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Differential habitat use by waterbirds in a managed wetland complex

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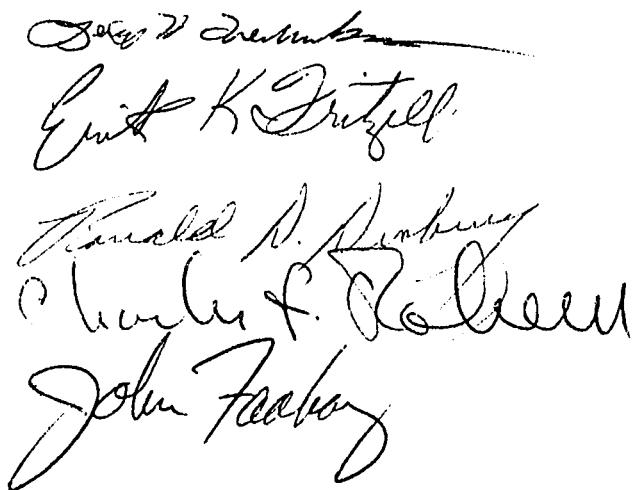
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WETLAND COMPLEX

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David W. Dennis
Eric K. Grifell
Donald P. Lohrey
Charles F. Colleen
John Farley



DIFFERENTIAL HABITAT USE BY WATERBIRDS
IN A MANAGED WETLAND COMPLEX

A Dissertation
Presented to
the Faculty of the Graduate School
University of Missouri-Columbia

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

by
FREDERIC ARTHUR REID

Leigh H. Fredrickson

Dissertation Supervisor

December, 1989

DIFFERENTIAL HABITAT USE BY WATERBIRDS
IN A MANAGED WETLAND COMPLEX

Frederic Arthur Reid

Leigh H. Fredrickson

Dissertation Supervisor

ABSTRACT

Patterns of habitat use in relation to changing water conditions were compared among several common waterbirds in a managed wetland complex within the floodplain of the Mississippi River from 1981-1985. Differential habitat use of seasonally flooded wetlands was compared among migrant rails and bitterns on the Ted Shanks Wildlife Area, Missouri. King rails' (Rallus elegans) use of seasonal wetlands for breeding and foraging was investigated. Wading bird response to controlled drawdown of a managed wetland and the relationship to potential aquatic prey were tested among years.

A clear pattern of spatial segregation is revealed for migrant rallids in relation to water depth. Soras (Porzana carolina) are located in the deepest sites, Virginia rails (Rallus limicola) are found at saturated soils or very shallow water depths, whereas king rails use intermediate

depths. Rails used shallower water depths with shorter and denser vegetation than bitterns used.

King rails nested at damp sites dominated by dense perennials. Nest success was high (span rate 0.695 ± 0.071) and regression analysis related it to water depth and distance to open water. Nests in the interior of management units, not artificially drawdown during the nesting period, showed the greatest nest success. This semi-preocial species displayed dramatic shifts in foraging habitat among migration and breeding periods, in relation to water depth and vegetation cover. Differences among breeding periods indicated brood sites yielded a more predictable prey base with greater densities of potential prey, whereas the nesting and migration periods had patchy food resources at foraging sites.

Wading birds and aquatic prey displayed increasing densities in relation to controlled drawdown conditions. Total heron, great blue heron (Ardea herodias), and great egret (Casmerodius albus) densities were ranked correlated to total prey biomass and densities, tadpole biomass and densities, and crayfish biomass and densities for all years combined. Slower drawdowns (9-10 days) produced greater wading bird response, both in total use days and peak densities, than rapid drawdowns (5 days). Wading bird response to drying or controlled drawdown on a given wetland is regulated by the timing and duration of drawdown, and status of other wetlands within the complex.

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CHAPTER I

INTRODUCTION

Among the proximate cues apparently used by birds in habitat choice are structural features of micro-habitats, foraging opportunities, and the presence of other species. These factors may operate independently, sequentially, or synergistically (Cody 1968, James 1971, Wiens 1974). Of the methods of resource subdivision that are widely recognized, habitat preference among different vegetation types and site selection for foraging within habitats appear to be dominant patterns (Hildén 1965, Cody 1985). The added dimension of water depth may provide an important proximate cue to habitat use and spatial segregation of resources among wetland species (Weller and Spatcher 1965, Burger 1985). The investigation of patterns of micro-habitat use along structural components in floodplain wetlands may provide specific clues for habitat manipulation that can affect vegetation or water depth and in turn influence foraging or nesting success.

Historically the floodplains of the Mississippi River have been seasonally inundated with floodwaters in relation to regional hydrologic cycles. Many species of waterbirds have adapted life history strategies that allow them to exploit the seasonal resources these wetlands provide for

breeding, wintering, or migration. Like palustrine wetlands throughout North America, most of these habitats are now converted to agricultural developments or degraded in quality (Tiner 1984). Although most of the remaining wetland habitats have been protected under public ownership, many lack dynamic water regimes which influence habitat quality (Korschgen 1989, Reid et al. 1989). The specific impacts of water regimes on waterbird breeding and foraging are also poorly understood (Weller and Fredrickson 1974, Kushlan 1976a) and knowledge of biological processes that can be implemented for management is limited.

Among the most common families of waterbirds that use the palustrine wetlands of the Mississippi River floodplain are Rallidae and Ardeidae, yet specific understanding of how these birds use wetlands and how this knowledge can be translated to managers is limited (Rundle and Fredrickson 1981, Fredrickson and Reid 1986). More specifically the patterns of habitat use in relation to changing water conditions have neither been quantified nor compared for many of these species. This dissertation addresses several questions related to dynamic water regimes and bird use. Differential habitat use of seasonally flooded wetland habitat by migrant rails and bitterns is addressed in Chapter II. How king rails (Rallus elegans) use seasonally flooded wetlands for breeding and foraging is addressed in Chapters III and IV. More specific questions concerning the relationships of nesting success to habitat characteristics

and breeding chronology to habitat characteristics at foraging sites are addressed in those chapters. Wading bird response to controlled drawdown of a managed wetland and the relationship to potential aquatic prey are tested among years and addressed in Chapter V. A case study of habitat preference for waterbirds in managed floodplain wetlands is presented in Chapter VI as a summary.

CHAPTER II

DIFFERENTIAL HABITAT USE OF SEASONALLY FLOODED WETLANDS BY MIGRANT RAILS AND BITTERNS

The habitat preferences of a bird species are determined by its ability to obtain food and shelter successfully and to avoid potential competitors or predators in the habitat (Cody 1974, Wiens and Rotenberry 1981). The patterns of micro-habitat preferences for coexisting bird species across structural components of the habitat may suggest mechanisms of resource partitioning (Cody 1981). These same patterns may be used by land managers to supply target avian species or groups with preferred micro-habitats. However, many patterns of micro-habitat use for coexisting bird species are poorly understood during certain periods of the annual cycle, such as migration or wintering, or remain totally undescribed. Two waterbird groups which appear to coexist within similar freshwater wetland habitats are the rails and bitterns, yet description of micro-habitat characteristics upon which these groups may segregate is incomplete. Both groups are secretive in nature and generally prefer densely vegetated wetlands (AOU 1983). Comparisons of specific habitat conditions or interactions among these conditions are not available, despite the fact that 7 rallid species and 2 bittern species may coexist in the same North American wetland complex.

Although generally described in a qualitative manner, some habitat variables for rallids have been partially quantified. Both Virginia rail (Rallus limicola) and sora (Porzana carolina) tend to nest in relatively deep waters [20-50 cm depth (Johnson and Dinsmore 1986)], but nesting also occurs in shallow marshes [<15 cm water depth (Griese et al. 1980)]. Saturated soils or shallow water depths (<5 cm) are preferred by migrant Virginia rails, whereas migrant soras prefer depths between 5-15 cm (Sayre and Rundle 1984) in seasonally flooded wetlands of the northern Mississippi Alluvial Valley. King rails (Rallus elegans) have been described as a "damp habitat species" (Meanley 1953), but water depths of approximately 60 cm have been reported for nesting sites (Trautman 1940). All 3 of these rallid species select tall, dense vegetation (Meanley 1969, Sayre and Rundle 1984). Yellow rails (Coturnicops noveboracensis) nest in short sedge dominated wetlands that range from saturated soil to 30 cm of water (Bookhout and Stenzel 1987). The 2 North American bittern species, American bittern (Botaurus lentiginosus) and least bittern (Ixobrychus exilis) nest in dense marshes (Weller and Spatcher 1965), but quantitative habitat information is lacking (Hancock and Kushlan 1984).

Acquisition of nutrients during spring migration is critical for temperate rallids and herons because nutrients must be obtained in a short period to maintain energy for migration and to potentially build body reserves for

territorial defense or breeding. Body condition on departure from spring staging areas may be the critical factor limiting reproductive output (Drent and Daan 1980). This may be especially true for large bodied waterbirds such as swans, geese, cranes and large herons which can gain nutrient reserves for breeding on wintering or staging areas (Ankney and MacInnes 1978, Raveling 1979, den Held 1981). The lipid demands for long hemispheric migrations of small-bodied waterbirds, such as arctic nesting sandpipers, limits nutrient storage capabilities during migration; however, staging areas are very important to rebuild lipid concentrations spent in migration (Ross 1979, Myers et al. 1987). American coots (Fulica americana), the largest of North American rallids, store all lipids required for egg production as reserves prior to arrival on breeding grounds (Alisauskas and Ankney 1985). This suggests that the condition of wintering or migrational habitats directly influences whether a coot will nest and the size of her clutch (Alisauskas and Ankney 1985). The specific strategies of nutrient acquisition before and during reproduction are unknown for most rallids and bitterns, but spring migration areas that provide quality foraging habitats may allow birds to arrive in better condition to attempt nesting. During fall migration, foods are needed for maintenance, migration and, in some cases, molt. The specific characteristics of quality wetland habitat that provide the food and cover resources for migrant rails and

bitterns is poorly documented. Unfortunately, palustrine, emergent wetlands of North America, probably the most important habitat type for rallids and bitterns, have been lost to agricultural expansion at a very rapid rate (Tiner 1984). Continued habitat degradation and declines in several rallid and bittern populations have resulted in the placement of many of these species on Midwest states' threatened or endangered faunal lists (Eddleman et al. 1988). Knowledge of specific micro-habitat characteristics such as water depth, vegetation height and vegetation stem density at site of rallid or bittern use would be valuable for wetland acquisition and management. This study was conducted to provide a quantitative comparison of habitat use by migrant rails and bitterns.

