlands, (2) microhabitat zones, (3) days, (4) day-night periods within days, and (5) heights above the water surface. To address our objective, we sampled wetland flying insects during a period that coincided with peak dabbling duck hatching in this region (Higgins et al. 1992).

METHODS

Study Area

The Woodworth Study Area (WSA) is located in northwestern Stutsman County about 5 km east of Woodworth, North Dakota, USA, and 56 km northwest of Jamestown, North Dakota (47° 8' N, 99° 15' W) (Higgins et al. 1992, Johnson et al. 1996). WSA is

located on the east side of the Missouri Coteau. The Coteau region extends from east-central South Dakota, through North Dakota, and into Saskatchewan. The study area is a large block of continuous prairie pothole habitat over 12 km² in size. There are 548 wetland basins on WSA, covering a range of wetland classes typical of the Prairie Pothole Region (PPR).

Three semi-permanent (Stewart and Kantrud 1971) native prairie wetlands (wetlands in native prairie grassland with no prior tillage history) were selected randomly as study sites from many that were very similar in basin size and morphometry (Gleason and Euliss 1996). Prior to our work, these wetlands were systematically given the codes 7-17, 7-18, and 16-15 based on their location on the WSA. Their emergent macrophyte communities were dominated by three species: *Polygonum amphibium* L. (smartweed), *Carex atherodes* Spreng. (slough sedge), and *Scolochloa festucacea* (Willd.) Link (whitetop). *Utricularia vulgaris* L. (bladderwort) was the dominant submergent macrophyte, and *Lemna minor* L. (duckweed) was an abundant floating species.

Sampling

Insect sampling was conducted using floating sticky traps (Figure 1). The trap consisted of one 15-cm × 15-cm × 2.5-cm styrofoam float, one 6.25-cm diameter × 30-cm long gray plastic pipe section, one 21.5-cm × 28-cm overhead transparency sheet (which had a 1-cm × 1-cm grid photocopied onto it for potential subsampling), two 1.5-cm width rubber bands, and Tangle-Trap Insect Trap Coating (Tanglefoot Co., Grand Rapids, MI). The trap was assembled stepwise, first with the transparency sheet wrapped over the circumference of the plastic pipe section and fixed at one end by the rubber band. The other end of the pipe was then secured into the center of the styrofoam float, which had a hole cut to the pipe's diameter. The pipe was pushed down into the float just far enough to secure the base of the transparency sheet. A second rubber band was cut and fastened by short tacks on two opposing sides of the float, where it bisected the diameter of the underside opening and prevented the pipe from sliding down below the designated position. The final step was the application of a thin layer of Tangle-Trap material onto the transparency. This coating was best applied by an extra-wide putty knife.

Our experimental design entailed sampling 3 microhabitat zones (emergent macrophytes, edge-transition, and open water) within each study wetland. Wetlands were divided by 5 evenly spaced transects, which radiated from the center (lowest elevation) to the land-water interface. We did not conduct an extensive *a priori* power analysis to project an appropriate sample

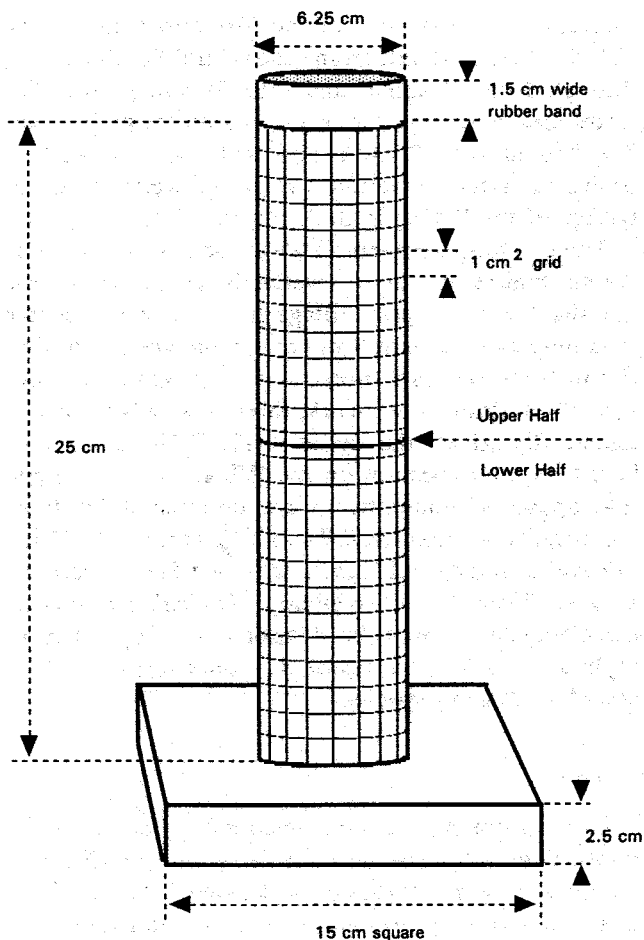


Figure 1. Dimensions of the sticky flight trap used in the study wetlands of the Woodworth Study Area in 1995.

size using sticky traps because the duckling hatching period already had begun upon our arrival to the WSA. However, we did deploy 3 traps in each zone of one wetland for 24-h (6 June 1995). Large numbers of insects (> 500) were captured on all traps and suggested that variance within zones was relatively small (Murkin et al. 1994). To increase our ability to detect differences among levels of effects, we placed a sticky trap in each zone adjacent to each transect, giving 5 replicate traps in each zone, with a total of 15 traps in each wetland. Traps were held in position with metal posts that extended above the water surface by about 50-cm after they had been driven into the wetland substrate. Traps were positioned by sliding the trap over the post, float first. Posts fixed the horizontal position of the traps but permitted them to move up and down if water levels changed.

We placed all traps in the wetlands on the same day and removed them 24-h later. Each location was sampled on a weekly basis throughout the peak dabbling duck hatching period (12 June–4 July 1995). We selected the 24-h interval because of the high density of

insects captured during the pilot sampling period. Longer intervals would have saturated the traps and reduced efficiency.

We used a slightly different sampling design to estimate differences in diel availability of insects. Traps were set from dawn until dusk (05:50–21:30), collected, and replaced by a second set of traps that sampled from dusk until dawn (21:30–05:50). The diel study would have required twice the number of traps ($n = 90$) because traps were collected and replaced by fresh ones simultaneously. However, we did not have enough traps or freezer space for sample storage to do this; therefore, we randomly selected 3 transects from the five in each wetland, yielding 3 replicate traps in each zone per wetland. Our diel study was conducted over 3 consecutive 24-h periods (22–24 June 1995). At the end of each sampling period, transparencies were removed from the traps, turned inside-out, placed in freezer bags, and frozen.

We also sampled additional insects to estimate dry mass of species captured on sticky traps. Insects were captured using sweep nets in upland, emergent, and neuston habitats and frozen immediately. Sweep-net specimens served as surrogates for insects captured on sticky traps because trap-caught insects often had Tangle-Trap residue on them and were damaged and when removed, therefore rendering them unusable for biomass estimates.

Sample Processing

Transparencies were examined using a dissecting microscope. Insect counts were recorded separately for the top and bottom sections (12.5-cm) of the transparencies. We did not subsample. Insects were identified initially to the level of taxonomy that distinguished specimens from one another (i.e., "morphospecies"). A few specimens of each morphospecies encountered were removed with commercial paint thinner (a solvent for the Tangle-Trap coating), preserved in 70% ethanol, and used as voucher specimens for tallying. All individuals that were later determined to constitute greater than 5% of the total number or biomass were identified to genus or species, if possible. Other species were keyed to family with the exception of specimens that were rarely caught or in poor condition. These specimens were identified to order.

Insect counts recorded from the sticky traps were used to estimate available biomass (mg dry weight) of potential duckling food. Sweep-net specimens were sorted and matched with sticky trap specimens. Net-caught individuals were dried for 48 h at 60° C and weighed. While dominant species sampled on the traps were well-represented in the sweep net samples, dry mass of some of the rare morphospecies was estimated

using length-mass regression equations from other studies (i.e., Sage 1982, Wrubleski and Rosenberg 1990, Sample et al. 1993). Insects were measured for total length (mm), with the exception of chironomids, which were measured from the pronotum to the penultimate abdominal segment, using an ocular micrometer. Median lengths were used in the length-mass regression equations.

Statistical Analysis

We assessed the effects of date (4), site (3), micro-habitat zone (3), and height above the water surface (lower 12.5 cm vs. upper 12.5 cm) on counts and biomass of total insects and chironomids from the four 24-h study periods using mixed-model analysis of variance (ANOVA). Since we selected sites randomly from a large population, the site main effect and all of its interactions with date, zone, and height were treated as random effects in our models. Date, zone, and height and all respective interactions among these effects were fixed. We conducted analyses using PROC MIXED of SAS (SAS Institute, Inc. 1997). Since insects were sampled from the same sites repeatedly over time, we used PROC MIXED because it models this dependency in the data and allows specification of an appropriate covariance structure (e.g., Jennrich and Schluchter 1986). This procedure accounted for potential serial correlation among our observations. Prior to analysis, all insect count and biomass data required a $\log_{10}(x + 1)$ transformation, which normalized residuals and increased variance homogeneity. ANOVA is also robust with regard to these assumptions when data are balanced (Rice 1988).

Data from the diel study were analyzed similarly using mixed-model ANOVA with site (3) as random and date (3), zone (3), period (day vs. night), and height (2) as fixed effects. While dates in the four 24-h study were selected on a weekly interval to examine seasonal effects and therefore fixed, dates in the diel study were not as clearly "fixed." However, we had chosen diel dates as consecutive 24-h periods and therefore could not sufficiently justify them as dates selected randomly (Bennington and Thayne 1994).

Probabilities of Type I error for fixed effects were estimated from Type III *F* statistics. Significance of random effects was estimated using -2 REML log likelihood ratio statistics between full and reduced models (SAS Institute, Inc. 1997). We calculated log likelihood ratios only for random effects with covariance parameter estimates > 0 . Tests were carried out by individually removing each covariance parameter, fitting the reduced model, and comparing the resulting statistic with χ^2 distributions (1 df). Main effects and

interactions were considered significant when $p \leq 0.05$.

We used multi-panel box plots to interpret significant interactions among effects rather than multiple mean comparisons. Box plots provide visualization of all data and complement hypothesis tests deemed significant from analyses, especially higher-order interactions (Cleveland 1993). We made and compared plots only for levels of fixed effects. We did not graphically compare or discuss specific levels of random effects because such comparisons were not consistent with our assumption that study wetlands were representative of a larger population of sites. Plots were generated using Trellis graphics of S-Plus (Mathsoft, Inc. 1995).

RESULTS

Our sticky traps captured 28,527 insects and spiders totaling approximately 32 families and 150 species (Table 1). Diptera was the dominant order, with at least 17 families and 89.3% and 69.5% of total counts and biomass, respectively. Most of these dipterans were chironomids, which constituted 60% of total counts and 32.9% of total biomass. Overall, the most numerically abundant taxa were the chironomids *Corynoneura* spp. (30.9%) and *Chironomus pallidivittatus* Malloch (16.7%). *Chironomus pallidivittatus* was also an important component of biomass (29% and 88% of total and chironomid biomass, respectively), but *Corynoneura* spp., while in large numbers, were so small that they contributed only 0.5% and 1.7% to total and chironomid biomass. Other abundant groups included ephydrids (marsh flies), sciomyzids (snail-killing flies), and coenagrionids (damselflies) (Table 1).

Considering random effects, ANOVAs on data from the four 24-h study showed that insect availability to ducklings varied significantly among sites, zones, and heights (total counts) and sites and dates (chironomid biomass) (Table 2). Total biomass and chironomid counts, however, were not different among sites (Table 2). Significance of these random effects suggested that a population of similar undisturbed wetlands may show differences in insect community structure and, in response, have differences in distribution of insect abundance over time and space.

In spite of significant random effects, two- and three-way interactions between or among the fixed date, zone, and height effects significantly influenced insect availability in the four 24-h study (Table 2). Generally, insects were more abundant at the lower trap-height in all zones but to the greatest degree in the open water (Figures 2, 3). Insects were more evenly distributed between trap-heights in and along stands of emergent vegetation (Figures 2, 3). However, this

Table 1. Counts and estimated biomass (mg dry weight) of flying insects trapped on the Woodworth Study Area in 1995. Number of morphospecies in each family or order are in parentheses. All insects with >5% of total numbers or biomass are shown to genus or species.