STUDY SITE AND METHODS

The study site was located within the 1,015 ha block of fields, marshes and seasonally flooded wetlands on the Ted Shanks Wildlife Area (WA) in northeastern Missouri ($39^{\circ}30'N$, $91^{\circ}W$). Historically, this site was a floodplain wetland at the confluence of the Mississippi and Salt rivers. Clearing for agricultural purposes occurred in the early and mid-twentieth century; however, wetland restoration activities in the last 15 years have recreated wetland conditions. Three marsh units (Unit 2A - 13 ha, Unit 9A - 7 ha, and Burreed Natural Area - 8 ha) and two seasonally flooded units (Unit 8A - 38 ha and Unit 2D - 42

ha [1984-85 only]) were systematically searched for migrant rails and bitterns between 1 April - 31 May and 15 August - 15 October from 1982-85. Two of the marsh units (2A and 9A) were searched completely, while strip transects were searched in the other wetlands. Several investigators searched vegetation for flushing rails or bitterns between 0700 to 1000 hours or between 1700 to 2000 hours in an attempt to gather data more reflective of foraging location (Rundle and Sayre 1983). Once a specific flush site was located, water depth, vegetation height, plant species composition, and stem density (recorded as stems/[20 cm x 20 cm] and converted to stems/m² prior to analysis) were recorded. Data were not collected if the bird appeared to be moving away from the observer, had potentially been flushed from another area, or a specific flush site was not clearly identified. Attempts were made to gather data from approximately 15 flush sites for each species, each year. Although American coot and common moorhen (Gallinula chloropus) were present, data were not collected on these species that occupied deeper and more open sites than the other rallids (Eddleman et al. 1988). Habitat characteristics of least bittern feeding platforms were also recorded during the period 15 May - 1 July to compare to migrant flush data.

RESULTS

Habitat usage in spring

A total of 152 flush sites for 3 rail species and 86 flush sites for the 2 bittern species were recorded in spring. Sora use occurred in the deepest water sites (Table 1) among the rail species (Fig. 1), while Virginia rail use occurred in sites with the shallowest water. All rail species were significantly different ($P < 0.05$) from each other rail in relation to their use of water depth (Student's T [LSD] and Tukey's Studentized range [HSD]). All rails used significantly shallower water than both bitterns (Fig. 1). Least bitterns displayed a slightly greater range of water depth tolerances, whereas American bitterns flushed from slightly greater mean water depths than the smaller bittern species. This relationship was statistically significant under one means comparison procedure (LSD) but not another (HSD), suggesting that a difference may exist. Whether such a difference is biologically meaningful is open to question (Fig. 1).

Soras occurred in the tallest vegetation (Table 2) among the rails studied (Fig. 2), whereas Virginia rails used the shortest vegetation, but none of the comparisons were significantly different (Least Square Means [LSM], sora v. king rail $P = 0.886$; sora v. Virginia rail $P = 0.139$; king rail v. Virginia rail $P = 0.199$). All 3 of the rail species consistently were flushed from significantly shorter vegetation than both bitterns (LSM, $P < 0.05$) (Fig. 2).

Although least bitterns were present in both shorter and taller vegetation than American bitterns, mean vegetation height at flush sites was not significantly different between the two species (LSM, $P = 0.822$).

Among the rail species, the mean stem density at flush sites was greatest for king rails (Table 3) and least for Virginia rails (Fig. 3), and significantly different between the 2 species (LSM, $P = 0.043$). Comparisons of stem densities at sites used by soras and Virginia rails and between soras and king rails were not significant (LSM, $P = 0.119$ and $P = 0.563$ respectively). Stem density was significantly different between sites used by sora and American bittern ($P = 0.002$) and those used by king rail and American bittern ($P < 0.001$), but sites used by Virginia rail and American bittern were similar ($P = 0.149$). None of the rail species used sites that had stem densities that were significantly different than sites used by least bitterns ($P > 0.05$), but sites used by the 2 bittern species were different ($P < 0.001$). The distribution of stem densities of sites that the bitterns use (Fig. 3) is concentrated on less dense values than that of sites used by rails.

All 3 rail species were closely associated with perennial vegetation (ranging from 100% at king rail sites to 86% at Virginia rail sites), but vegetation was dominated by moist-soil plants (ranging from 74% at Virginia rail sites to 62% at sora sites) rather than robust emergents.

Sora sites were dominated by ricecut grass (Leersia oryzoides) at 28% of flush sites and Carex sedges at 18% of flush sites. King rail flush sites were dominated by ricecut grass at 45% and burreed (Sparganium eurycarpum) at 16%. Virginia rail sites were dominated by ricecut grass at 40% and Carex sedges and cattail (Typha spp.) both at 14%. The bittern species were almost exclusively associated with perennial vegetation (ranging from 100% at American bittern sites to 97% at least bittern sites), but vegetation was dominated by robust emergents (ranging from 78% at American bittern sites to 57% at least bittern sites). American bittern sites were dominated by river bulrush (Scirpus fluviatilis) at 24%, burreed at 22%, and cattail at 20%. Least bittern sites were dominated by burreed at 33% and water smartweed (Polygonum coccineum) at 23%

Habitat usage in fall

A total of 108 flush sites for 4 rail species and 50 flush sites for the 2 bittern species were recorded in fall. Sora used deeper water depths (Table 4) than any other rail species (Fig. 4), while Virginia rails used the shallowest water. Excluding the yellow rail from comparisons (because of low sample size), each rail species was significantly different ($P < 0.05$) from the other rails in relation to water depth (LSD and HSD). All water depths at sites used by rails were significantly shallower than those used by both bitterns (Fig. 4), but the bittern species were not

significantly different ($P > 0.05$, LSD and HSD) in their use of water depth.

King rails typically occurred in the tallest vegetation (Table 5) among the rail species (Fig. 5). King rails used significantly taller vegetation than did soras and Virginia rails (LSM, $P = 0.001$ and $P = 0.009$ respectively). A comparison of vegetation height used by soras and Virginia rails was not significant ($P = 0.269$). Soras and Virginia rails were found in shorter vegetation than both bittern species ($P < 0.002$), but vegetation height at sites used by king rails was not different from sites used by either American bitterns ($P = 0.259$) or least bitterns ($P = 0.219$). No difference existed for height of vegetation used by the 2 bittern species ($P = 0.732$).

Virginia rails and yellow rails occurred in the densest vegetation (Table 6), but because of low sample size, yellow rails were excluded from statistical treatment. Among the rail species, Virginia rails were found in significantly denser vegetation than soras (LSM, $P = 0.018$) or king rails ($P = 0.012$), but soras and king rails used sites that had similar densities ($P = 0.567$) (Fig. 6). All rail species used denser vegetation than the bitterns ($P < 0.05$), but American and least bitterns used vegetation of similar density ($P = 0.482$).

Soras and yellow rails were associated with annual vegetation (71% and 75% respectively), whereas king rails and Virginia rails were associated more with perennial

vegetation (72% and 100%, respectively). Vegetation was dominated by moist-soil plants (100% for both Virginia rails and yellow rails, 91% for soras, and 68% for king rails) rather than robust emergents. Soras used sites that were dominated by a barnyard grass - nutsedge mix (Echinochloa spp. and Cyperus spp.) at 50% and marsh smartweed at 15%. Virginia rails flushed from ricecut grass 3 times and from flat culm spikerush (Eleocharis macrostachya) and water smartweed once. Yellow rails flushed from ricecut grass, sprangletop (Leptochloa sp.), beggarticks (Bidens sp.) and cockleburr (Xanthium sp.). King rails were associated with 6 sites in open mudflat, but of the vegetated sites, barnyard grass dominated at 32%, with cattail and burreed important at 20% and 12% respectively. In contrast to the rallids, the bitterns were associated with robust emergent vegetation. American bitterns used sites that were associated with 89% perennial and 57% robust, emergent vegetation, whereas least bitterns used sites that were associated with 100% perennial and 73% robust emergents. Sites used by American bitterns were dominated by cattail (34%), water smartweed (20%) and burreed (14%). Least bitterns were found in vegetation dominated by cattail (47%), water smartweed (27%) and burreed (20%).

Comparison among seasons

Comparisons were made between fall and spring habitat variables for each of the waterbird species. A general linear ANOVA model was conducted for species, season, and

species-season interaction for each of the three dependent habitat variables (water depth, vegetation height, and stem density) to elucidate the patterns of bird usage with wetland habitat characteristics.

In computing a general linear ANOVA model for species, season and species-season interaction for the dependent variable of water depth, only species were significantly different to develop the model ($F = 107$, $P < 0.001$).

In comparing vegetation height between spring and fall seasons for the 3 rallids and 2 bitterns, all of the comparisons were significantly different at $P < 0.001$, except Virginia rail which was significantly different at $P = 0.034$ (LSM). A general linear ANOVA model for species, season and species-season interaction for the dependent variable of vegetation height found species ($F = 15$, $P < 0.001$), season ($F = 224$, $P < 0.001$) and species-season interaction ($F = 3$, $P < 0.018$) all significant to develop the model.