Insect Taxon	Individuals Trapped	% Total Count	Biomass Trapped	% Total Biomass
Order Diptera	25,478	89.3	23,457.2	69.5
Calliphoridae (4)	56	0.2	173.8	0.5
Ceratopogonidae (4)	1,590	5.6	1,113.1	3.3
Chaoboridae (1)	14	0.1	13.0	<0.1
Chironomidae (29)	17,112	60.0	11,090.9	32.9
<i>Chironomus pallidivittatus</i> Malloch	4,774	16.7	9,763.1	29.0
<i>Corynoneura</i> spp.	8,802	30.9	184.0	0.5
<i>Tanytarsus</i> sp. 2	2,030	7.1	127.3	0.4
Culicidae (1)	4	<0.1	5.3	<0.1
Dolichopodidae (6)	431	1.5	524.3	1.6
Ephydriidae (8)	4,114	14.4	2,713.8	8.1
<i>Notiphila</i> sp. 1	1,463	5.1	2,222.0	6.6
Lonchopteridae (1)	3	<0.1	1.1	<0.1
Muscidae (3)	825	2.9	1,299.4	3.9
Opomyzidae (1)	3	<0.1	2.6	<0.1
Phoridae (1)	4	<0.1	0.8	<0.1
Sarcophagidae (1)	4	<0.1	21.0	<0.1
Scathophagidae (6)	52	0.2	72.9	0.2
Sciomyzidae (5)	732	2.6	2,754.0	8.3
<i>Sepedon</i> sp. 1	583	2.0	2,558.0	7.6
Syrphidae (11)	137	0.4	2,082.7	6.2
Tabanidae (2)	3	<0.1	100.0	0.3
Tipulidae (4)	243	0.9	1,451.7	4.0
Other Diptera (5)	74	0.3	42.2	0.1
Order Hymenoptera (10)	423	1.5	449.7	1.3
Order Odonata	693	2.5	5,734.4	17.0
Coenagrionidae (2)	672	2.4	5,159.5	15.5
<i>Ischnura</i> spp.	654	2.3	4,782.2	14.2
Lestidae (1)	19	0.1	416.4	1.2
Libellulidae (1)	2	<0.1	72.6	0.2
Order Trichoptera	81	0.3	1,517.8	4.5
Phryganeidae (1)	34	0.1	1,448.0	4.3
Polycentropodidae (1)	47	0.2	68.1	0.2
Order Hemiptera—Gerridae (2)	127	0.4	385.0	1.1
Order Coleoptera	545	1.9	1,472.1	4.4
Chrysomelidae (3)	358	1.3	1,120.3	3.3
Curculionidae (5)	103	0.4	123.0	0.4
Dytiscidae (3)	27	0.1	173.2	0.5
Other Coleoptera (6)	56	0.2	66.3	0.2
Order Homoptera—Cicadellidae (4)	1,048	3.7	297.5	0.9
Order Ephemeroptera	16	0.1	28.8	0.1
Baetidae (1)	11	<0.1	26.0	0.1
Caenidae (1)	5	<0.1	2.8	<0.1
Class Arachnida (7)	115	0.4	399.0	1.2
Totals	28,527	100%	33,667.2	100%

Table 2. Probabilities of Type I error associated with F ratios (fixed effects) and -2 REML log likelihood ratios (random effects) from mixed-model ANOVA (date \times site \times zone \times height) on insect count and biomass data (no. trap-height⁻¹·24 h⁻¹) from the four 24 h study. Log likelihood ratio values (χ^2 distribution, 1 df) were calculated only for random effects with covariance parameter estimates > 0 . All significant effects ($P \leq 0.05$) are indicated by bold type. D = date, S = site, Z = zone, and H = height.

Source of Variation	NDF	DDF	Total		Chironomid	
			Counts	Biomass	Counts	Biomass
Fixed effects						
D	3	6	0.0001	0.0002	0.0001	0.0037
Z	2	4	0.6758	0.6036	0.1849	0.0670
H	1	2	0.0203	0.0224	0.0279	0.0268
D \times Z	6	12	0.1023	0.0004	0.0345	0.0022
D \times H	3	6	0.1829	0.5902	0.0683	0.1613
Z \times H	2	4	0.2898	0.1710	0.0253	0.0161
D \times Z \times H	6	12	0.0421	0.9729	0.1234	0.2596
Random effects						
S			—	0.9002	0.8584	—
S \times D			0.4848	0.5981	0.1552	0.0031
S \times Z			—	0.4319	0.3214	0.0867
S \times H			—	—	—	—
S \times D \times Z			0.0527	0.7657	0.1544	0.6442
S \times D \times H			0.0999	0.0601	0.8027	—
S \times Z \times H			0.0119	0.3887	0.6610	0.5838
S \times D \times Z \times H			—	—	—	—

trend depended significantly upon date of sampling for total counts (Table 2, Figure 2). Similarly, distribution of total biomass and chironomid counts and biomass among zones varied significantly by dates (Table 2, Figures 2b, 3). Weather and changes in community structure over time were most likely responsible for these significant interactions. Cool, windy weather on 28 June reduced abundance and activity of insects, especially chironomids (Figure 3). Most insects on 28 June were in stands of emergent vegetation and stratified at the lower height (Figure 2). *Chironomus pallidivittatus*, the dominant large chironomid from our study wetlands, was virtually absent on 28 June and thus contributed to significant interactions among date, zone, and height. It was captured chiefly in open areas near the water surface on all other dates (Figure 3b).

Results from ANOVAs on data from the diel study showed that total insect biomass varied significantly among sites when considering dates, diel periods, and zones (Table 3). However, other dependent variables were not significantly influenced by site effects (Table 3). Differences in abundance of dominant species among wetlands were likely responsible for the significant random effect since insect biomass was distributed differently within wetlands. Relative abundance of large-bodied *Chironomus pallidivittatus*, *Ischnura* spp., and *Notiphila* sp. 1 especially varied among sites. Because these species showed similar patterns in their distribution across wetlands, they

therefore influenced proportional distribution of insect biomass over time and space.