A comparison of stem densities between spring and fall seasons for each species revealed significant differences for Virginia rail (LSM, $P < 0.001$) and least bittern ($P = 0.024$), but differences were not significant for sora ($P = 0.069$), king rail ($P = 0.751$) or American bittern ($P = 0.243$). A general linear ANOVA model for species, season and species-season interaction for the dependent variable of stem density found species ($F = 8$, $P < 0.001$), season ($F = 7$, $P = 0.009$) and species-season interaction ($F = 5$, $P <$

0.001) all significant to develop the model.

Seasonal differences among vegetation types and dominant plant species existed for each waterbird species. The most dramatic seasonal difference in vegetation type was demonstrated by sora, where that species was 6.4 (\hat{OR} = odds ratio) times more likely to be in robust vegetation in spring than in fall. Virginia rails and American bitterns were 1.7 and 2.4 (\hat{OR}), respectively, times more likely to be in robust vegetation in spring than in fall, whereas, king rails and least bitterns were more likely found in robust vegetation in fall than in spring (1.2 and 2.0 [\hat{OR}] times respectively).

Least bittern feeding platforms

Adult least bitterns often constructed feeding platforms that allowed both adult birds and chicks to forage without grabbing emergent vegetation. Such activities were typically associated with the late stages of incubation to brood rearing. Additional vegetation was added to a foraging site and stems from adjacent plants usually were bent over, but this construction was distinct from nest building (Weller 1961, Reid unpubl.). To compare feeding platform sites from flush sites, 52 platform sites were measured (Table 7). Although there was a significant difference between spring flush sites and platform sites for water depth (HSD, $P < 0.05$), no difference existed between fall flush sites and platform sites ($P > 0.05$). Spring, fall and

platform vegetation height values were all significantly different (HSD, $P < 0.05$). Whereas comparisons of spring and fall and a comparison of spring and platform sites were significantly different (HSD, $P < 0.05$) for stem density, fall and platform sites were not significantly different ($P > 0.05$).

DISCUSSION

To clarify the patterns of differential wetland habitat use among the rails and bitterns, habitat variables are examined for rallids first, then for the bitterns, and finally the two migrant groups are compared. A clear pattern of spatial segregation is revealed for migrant rallids in relation to water depth (Figs. 1 and 4). Soras are located in the deepest sites, Virginia rails use saturated soils or very shallow water depths whereas king rails use intermediate depths. The same pattern holds for both spring and fall habitat usage, yet deeper sites are used by all species in spring. Water depths used by yellow rails probably fall between those used by Virginia and king rails, but data for yellow rails are limited to only 4 fall flushes. Virginia and king rails were often associated with water/soil interfaces in spring and fall, however these were not quantified. A similar pattern of differential habitat use based on water depth was documented for migrant Virginia rails and soras in seasonally flooded wetlands of southeastern Missouri (Sayre and Rundle 1984), but the water

depths used by soras were shallower in both seasons. No differences were evident, however, in habitat use for breeding Virginia rails and soras in glaciated marshes of northwestern Iowa (Johnson and Dinsmore 1986). Both nesting species used territorial sites (means between 38-41 cm in depth) that were not significantly different in depth. Preference for deeper sites to protect nests from mammalian predators may cause selection for deeper wetland basins by both species on breeding grounds.

The structural component of vegetation height revealed few use patterns among avian species. All rallids used similar vegetation in spring. In fall king rails used taller vegetation than soras or Virginia rails. The close association of king rails with perennial vegetation in fall may explain this difference. Use of vegetation density was different for king and Virginia rails for both seasons, but king rails used denser vegetation in spring, whereas Virginia rails used denser vegetation in fall. Part of this apparent anomaly might be explained by temporal differences in the fall migration of these two species. Virginia rails migrate later than king rails, thus they may use the dense vegetation present in newly flooded areas in early October. The difference in use of vegetation may merely be an artifact of small sample size for fall migrating Virginia rails. Probably the strongest pattern related to wetland plants and habitat use by migrant rails is the ubiquitous use of perennial vegetation by all species in spring, but

the fall segregation by soras and yellow rails to sites with annual vegetation, whereas king and Virginia rails use sites dominated by perennial vegetation.

The cline of use among species related to water depth and the differential selection of plant types in the fall is most probably related to differences in foraging modes of the species. Soras have the ability to forage in deeper water sites because they cling to aquatic plants or are supported by floating, rank vegetation. Sedge seeds and adult invertebrates (principally beetles and snails) dominate spring diets in migration, whereas seeds of annual grasses and smartweeds are important in fall (Meanley 1965, Rundle and Sayre 1983). The peak of fall migration in northeastern Missouri appears initially timed to the exploitation of maturing barnyard grass and sprangletop, while later migrants appear to exploit smartweeds and crabgrass. Sora may strip maturing seed heads from the aquatic plants as the most efficient means of gaining large numbers of seeds rapidly (Meanley 1965, Rundle and Sayre 1983). The smaller yellow rail may also exploit seed resources, but in shallower sites. Virginia and king rails both possess long, slightly curved bills that can be used to probe mud substrates or capture aquatic invertebrate prey in water. Snails and insects dominate preferred foods on Iowa breeding grounds for Virginia rail (Horak 1970), whereas crayfish and aquatic insects were most important for king rails in marshes of Arkansas (Meanley 1956). Foraging in

very shallow water sites or at water-mud interfaces is the most efficient location to exploit such animal prey (Chapter 3).

Rallids demonstrated a strong segregation of habitat use based on water depth, whereas segregation by micro-habitat types between the two bitterns did not appear to exist. Water depths used by the two bittern species in spring and fall were not significantly different.

Vegetation height was not an important variable. Least bitterns used denser vegetation than American bitterns in spring, but no difference occurred in fall. American bitterns were associated with robust vegetation slightly more frequently in spring, especially river bulrush, than least bitterns, which are more associated with water smartweed. Least bitterns were slightly more associated with robust vegetation in fall than American bitterns.

Feeding platforms of least bitterns were at sites deeper and with less dense vegetation than spring flush sites. Least bitterns feed on macroinvertebrates, amphibians, and fish at the water surface (Eastwood 1932, Weller 1961).

Construction of feeding structures may allow breeding adults and chicks to forage at the surface of deeper sites where dense, robust vegetation is lacking. Construction of feeding platforms and behavior of grasping emergent vegetation when foraging allows this smallest representative of the Ciconiiformes to feed in relatively deep wetland basins. Least bitterns may forage in deep sites where

floating vegetation exists, but this was not the case for American lotus (Nelumbo lutea) sites in this study.

The general pattern of habitat use by migrant rails and bitterns is that rails used sites with shallower water and shorter and denser vegetation where moist-soil plants rather than robust emergents are dominant. The only exceptions to this pattern of use were: (1) vegetation heights in fall for king rails and both bitterns, (2) vegetation densities in spring for Virginia rails and American bitterns, and (3) vegetation densities in spring for all rails and least bitterns. The exceptions to these general patterns of use are not significantly different, thus none of the exceptions contradict the pattern.

The patterns of differential habitat use among rails and bitterns have been broadly described around clines of water depth and vegetation structure (Weller and Spatcher 1965, Rundle and Fredrickson 1981). This investigation quantified specific micro-habitat use during migration. The extremes of micro-habitat preference suggest that neither migrant rails, nor migrant bitterns use seasonally flooded wetlands in the spring with water depths greater than 44 cm. Even the sora, which forages at the deepest sites of all the rallids, prefers depths less than 25 cm during spring migration. Both bitterns prefer water depths between 15 to 35 cm. Rallids prefer vegetation densities between 100 to 400 stems/m², whereas, bitterns prefer less dense, more robust vegetation in spring. Rails did not use water depths

greater than 31 cm during fall migration. Even though soras foraged in sites with deeper water than all of the other rallids, water depths of less than 20 cm were preferred. As during spring migration, bitterns preferred water depths between 15 to 35 cm during fall migration. Similar patterns of habitat preference may exist during the nesting period (Weller and Spatcher 1965, Fredrickson and Reid 1986), however, differences between sites used by Virginia rails and soras may be far more subtle (Andrews 1973, Giese et al. 1980, Johnson and Dinsmore 1985) than during migration. Patterns of habitat use on wintering grounds need elucidation (Eddleman et al. 1988). These data will provide managers with specific habitat characteristics. With recent declines in several North American rallid and bittern populations (Eddleman et al. 1988), this information is needed immediately. Similar dramatic declines in Rallus and Porzana species in Europe over the last twenty years (Reichholf 1982) suggest that the North American situation is not a unique conservation problem.

Wetlands of the midwestern and southeastern United States may contain up to 7 species of migrant rallids and 2 species of bitterns concurrently. Reed-cattail marshes of central Europe may contain 4 species of rallids and 5 species of herons, including 2 species of bitterns (Oksanen et al. 1979). In the latter instance, the weights of species tend to make up a geometric series. The size of food items is suggested to be one possible niche dimension

among sympatric competitors (Oksanen et al. 1979), and differences in habitat preference may be relative to differences in foraging ecology and behavior in the context of alternative aspects of resource partitioning (Cody 1974, Cody 1981). If the waterbird species of this study are separated into foraging guilds, then patterns relative to the structural habitat component of water depth are distinct. For the granivores, soras forage in deeper water than yellow rails; whereas, for the aquatic invertebrate predators, king rails forage in deeper water than Virginia rails. The picivorous/insectivorous predators, least bitterns and American bitterns, forage in deeper water than any of the rallids, however, the bitterns themselves show little difference between species in micro-habitat preference relative to water depth. Instead, differences in body size, prey size and foraging behavior may be important. Because least bitterns forage at the water surface and American bitterns forage in the water column, there may be a distinct partitioning of food resources across a vertical gradient. The evolution of micro-habitat preferences is determined by, and determines, a bird species' morphological structure and behavioral functions which allow food acquisition and predator avoidance within a habitat (Hilden 1965, Cody 1985). Migrant rallids and bitterns of North America appear to use body size, tarsal length, bill type and foraging behaviors as isolating mechanisms that allow them to coexist within the same wetland.

TABLE 1. Water depths (mm) at spring flush sites of migrant rails and bitterns.

Species	Mean \pm SE	Range	CV
Sora (N = 60)	181 \pm 12	27 - 433	52
King rail (N = 49)	97 \pm 6	25 - 200	42
Virginia rail (N = 43)	52 \pm 5	0 - 141	56
Least bittern (N = 61)	228 \pm 12	70 - 421	40
American bittern (N = 25)	256 \pm 10	120 - 340	25

TABLE 2. Vegetation heights (cm) at spring flush sites of migrant rails and bitterns.

Species	Mean \pm SE	Range	CV
Sora (N = 60)	51.4 \pm 2.9	22 - 140	44
King rail (N = 49)	50.6 \pm 1.8	31 - 84	24
Virginia rail (N = 43)	42.8 \pm 2.5	22 - 90	38
Least bittern (N = 61)	64.1 \pm 3.5	22 - 146	43
American bittern (N = 25)	62.9 \pm 2.4	31 - 97	26

TABLE 3. Vegetation stem densities (stems/m²) at spring flush sites of migrant rails and bitterns.

Species	Mean \pm SE	Range	CV
Sora (N = 60)	273 \pm 28	25 - 1150	81
King rail (N = 49)	293 \pm 29	50 - 1000	70
Virginia rail (N = 43)	214 \pm 20	25 - 550	62
Least bittern (N = 61)	287 \pm 33	75 - 1200	89
American bittern (N = 25)	157 \pm 25	25 - 875	107

TABLE 4. Water depths (mm) at fall flush sites of migrant rails and bitterns.

Species	Mean \pm SE	Range	CV
Sora (N = 68)	148 \pm 6	54 - 301	36
King rail (N = 31)	76 \pm 9	10 - 245	65
Yellow rail (N = 4)	48 \pm 29	0 - 113	119
Virginia rail (N = 5)	19 \pm 9	0 - 40	105
Least bittern (N = 15)	244 \pm 26	88 - 421	41
American bittern (N = 35)	253 \pm 14	74 - 365	33

TABLE 5. Vegetation heights (cm) at fall flush sites of migrant rails and bitterns.

Species	Mean \pm SE	Range	CV
Sora (N = 68)	86.9 \pm 4.1	63 - 204	39
King rail (N = 25)	109.2 \pm 8.8	65 - 195	40
Yellow rail (N = 4)	78.0 \pm 6.7	62 - 94	17
Virginia rail (N = 5)	72.0 \pm 2.5	66 - 80	8
Least bittern (N = 15)	120.9 \pm 10.5	59 - 181	34
American bittern (N = 35)	117.9 \pm 8.4	55 - 208	42

TABLE 6. Vegetation stem densities (stems/m²) at fall flush sites of migrant rails and bitterns.

Species	Mean \pm SE	Range	CV
Sora (N = 68)	333 \pm 17	50 - 625	42
King rail (N = 25)	308 \pm 36	50 - 750	59
Yellow rail (N = 4)	456 \pm 74	275 - 600	32
Virginia rail (N = 5)	540 \pm 116	325 - 975	48
Least bittern (N = 15)	165 \pm 24	75 - 375	56
American bittern (N = 35)	206 \pm 24	50 - 625	69

TABLE 7. Physical characteristics of least bittern feeding platforms.

Variable (N = 52)	Mean \pm SE	Range	CV
Water depth (mm)	293 \pm 12	183 - 487	28
Height platform above water (cm)	4.9 \pm 0.3	2 - 11	48
Vegetation height (cm)	82.8 \pm 4.4	48 - 167	38
Vegetation stem density (stems/m ²)	199 \pm 13	100 - 700	47

Fig. 1 Box plots showing a comparison of water depths (mm) used by spring migrant rails and bitterns. Vertical lines show extremes, while box represents upper and lower quartiles.

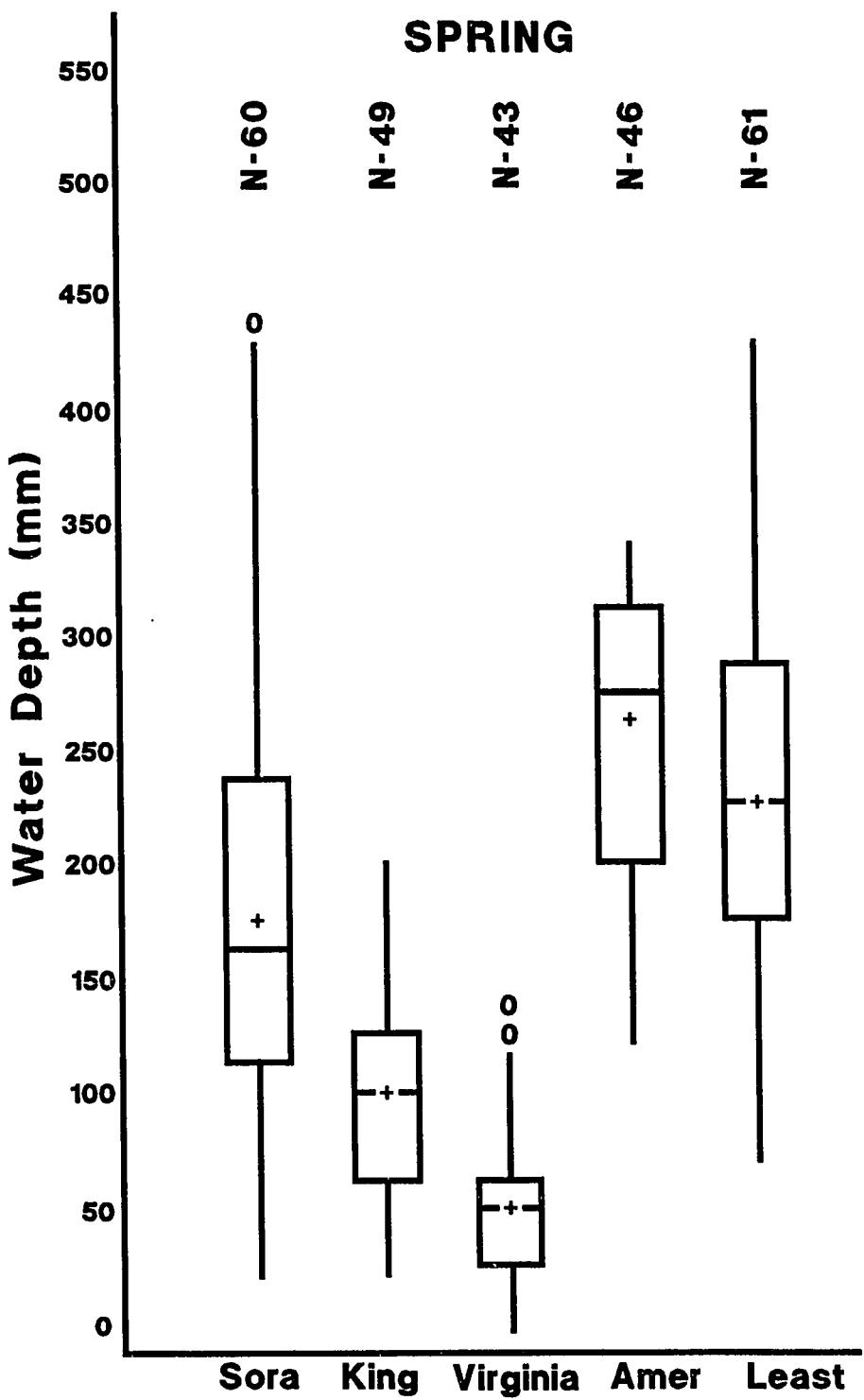


Fig. 2 Box plots showing a comparison of vegetation height (cm) for flush sites of spring migrant rails and bitterns. Vertical lines show extremes, while box represents upper and lower quartiles.