Significant fixed effects from diel study ANOVAs demonstrated distinct spatial-temporal trends in insect availability in spite of variability in community structure among wetlands. A significant diel pattern in insect availability existed among zones, but this interaction also varied by trap-height (chironomid biomass) or date (chironomid counts and biomass) (Table 3). Generally, insects were most abundant in stands of emergent vegetation during daylight but occurred in greatest numbers in open water at night (Figures 4–6). This was especially true on 22 June for chironomid counts and biomass (Figure 5) and at the lower height for chironomid biomass (Figure 6). Total insect counts and biomass also varied by date, but their significant period \times zone interaction was consistent across dates (Table 3, Figure 4). Significant date effects were primarily due to large numbers of *Chironomus pallidivittatus* available on 22 June but somewhat reduced abundance on the following two dates (Figure 5). *Chironomus pallidivittatus* also was captured almost exclusively in open water at night at the lower trap-height, as seen by the dearth of chironomid biomass during daytime (Figure 5b, 6). Daytime chironomids were small (mostly *Corynoneura* spp. and *Tanytarsus* sp. 2) and predominantly trapped in stands of emergent vegetation (Figure 5).

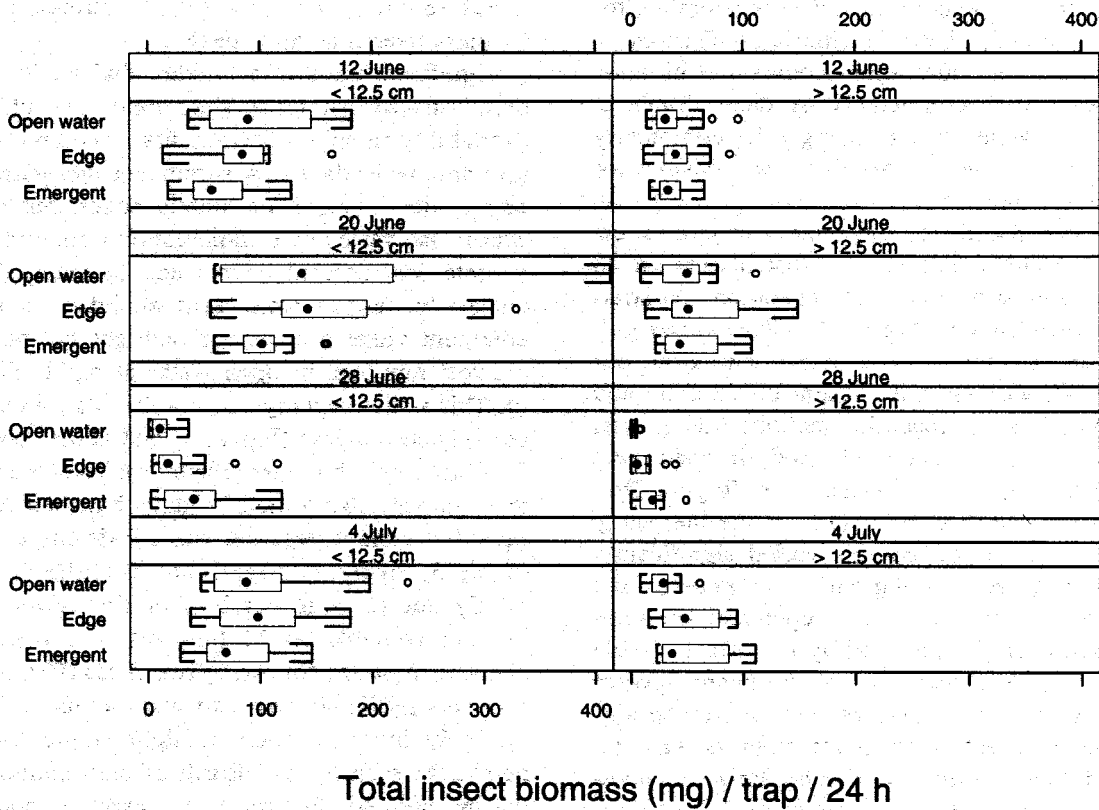
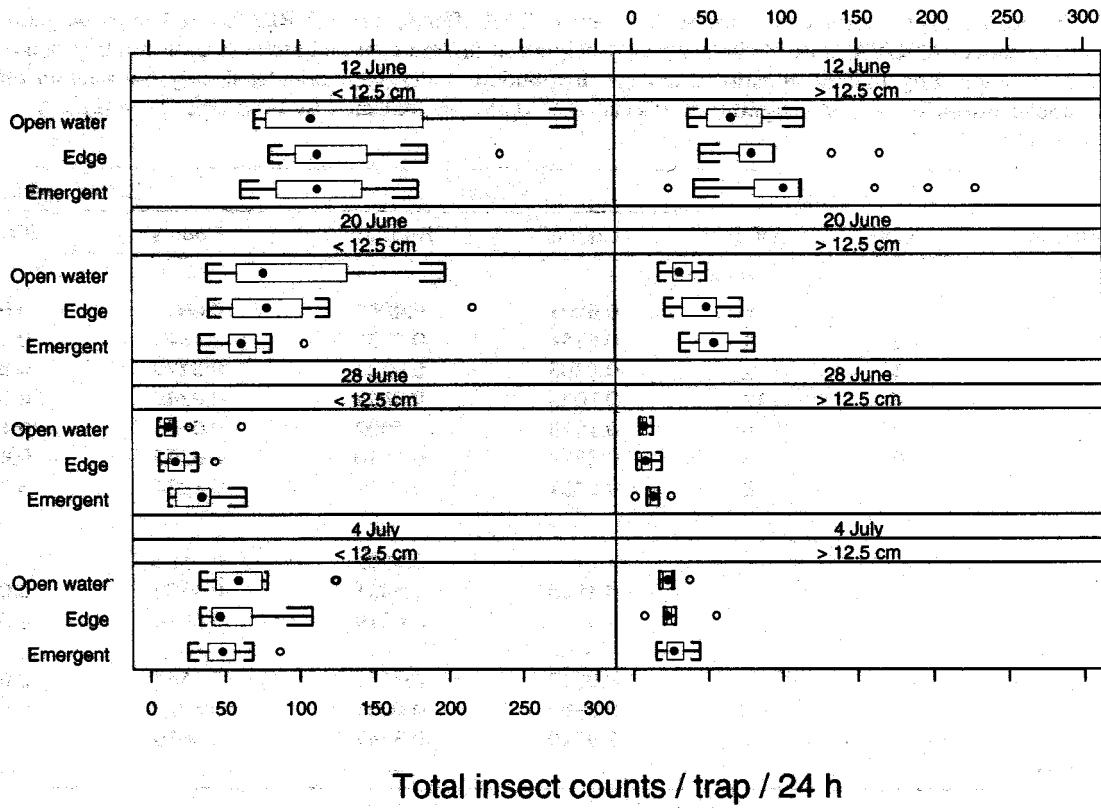
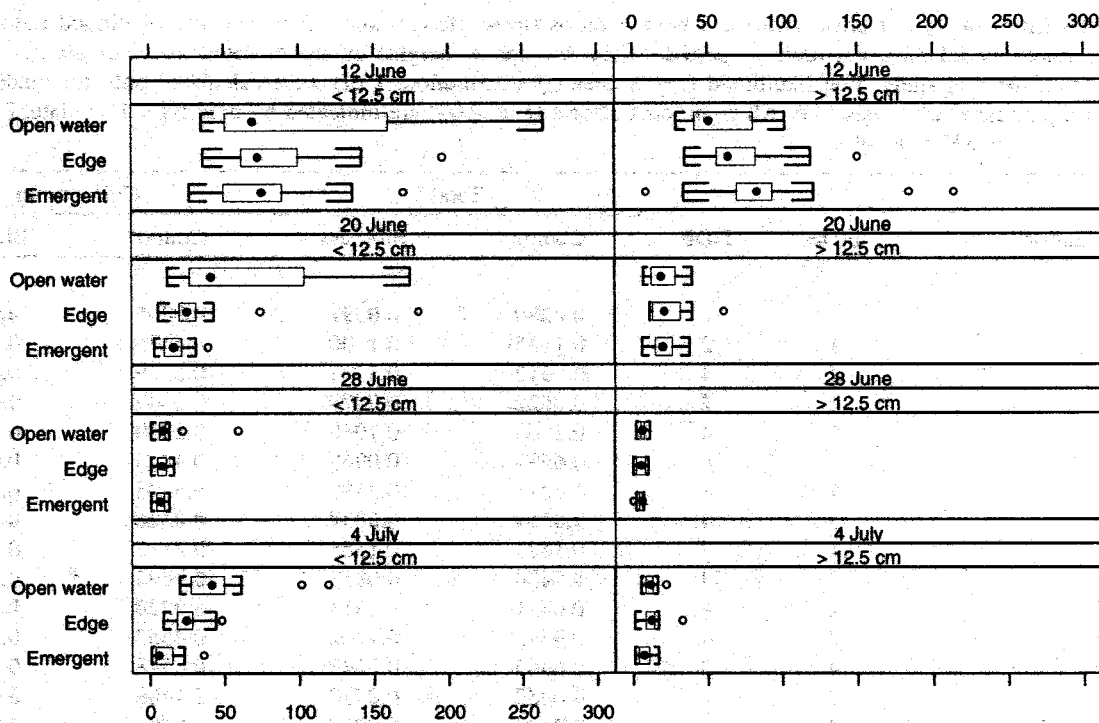
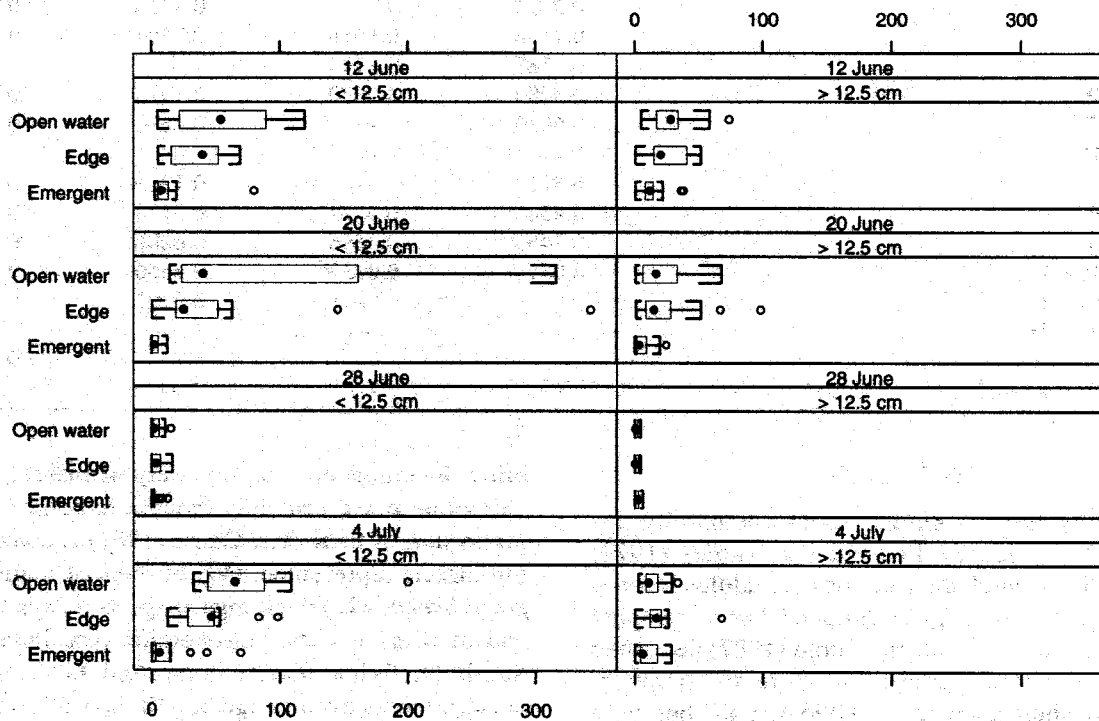