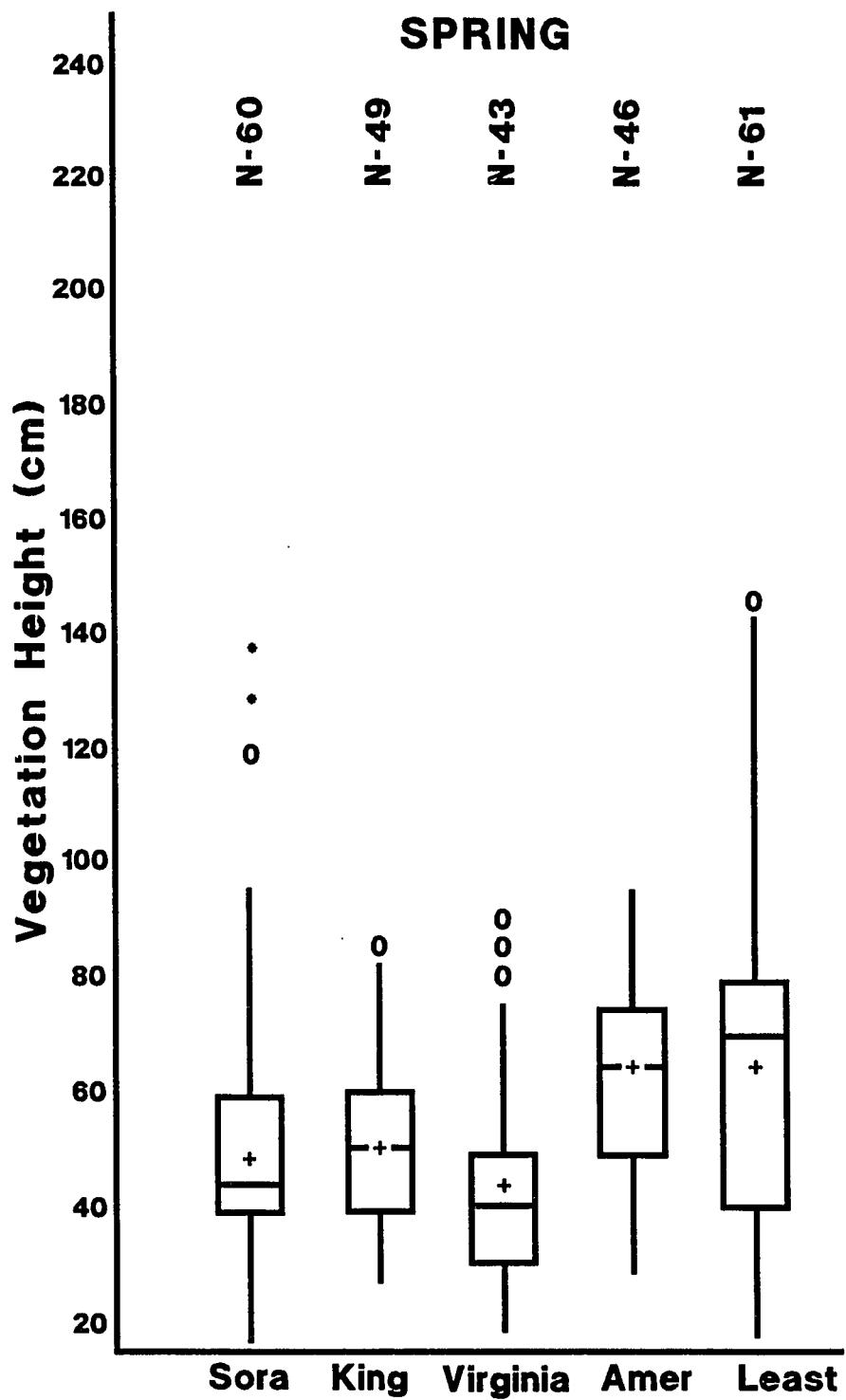


Fig. 3 Box plots showing a comparison of vegetation
stem density ($\text{stems/m}^2 \times 100$) for flush sites
of spring migrant rails and bitterns.
Vertical lines show extremes, while box
represents upper and lower quartiles.

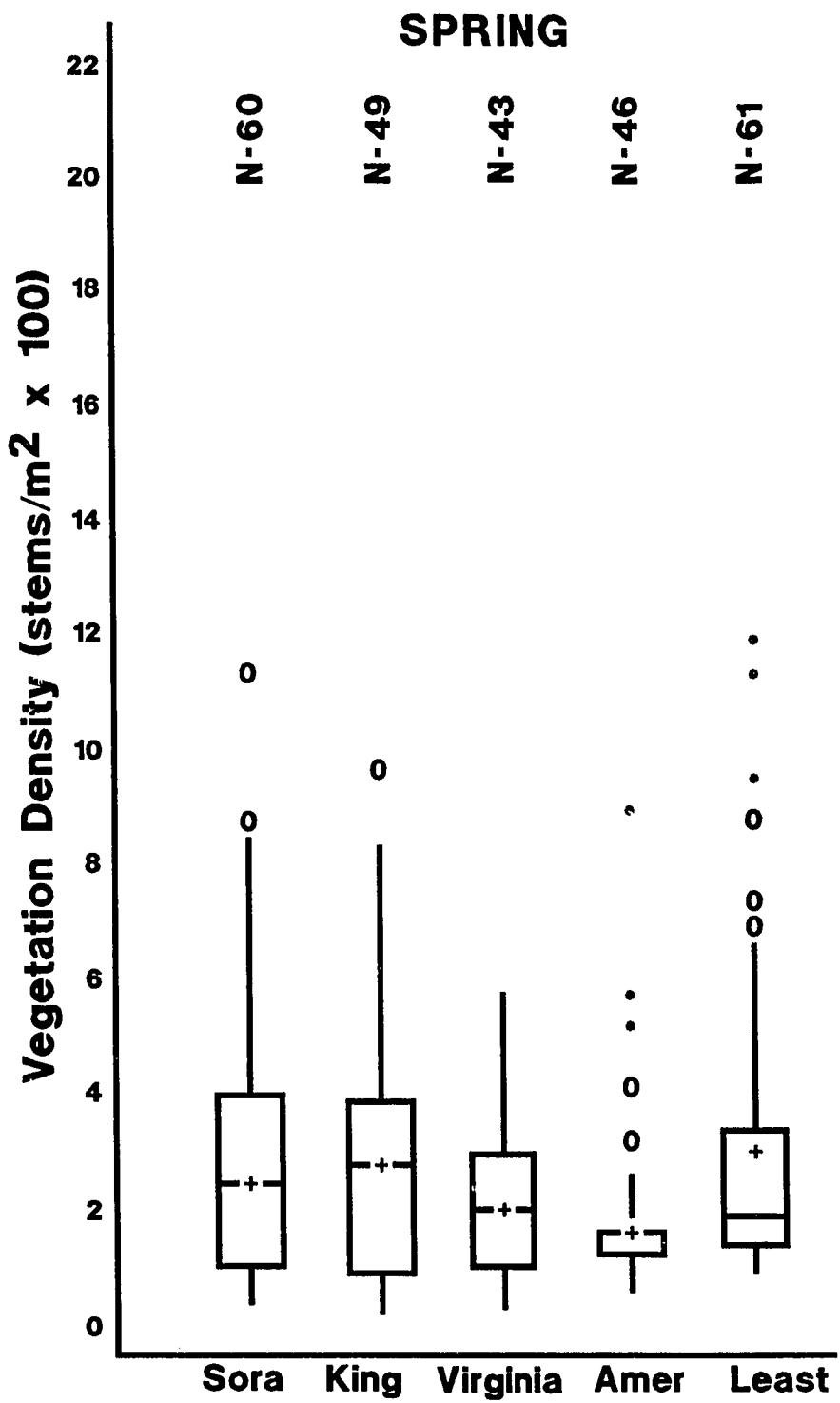


Fig. 4 Box plots showing a comparison of water depths (mm) used by fall migrant rails and bitterns. Vertical lines show extremes, while box represents upper and lower quartiles.

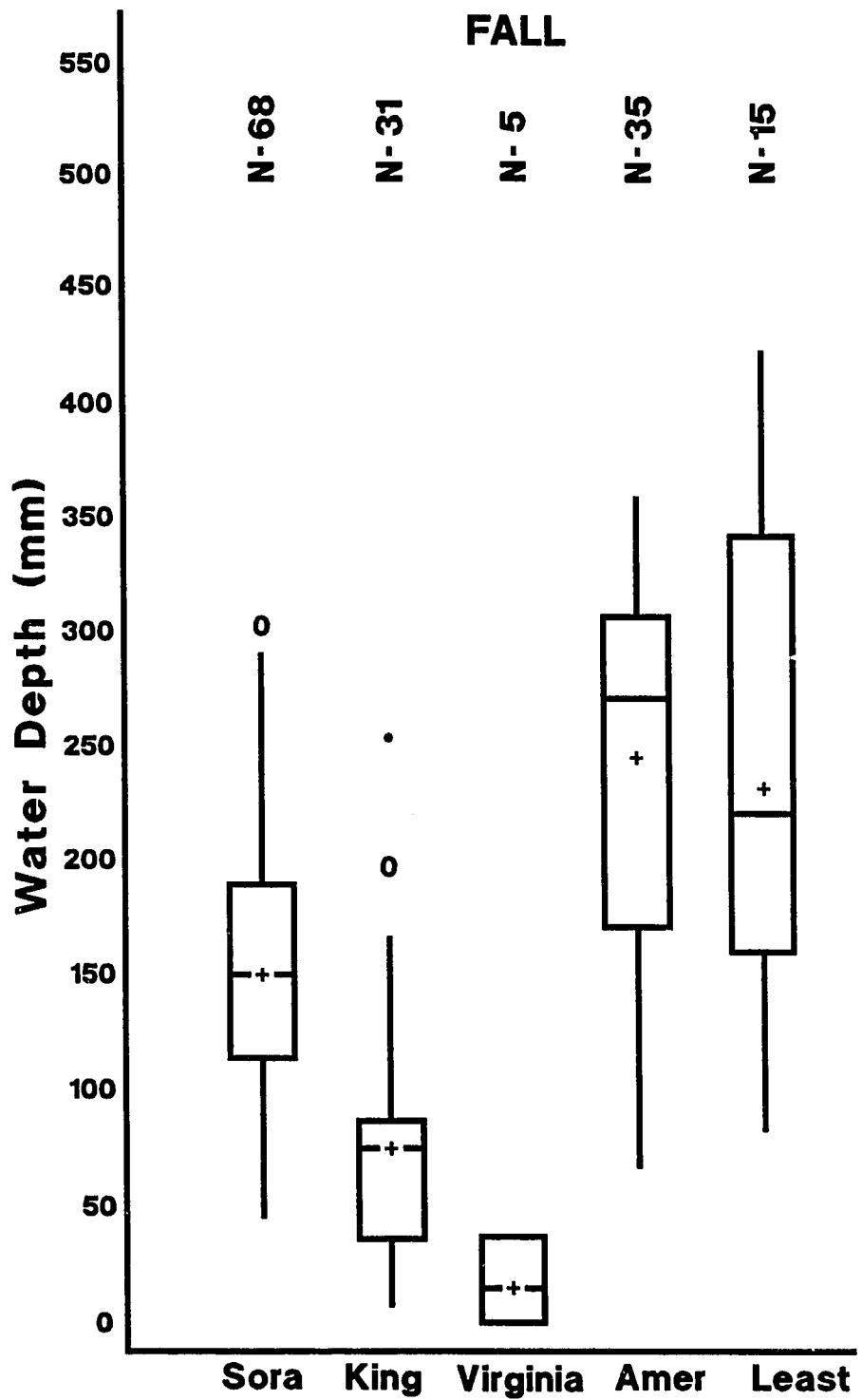


Fig. 5 Box plots showing a comparison of vegetation height (cm) for flush sites of fall migrant rails and bitterns. Vertical lines show extremes, while box represents upper and lower quartiles.