Figure 2. Box plots showing total insect (a) counts and (b) biomass trapped on dates and at trap-heights (< 12.5-cm and > 12.5-cm) by zones (n = 15) from the four 24-h study. The filled circle is the median, the box encodes the interquartile range (25th-75th percentiles), bars indicate the nearest adjacent value to 1.5*(interquartile range), and open circles are outlier values (Cleveland 1993).



Chironomid counts / trap / 24 h



Chironomid biomass (mg) / trap / 24 h

Figure 3. Box plots showing chironomid (a) counts and (b) biomass trapped on dates and at trap-heights (< 12.5-cm and > 12.5-cm) by zones (n = 15) from the four 24-h study. The filled circle is the median, the box encodes the interquartile range (25th-75th percentiles), bars indicate the nearest adjacent value to 1.5*(interquartile range), and open circles are outlier values (Cleveland 1993).

Table 3. Probabilities of Type I error associated with F ratios (fixed effects) and -2 REML log likelihood ratios (random effects) from mixed-model ANOVA (date \times period \times site \times zone \times height) on insect count and biomass data (no. trap-height $^{-1}$ h $^{-1}$) from the diel study. Log likelihood ratio values (χ^2 distribution, 1 df) were calculated only for random effects with covariance parameter estimates > 0 . All significant effects ($P \leq 0.05$) are indicated by bold type. D = date, P = period, S = site, Z = zone, and H = height.

Source of Variation	NDF	DDF	Total		Chironomid	
			Counts	Biomass	Counts	Biomass
Fixed effects						
D	2	4	0.0280	0.0397	0.0866	0.0402
P	1	2	0.1635	0.1100	0.5675	0.0986
Z	2	4	0.9312	0.5732	0.6779	0.1098
H	1	2	0.0622	0.0479	0.3649	0.1749
D \times P	2	4	0.1863	0.1065	0.2389	0.0637
D \times Z	4	8	0.6581	0.0968	0.4823	0.0218
D \times H	2	4	0.7211	0.2537	0.5405	0.5207
P \times Z	2	4	0.0091	0.0034	0.0326	0.0183
P \times H	1	2	0.1423	0.1385	0.2112	0.1909
Z \times H	2	4	0.0434	0.0853	0.0444	0.0182
D \times P \times Z	4	8	0.0731	0.1314	0.0220	0.0038
D \times P \times H	2	4	0.9645	0.1402	0.4553	0.7640
D \times Z \times H	4	8	0.6963	0.3649	0.8548	0.5860
P \times Z \times H	2	4	0.0852	0.0718	0.1408	0.0237
D \times P \times Z \times H	4	8	0.9803	0.9268	0.9490	0.7701
Random effects						
S			—	0.4632	—	—
S \times D			—	0.4579	—	—
S \times P			0.2495	0.7379	0.2414	0.2056
S \times Z			0.1138	0.1016	0.3207	0.3540
S \times H			0.4187	0.4944	—	—
S \times D \times P			0.3083	0.3680	0.1915	0.0721
S \times D \times Z			0.6910	—	0.2636	0.6094
S \times D \times H			—	—	—	—
S \times P \times Z			0.3210	—	0.1213	0.1148
S \times P \times H			0.4348	0.3227	0.5174	0.2510
S \times Z \times H			0.2453	0.4696	0.6206	0.3458
S \times D \times P \times Z			0.0894	0.0253	0.4666	0.2117
S \times D \times P \times H			—	—	0.9203	—
S \times D \times Z \times H			—	—	—	—
S \times P \times Z \times H			—	—	—	0.7195
S \times D \times P \times Z \times H			—	—	—	—

DISCUSSION

Surprisingly little is known about community dynamics of flying insects in wetlands. Titmus (1979) examined diel spatial distributions of adult chironomids along a wet gravel pit in England, but he sampled only nearshore areas. Todd and Foote (1987) described spatial and temporal patterns in shore fly (Diptera: Ephydriidae) abundance in an Ohio marsh, but only Chura (1961) examined abundance of all types of flying insects in wetlands (emergent vegetation only). He reported that 54.76% of the insects captured within stands of macrophytes were chironomids. In our study, chironomids also comprised a large percentage of the total number and biomass of insects sampled. Dab-

bling ducklings prey on a variety of insects, but adult chironomids are generally thought to comprise a large proportion of their diet. Chura (1961) showed that flying insects represented 84% of diets of mallard (*Anas platyrhynchos* L.) ducklings at age 1–6 days (Class Ia), and of these insects, chironomids constituted 75.9%. Similarly, flying insects comprised 68% of mallard duckling diets even at age 13–18 days (Class Ic), with adult chironomids making up 93% of total flying insects ingested (Chura 1961). These percentages may indicate selective feeding by ducklings or that chironomids are simply easier to catch. Collias and Collias (1963) described dabblers as quite adept at catching flies, but they did not indicate preferences toward or