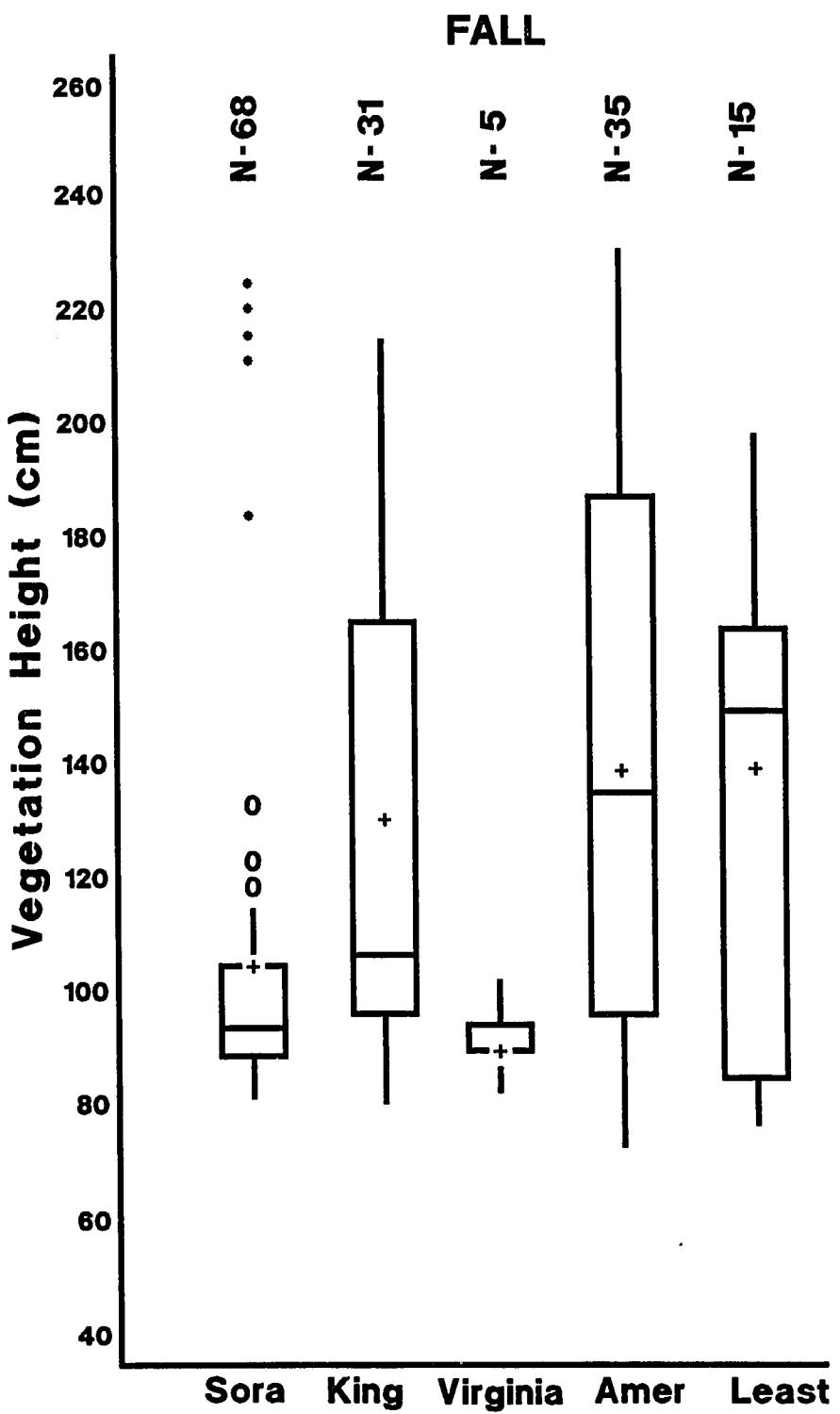
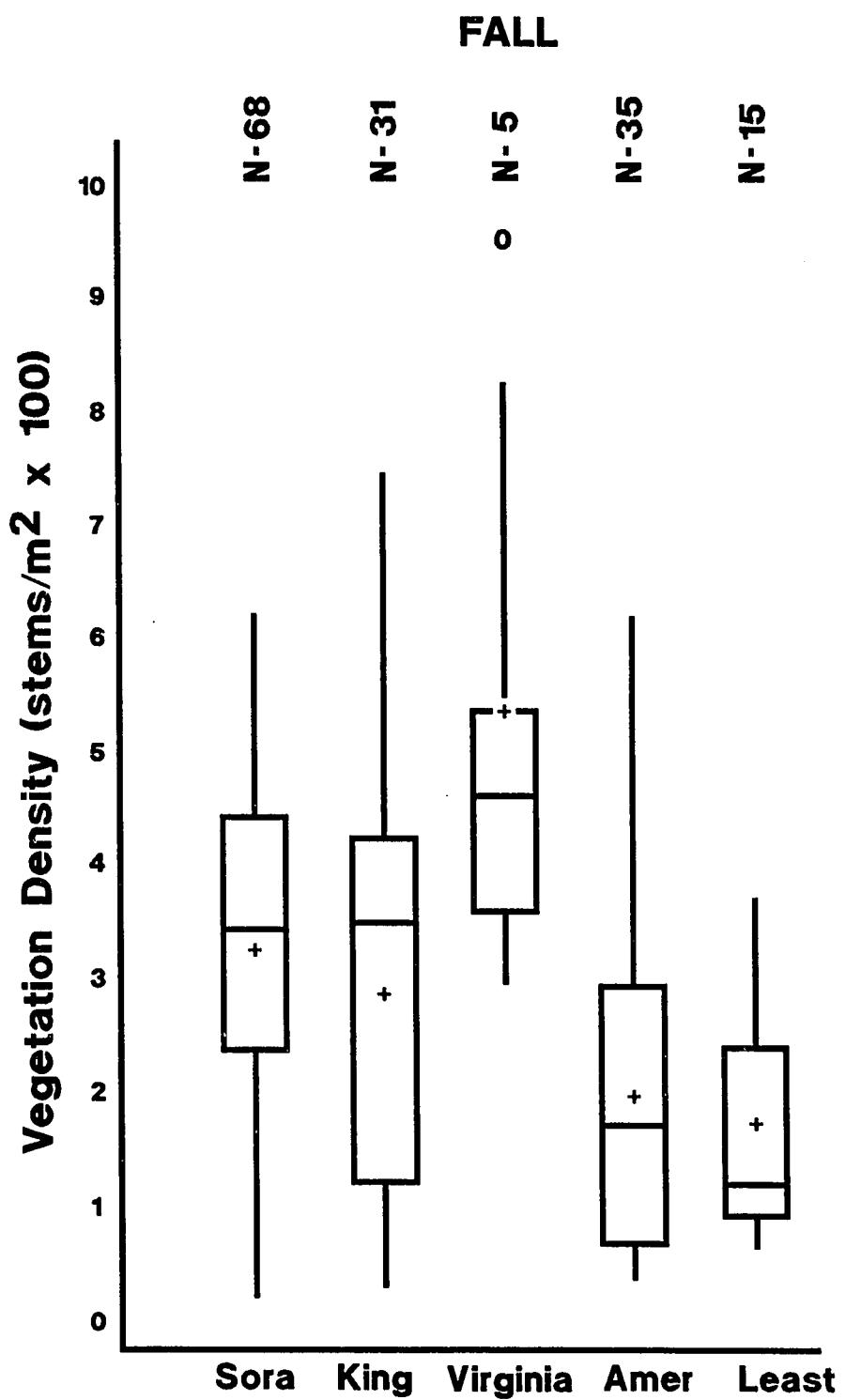


Fig. 6 Box plots showing a comparison of vegetation stem density ($\text{stems/m}^2 \times 100$) for flush sites of fall migrant rails and bitterns. Vertical lines show extremes, while box represents upper and lower quartiles.



CHAPTER III
BREEDING ECOLOGY OF KING RAIL IN A MANAGED
MISSISSIPPI RIVER FLOODPLAIN WETLAND

The King rail (Rallus elegans) has a broad distribution across eastern North America, ranging from the Gulf of Mexico to southern Canada and from the Great Plains to the Atlantic coast (AOU 1983). This rallid breeds in a great diversity of freshwater and brackish wetlands (Meanley 1969). Despite this broad geographic and habitat distribution, alarming declines in populations of this species have occurred in the last 30 years (Ripley 1977). Specific locations of recent declines include the southwestern shore of Lake Erie, the glacial marshes of northwestern Iowa, the western shore of Maryland, the Smyrna River marshes of Delaware, and the Arkansas rice belt (Meanley 1969, Weller 1979, Eddleman et al. 1988). Much of this decline can be directly related to wetland habitat losses and perturbations across North America. Approximately 54% of the original wetlands in the conterminous United States have been lost (Tiner 1984); agriculture specifically has accounted for 87% of wetland losses from the mid-1950s to mid-1970s (Frayer et al. 1983). Palustrine, emergent wetlands (Cowardin et al. 1979) are probably the most important habitat type for king rails (Meanley 1969), and have declined by 1.9 million ha during

that 20-year period (Frayer et al. 1983). These losses represented approximately 17% of all existing conterminous palustrine wetlands.