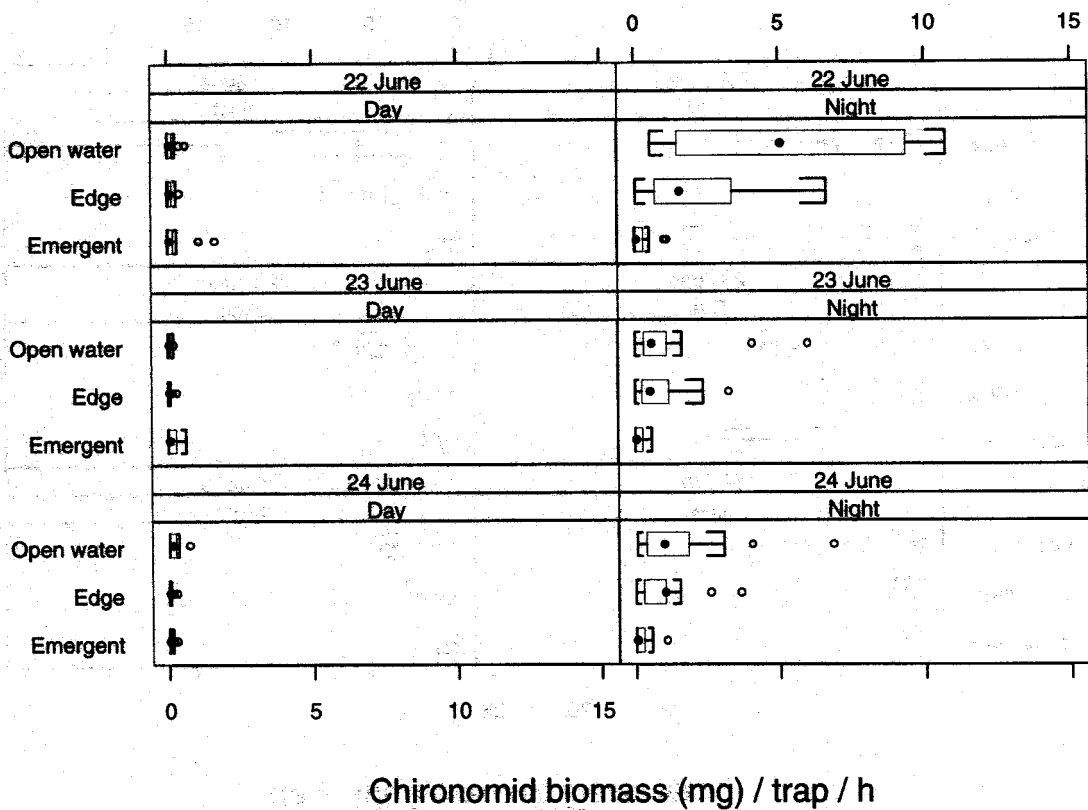
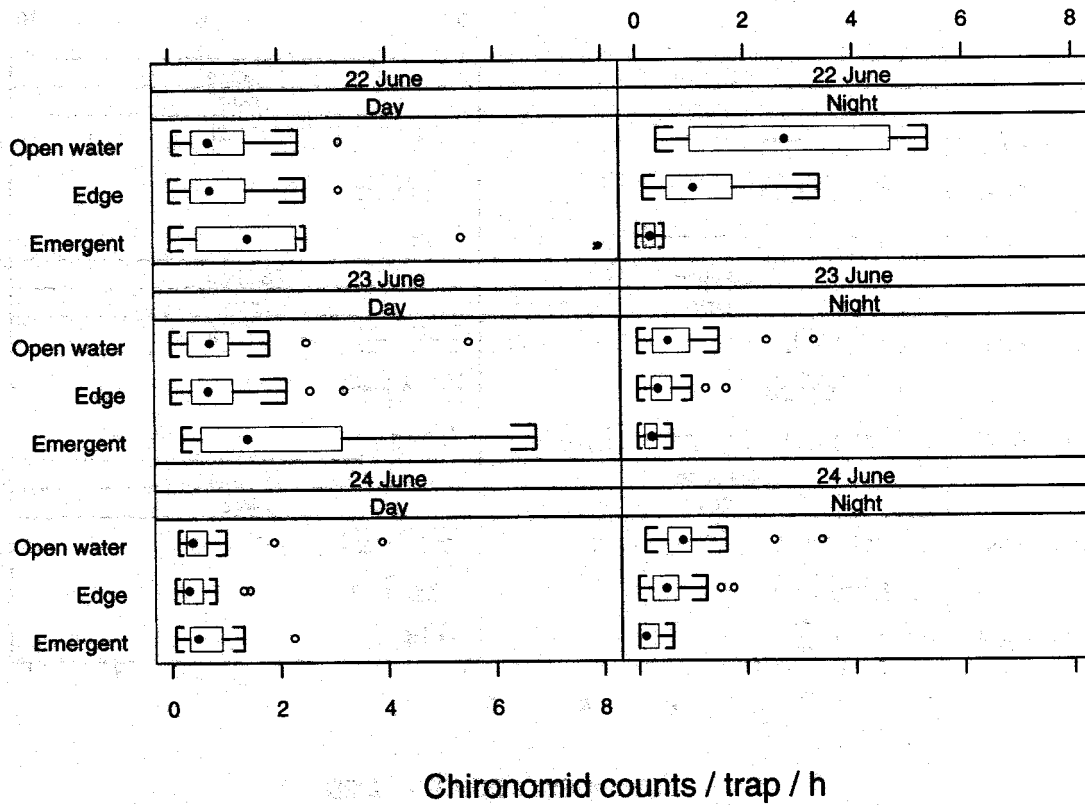


Figure 5. Box plots showing chironomid (a) counts and (b) biomass trapped on dates and during diel periods by zones (n = 9) from the diel study. The filled circle is the median, the box encodes the interquartile range (25th-75th percentiles), bars indicate the nearest adjacent value to 1.5*(interquartile range), and open circles are outlier values (Cleveland 1993).

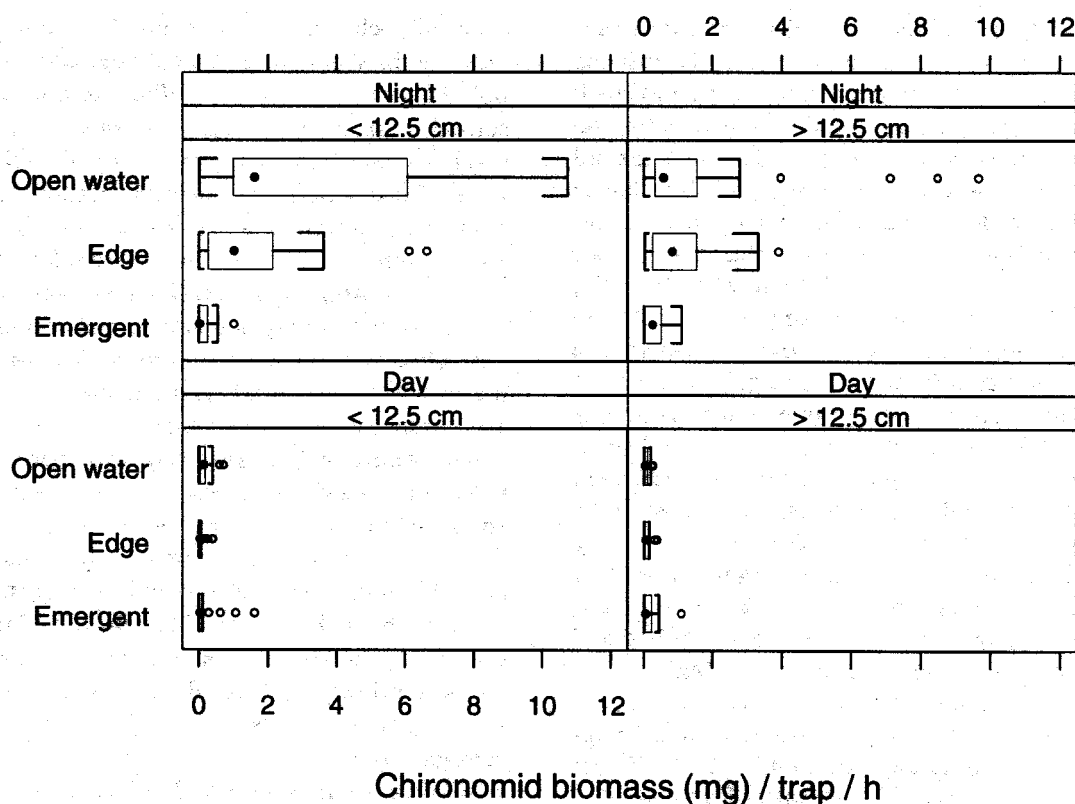


Figure 6. Box plots showing chironomid biomass trapped during diel periods and at trap-heights (< 12.5-cm and > 12.5-cm) by zones ($n = 27$) from the diel study. The filled circle is the median, the box encodes the interquartile range (25th–75th percentiles), bars indicate the nearest adjacent value to 1.5*(interquartile range), and open circles are outlier values (Cleveland 1993).

availability of particular flying insect groups. Chura (1961) noted that size, coloration, transparency, camouflage, and movement are all likely determinants of the availability of a particular insect taxon as food. Obviously, insect presence is not synonymous with availability; in fact, food availability may be entirely impossible to measure. We recognize this limitation in our data and suggest future work in this area is needed to clarify which insects are truly “available” as food.