With continued wetland degradations and declining populations, several states have listed the king rail among state endangered or threatened species. Missouri is among this group, and lists only 8 counties that have recent nesting records (MDC 1984). In contrast, 13 southern Atlantic and Gulf Coast states still allow sport hunting of king rails, principally in association with clapper rail (R. crepitans) hunting (USFWS 1987). Even though the king rail is considered endangered in central portions of its breeding range and hunted in southern regions, basic information on breeding and specific habitat needs is lacking. The secretive nature of this species has restricted collection of even basic information, such as occurrence, over much of its range. Despite its wide breeding range, only the wetland habitat of the Grand Prairie region of Arkansas has been quantitatively described for breeding king rails (Meanley 1953, Meanley 1969).

The present study was undertaken to develop a quantitative description of nesting habitat, to record the chronology of nesting, and to document the relationship among nesting success and habitat variables in a managed wetland in the floodplain of the Mississippi River.

STUDY AREA AND FIELD METHODS

The study area was located on the Ted Shanks Wildlife

Area (WA) in northeastern Missouri ($39^{\circ} 30'N$, $91^{\circ}W$), a public wetland managed by the Missouri Department of Conservation. This 4,480 ha area lies at the confluence of the Mississippi and Salt rivers. Although most of the area consists of bottomland hardwoods, fields, marshes and seasonally flooded wetlands account for a 1,015 ha block of nonforested habitats. Although area of nonforested habitats increased through clearing prior to public acquisition, palustrine, emergent wetlands within large openings in riverine bottomland forests have historically existed, as evidenced by the 1812 map of this area constructed by Zebulon Pike.

All marsh and seasonally flooded impoundments, known as units, were systematically searched for rail nests between 15 April and 15 August from 1981-85. Several investigators searched vegetation via transects that divided the habitats at 3 m intervals. Habitats were searched at least biweekly and often more frequently. Herbaceous wetland habitat ranged from 138 ha to 221 ha in 17 management units among years, but much of this habitat was either dry or deep, open water in several years. Dewatering (drawdown) was conducted on many seasonally flooded units in accordance to moist-soil techniques (Fredrickson and Taylor 1982). When a nest was located, nest characteristics (water depth at site, distance to open water, dominant vegetation species, height and density, nest bowl size, and number of eggs) were measured. We attempted to minimize disturbance to nests and

surrounding vegetation, and repeat visits were limited to specific checks for nest fate. Nest success was calculated using the Mayfield method (Mayfield 1975).

RESULTS

Arrivals and Rallid Nesting within the Study Area

Adult king rails were first flushed between 15 April and 1 May, with a mean first sighting of 24 April, for the years 1981-85. Adults may have been present earlier, but short, senescent vegetation restricted use of potential habitats. A total of 67 king rail nests were located during the 5 years of study. One common moorhen (Gallinula chloropus) nest and one American coot (Fulica americana) nest were found, but both were depredated. Although this area falls within the recorded southern breeding range of Virginia rail (Rallus limicola), sora (Porzana carolina) and black rail (Laterallus jamaicensis) (AOU 1983), and although the former two species are common migrants at Ted Shanks WA, no nests for any of these species were found. Thus the king rail was the only rallid to successfully breed in this area during the years of this study.

Physical Nest Site Characteristics

All king rail nests were associated with perennial vegetation (Table 8). Three species, Hart Wright's sedge (Carex hyalinolepis), ricecut grass (Leersia oryzoides) and water smartweed (Polygonum coccineum) were present at 87% of

nest sites. Dominant vegetation at nest sites differed among early and late years of the study. The chance of finding a nest in ricecut grass or water smartweed was 16 (\hat{OR} = odds ratio) times greater than finding a nest in Hart Wright's sedge in 1981-82 than in 1983-85 ($\chi^2 = 16.74$, $P < 0.005$, 1 df), and 24 (\hat{OR}) times more likely in 1981-82 than in 1984-85 ($\chi^2 = 18.60$, $P < 0.005$, 1 df). When the dominant plant species (native plants only; cultivated rice at the Arkansas site was excluded in this analysis) at nest sites is compared between Ted Shanks WA, Missouri and the Grand Prairie of Arkansas (Meanley 1969), a significantly greater proportion ($z = -2.42$, $P = 0.008$) of sedges occurred at nests in the Arkansas site (60%) than at the Missouri site (45%). The proportion of grasses, however, between the Arkansas (28%) and the Missouri sites (30%) was not different ($z = 1.09$, $P = 0.137$).

Water depth ranged from moist to 22 cm at nest sites (Table 9). The majority of nests (66%) were actually over water, but water levels were very shallow ($\bar{x} < 8$ cm). The distance to open water at rail nests ranged from 1 to 15 m, but typically nests were not immediately adjacent to open areas. The height of the nest bowl base from the substrate was dependent on whether it was a moist or wet site. The wetter the site, the higher the bowl was set above water. The size of the nest bowl varied little among the population (Table 9).

Vegetation height at nest initiation was dependent on

plant species and date of initiation. Nests in smartweed had relatively short vegetation ($\bar{x} \pm SE = 48.5 \pm 3.9\text{cm}$), whereas nests in burreed (*Sparganium eurycarpum*) or giant bulrush (*Scirpus heterochaetus*) had taller vegetation ($\bar{x} \pm SE = 101.5 \pm 12.6\text{cm}$). Plants had reached higher growth forms in nests initiated later in the season. Stem/culm density varied greatly, 225-1,950 stems/ m^2 , but nests were typically in dense tussocks or clumps of vegetation (Table 9). The growth form of smartweeds was least dense ($\bar{x} \pm SE = 317 \pm 56 \text{ stems}/\text{m}^2$), whereas spikerush was most dense ($\bar{x} \pm SE = 1,463 \pm 689 \text{ culms}/\text{m}^2$).

Chronology of Nest Initiation, Incubation, and Hatching

The earliest nest initiation (date of first egg laid) in the 5-year study was 1 May. The mean date ($\pm SE$) of first nest initiation among the 5 years was 9 May \pm 5.7 days. The mean initiation date of all nests was 29 May (Table 10). The peak of initiation occurred between the 2nd week of May and the 2nd week of June (Fig. 7), with the greatest number of nests started in the 3rd week of May or the 1st week of June. The mean date ($\pm SE$) of last nest initiation among the 5 years was 26 June \pm 9.3 days. The latest nest initiation in the 5-year study was 8 July. The earliest hatch in the 1981-5 period was 1 June. The mean date ($\pm SE$) of first hatch among the 5 years was 10 June \pm 6.4 days. The mean hatch date of all successful nests was 30 June (Table 10). The mean date ($\pm SE$) of last hatch

among the 5 years was 26 July \pm 10.3 days. The latest hatch in the 5-year study occurred on 9 August. The mean period (\pm SE) from first egg laid to hatch was 31.5 ± 1.4 days ($N = 53$). The estimated mean incubation period (\pm SE) was 21.0 ± 1.1 days.

Clutch Size and Nest Success

Completed clutch size ranged from 8 to 13 eggs ($N = 55$) with a mean of 10.5 eggs (Table 10). A box plot comparison of clutch sizes for this population and populations from Arkansas (Meanley 1969), Ohio (Trautman 1940) and Delaware (Stone 1937 in Meanley 1969) reveals little variation among populations with means ranging from 10.5 to 11.2 eggs/clutch (Fig. 8). No trends in clutch size were apparent in relation to latitude or longitude. When data from all four populations of king rails are combined and compared to clutch size data for clapper rail from North Carolina (Adams and Quay 1958) and Virginia (Stewart and Meanley 1960) differences between the species are apparent (Fig. 9). Although the upper quartile of clapper rail clutch size overlaps with the lower quartile of king rail clutch size, clutch sizes are greater for the king rail than for the clapper rail. When clutch size is categorized as low (4-8 eggs), medium (9-11 eggs) and high (12-14 eggs), a significant difference between the species is obvious ($X^2 = 54.45$, $P < 0.001$, Cramer's $V = 0.438$, 2 df). Twenty-seven percent of the king rail population is in the high clutch size group, whereas only 2% of the clapper rail population

is in the high group. In contrast, 28% of the clapper rail population is in the low clutch size group, whereas only 4% of the king rail population is in the low group.

Of the king rail nests in this study, 54 (81%) of the nests were successful and 39 (58%) of the nests hatched complete clutches. All thirteen of the unsuccessful nests were apparently destroyed by mammalian predators. Two of the depredated nests had raccoon (Procyon lotor) tracks surrounding the nest. Analyses for nest success among egg laying and incubation periods (after Mayfield 1975) reveals daily survival rates ranging from 0.97 to 1.0 and interval survival rates ranging from 0.74 to 1.0 (Table 11). Span survival rate (\pm SE), from first egg laid to hatch, was 0.695 ± 0.071 .

Nest Success and Habitat Factors

Analyses of the relationships between nest site characteristics and nesting success were conducted in three parts. First, the nest site characteristics measured as continuous variables (water depth, distance to open water, vegetation height and vegetation stem density) were related to nest success. Success was considered as a binary random variable for each nest; 1 = success, 0 = failure. A separate logistic regression was conducted for nest success using each of these factors as explanatory variables. Regressions conducted with water depth and distance to open water as explanatory variables were significant ($P < 0.10$),

whereas those using stem density and vegetation height were not ($P = 0.24$ and $P = 0.83$, respectively) (Table 12). A logistic stepwise selection procedure using all four continuous factors as input variables produced a final model that included water depth ($X^2 = 6.25$, $P = 0.012$) and distance to open water ($X^2 = 5.47$, $P = 0.019$) (Table 13). Maximum likelihood parameter estimates and likelihood ratio test statistics were used throughout the model selection process, and no variables were forced into the model. In addition, protection against building a superfluous model was insured by examination of a chi-square statistic for jointly testing all candidate variables (Harrell et al. 1984). Although the estimated coefficient was positive for water depth and negative for distance to open water, as might be expected these two site characteristics were correlated with one another ($r = -0.37$, $P = 0.002$), rendering direct interpretation tenuous (Table 14). More importantly, when these two factors were considered in tandem, the combination strongly related to individual nest success, as indicated by the value of $C = 0.788$ (Table 13). The statistic C is a measure of the concordance of predicted success from the fitted model with observed success (see Leach 1979, Hanley and McNeil 1982). No other continuous habitat factors were intercorrelated (Table 14).