Trends in insect emergence have been reported in wetlands, but most indicate a peak in late spring and a gradual-to-abrupt decrease in emergence throughout the summer (e.g., Chura 1961, Danell and Sjöberg 1977, Sjöberg and Danell 1982, Nelson 1989, Jacobsen 1991, Wrubleski 1996). These studies focused almost exclusively on chironomids, however, and emergence does not correlate directly to availability. Our results indicate that community structure changed seasonally; some taxa diminished in number (e.g., *Ischnura* spp., *Corynoneura* spp.) while others became more abundant (e.g., *Notiphila* sp. 1, *Sepedon* sp. 1). This may illustrate an important function of species diversity in wetlands. Although community structure fluctuated, high taxon richness maintained relatively

stable levels of biomass (excluding weather-related effects on 28 June). It seems intuitive that disturbed, low diversity communities are much more likely to have gaps in food availability due to emergence phenologies that make dominant insects available too soon or too late for dabbler brood rearing.

Year-to-year variation in insect abundance is common in dynamic habitats such as prairie wetlands (e.g., Driver 1977, Wrubleski and Rosenberg 1990). This variability is most often attributed to yearly fluctuations in water levels common in the PPR (Murkin and Kadlec 1986, Wrubleski 1991). Our study was conducted only in one year, and we recognize that temporal variation across years may also influence availability of insects. While community structure and abundance of insect species may change year-to-year, spatial distribution of particular species should be similar (e.g., *Chironomus pallidivittatus* would likely be available in greatest abundance in open water areas regardless of year). Therefore, inferences drawn from our results should be robust when considering relative abundance of dominant taxa from our wetlands.

Inclement weather can also significantly influence wetland insect activity (Williams 1961). Swanson and

Sargeant (1972) and Wrubleski and Ross (1989) suggested that emergence of chironomids may be reduced by high wind or cool temperatures. Sjöberg and Danell (1982) found large numbers of chironomids resting on *Carex* shoots during cool, rainy periods. Our traps did not collect many insects on 28 June, probably due to a combination of depressed insect emergence and reduced flight activity in response to relatively low air temperatures, gusty winds, and light rain. We did, however, find that most insects sampled on that date were in the emergent zone at the lower trap-height, a phenomenon that contributed to the significant date \times zone and date \times zone \times height interactions from our ANOVA models. According to Sjöberg and Danell (1982), lethargic chironomids resting on emergent vegetation during cool, windy weather are easy prey. Additionally, air temperatures on cold days are likely to be more favorable in stands of emergent vegetation in comparison to open areas subject to wind. Thus, emergent macrophytes may provide both shelter and food for ducklings during inclement weather.

Wetland invertebrate productivity plays an important role in determining brood movements and foraging behavior (e.g., Stewart and Kantrud 1973, Talent et al. 1982, Bélanger and Couture 1988, Cooper and Anderson 1996). Wetlands with relatively low insect abundance cause broods to spend more time searching for food (Hunter et al. 1984, Pehrsson and Nyström 1988), and broods are much more likely to leave these wetlands (Talent et al. 1982, Mauser et al. 1994). Significant random-effect interactions from our ANOVA models suggest that insect availability among similar wetlands may be most dependent upon community structure in each wetland and respective spatial-temporal tendencies in distribution of dominant species. In our study, abundant species were present in each study wetland but in differing proportions relative to other species in each community. Thus, differences in availability were not merely site-dependent but spatially and temporally dependent among sites. Reasons for these differences in availability among wetlands are not clear but may influence brood use. Dabbler broods may favor or move among wetlands with greatest abundance of species that are more obtainable as food (i.e., "preferred" food items) (Sedinger 1992). Paired observations of flying insect abundance and brood movements across many wetlands would help to better understand these relationships.

Diel patterns in insect activity were significant determinants of insect spatial distribution in our wetlands. Insects were caught most often within and near stands of emergent vegetation during daylight hours, with the exception of chironomid biomass, which was quite low in all zones during the day. During night, however, insect abundance was greatest in open water,

especially chironomid biomass. Chironomid biomass was low in stands of emergent vegetation during daylight because *Chironomus pallidivittatus* was often observed near tops of emergent macrophytes, out of reach of our traps and above the duckling feeding zone. These period-microhabitat relationships help explain why differences in insect availability among zones from our four 24-h study were less apparent.

Our diel sampling results are consistent with reports of Swanson and Sargeant (1972) and Swanson (1977), who observed intensive waterfowl feeding on emerging insects (chironomids and mayflies) between sunset and midnight during summer in North Dakota wetlands. Additionally, Swanson and Sargeant (1972) found that duckling broods were less wary and more apt to venture into the open water at night. We found that insect counts and biomass, particularly chironomid biomass, were most abundant over the open water at night and thus provided an abundant food resource for ducklings. Our data also indicate that potential food resources for ducklings are greater in and at the edge of stands of emergent vegetation during daylight hours.

While ducklings are relatively small and appear dependent on food at the water surface, Chura (1961) noted that mallard ducklings even at age 1-6 days (Class Ia) are capable of jumping and reaching over three times their normal standing height to snap at objects above them. Therefore, even insects at the top of our sticky traps (25-cm) were potential food items. However, we found that the lower trap-height captured greater numbers and biomass of insects, especially chironomid biomass, in open water on all dates except 28 June. *Chironomus pallidivittatus*, a substrate-swarmer, emerged, mated, and oviposited in open areas on the water surface, hence the significant date \times zone and zone \times height effect for chironomids in our ANOVA models. Chironomid biomass was also significantly stratified at the lower trap-height in open water areas during the night. Vertical distribution of insects, especially for small chironomids, seemed random within and at the edge of stands of emergent vegetation, with insects flying not only close to the air-water interface but also up to the tops of macrophytes. Likely, less energy is required for ducklings foraging at times and in habitats where insects stratify near the water surface. Our results are consistent with the suggestion of McNeil et al. (1992) that waterfowl may prefer nocturnal feeding because night foraging is more profitable. Therefore, a trade-off may exist between low energy foraging in the open at night and potentially safer but less efficient foraging in stands of emergent vegetation during the day.

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