In the second portion of the analyses, a log-linear model was constructed for the variables nest success, nest location, and habitat type. Nest success was considered

binary as in the previous analysis; nest location was classified as either: (1) in the interior of a management unit without a drawdown during nesting, or (2) in a unit with a drawdown, adjacent to a levee or in a borrow ditch; habitat type comprised three categories: (1) marsh, (2) seasonally flooded wetland (moist-soil unit), or (3) borrow ditch. Because the process of building a log-linear model treats all of the variables involved in a symmetric manner (i.e., log-linear models use no dependent versus independent structure), primary interest centered on terms estimated to describe the interactions among these variables (see Freeman 1987). The final model chosen to describe such relationships was selected in a hierarchical manner (Freeman 1987). Two of the three possible 2-way interaction terms were included in the final model; interaction between success and location, and interaction between location and habitat (Table 15). Parameter estimates in the final model revealed that nests located in the interior of management units without drawdowns were positively related to nest success, and positively related to the probability of being in marsh habitat. The absence of an interaction term for success and habitat in the final model allows the data to be "collapsed" over habitat classification for this three variable model (Bishop et al. 1975, Whittemore 1978). The significance of this result is that the data may be appropriately displayed in a two-way contingency table using the variables success and location, without producing

confusion from the exclusion of an important factor (thus avoiding inappropriate analysis that has become known as Simpson's Paradox [Simpson 1951]). Analysis of success and location in a two-way table format revealed that nest success was not independent of nest location ($\chi^2 = 44.53$, $P < 0.001$) (Table 16). Use of the odds ratio as a measure of dependence for this two-way table (Freeman 1987) showed that nests located along the edges of management units, within units that are drawdown during the nesting period, or within borrow ditches were over 300 times as likely to result in failure as were nests located in the interior units that were not drawdown during that period (Table 16).

In the final step of the analyses of nest site characteristics and nest success, a logistic regression model was constructed for the probability of nest success as a function of all measured site characteristics, both continuous and categorical. A stepwise selection procedure as described above was again used to select the final model. The first variable selected to enter the model was location, and, given location, no other variables met the 0.15 significance level for entry into the model. As would be expected from the close explanatory variables with log-linear models and frequency-based contingency analysis (Freeman 1987), measures of association and other statistics for this model were similar to those reported above for the effect of location on nest success.

DISCUSSION

Whereas the king rail was considered a common summer resident in the marshes along Missouri's large rivers at the turn of the century (Widmann 1907), it is now considered very rare and classified as endangered (MDC 1984). The wetlands of the Ted Shanks WA probably represent one of the highest quality blocks of contiguous king rail breeding habitat left within the state.

Spring arrival dates in the Upper Mississippi Valley vary little, where the first king rails arrived 2 May in glacial marshes of northeastern Iowa (43°N , 95°W), and the height of migration was reached during the 1st week of May in 1951 (Tanner and Hendrickson 1956). First nest initiation began 13 May at the Iowa site, and the nesting period continued to last hatch on 23 June (Tanner and Hendrickson 1956). The peak nesting initiations between 15 May and 31 May in central Ohio (Trautman 1940) follow this pattern. A young brood siting on 1 June 1905 at Mudlake, St. Charles County, Missouri (39°N , $90^{\circ}30'\text{W}$) (Widmann 1907) suggests a late April nest initiation. A newly hatched brood of 7 young at Marais Temps Clair WA, Missouri (39°N , $90^{\circ}30'\text{W}$) on 7 June 1988 suggests an early May initiation (D. Matlock, pers. commun.). In contrast to the conditions in the Upper Mississippi Valley where king rail arrive in late-April or early-May and initiate nesting in mid-May to late-May, the Upper Mississippi Alluvial Valley may provide

a longer period for breeding. An adult king rail was seen in late February 1984 in the vicinity of Mingo NWR, Missouri (37°N , 90°W), and broods have been seen on the refuge as early as 5 April 1987 and 27 April 1988 (J. Ware, pers. commun.). By back-dating the early April brood, it appears that nest initiation began by late February or the 1st week of March. At the southern extreme of the U.S. breeding range, in Florida and Louisiana, the breeding season may last as long as 8 months (Meanley 1969).

All of the plants associated at nest sites typically occur in open swales of alluvial floodplain or wet meadows (Steyermark 1963). The difference in dominant vegetation between early and late years of the study is probably related to the successional establishment of Hart Wright's sedge in several sites. Height of vegetation is undoubtedly important only as long as a threshold level (≥ 45 cm), which hides adults, is reached. Sofrush, which was far more common in the Grand Prairie site (Meanley 1969), is probably a more important plant for nest cover in the Lower Mississippi Alluvial Valley.

The shallow water nest site selection, moist to 22 cm of water, is characteristic of this species. Six king rail nests at Dewey's Pasture, Iowa were located in slightly deeper water, ranging from 10 to 46 cm, with a mean of 27 cm (Tanner and Hendrickson 1956). Nesting in the Lake Erie marshes occurred at water depths of approximately 60 cm (Trautman 1940), but this value seems very large for a

species with a short tarsus (approximately 6 cm) that relies so heavily on walking. The description of the king rail as essentially a "damp habitat species" (Meanley 1953) seems most appropriate. Water depth at nest sites ranged from 15 to 20 cm in the Grand Prairie, Arkansas (Meanley 1953).

It has been proposed that clutch size in semi-precocial birds was primarily limited by the ability of parents to feed their young (Lack 1947, Williams 1966, Hogstedt 1980). Of semi-precocial birds, only the family Rallidae has clutch sizes that approach those of precocial birds, such as galliforms and anatids, that do not feed their young (Winkler and Walters 1983). Other studies have suggested that declining egg viability and the risk of nest predation can account for much of the selection pressure determining clutch size (Cody 1966, Koenig 1982, Arnold et al. 1987). Because clutch sizes of king rail populations were similar in Arkansas, Missouri, Delaware and Ohio (Fig 2), no pattern in clutch size relative to latitude or longitude was apparent. Such variation in clutch size would be surprising across this temperate region. However, variation may exist when clutch sizes of congenerics are compared between temperate and tropical zones (Cody 1966, Ripley 1977). Differences among king rail and clapper rail clutch sizes were apparent (Fig. 3). Some of this difference may be explained by smaller clutch sizes produced by clapper rails in second nesting attempts (Stewart and Meanley 1960), however, the greater percentage of large clutches (≥ 11

eggs) for king rails is unexplained. Covarying life-history traits expected under various environmental conditions might explain clutch size differences among closely related species (Pianka 1970, Schaffer 1974, Winkler and Walters 1983). Where environmental predictability is high for adults and juveniles, the number of young is relatively low, but quality of individual chicks is high. In contrast, low environmental predictability should lead to a relatively large number of young produced (Pianka 1970). Clutch size differences among king rail and clapper rail populations may reflect the unpredictability of freshwater habitats, as compared to more predictable coastal habitats, relative to food resources and nest predators.

Nest success was relatively high at the Missouri study site [81% of nests found and 70% span rate (Mayfield 1975)] and similar to the 75% apparent success rate observed in Arkansas (Meanley 1969). The cryptic plumage of both sexes and the secretive nature of adults certainly aid in success. Failed nests were probably depredated by raccoons or striped skunks (Mephitis mephitis) and less probably mink (Mustela vison) or red fox (Vulpes vulpes).

Water depth and distance to open water were important factors in predicting nest success among the continuous variables, but location of a nest within a management unit alone fit the log-linear model for categorical variables and the logistic regression model for all factors. This relationship suggests that small wetland units or units with

large shoreline development that yield greater "edge" area may be more susceptable to king rail nest failures. Man-impacted wetland area and travel lanes for predators have been implicated in wetland bird species declines (Brown and Dinsmore 1986, Peterson and Cooper 1987). Fragmentation of habitats can adversely affect nest predation for avian species in forested or herbaceous habitats (Wilcove 1985, Burger 1988).

Management Implications

King rails nest in floodplain habitats. As such, hummocky topography and natural swales should be maintained for nesting and foraging. Artificial land leveling should be discouraged. Beds of perennial vegetation, especially Hart Wright's sedge, ricecut grass and water smartweed, should be encouraged where water depths are moist to 22 cm. In a continuum of preferred water depths at nest sites for inland-breeding rallids, king rails and black rails nest in the most shallow water areas (Fredrickson and Reid 1986). These shallow, seasonally flooded sites are most easily drained and impacted by agriculture. Rowcrops, other than rice (Meanley 1969), have little value for any rallid species (Rundle and Sayre 1983). Improved nest success when nests were located in the interior of units suggests that beds of desired vegetation should be encouraged within the interior, not the periphery, of managed wetland units. Borrow areas along the edges of units may serve as travel lanes for mammalian predators. Ditches also may be

susceptable to rapid and higher flooding spates that can flood out nests (Meanley 1969). Borrow areas may, however, be the only remaining habitat available in intensively farmed regions (Meanley 1969) and roadside mowing of borrow areas should be discouraged during the nesting and brood period. On intensively managed refuges, a complex of wetland units should include marsh habitats that naturally dry during the summer and may include extensive perennial vegetation.

TABLE 8. Dominant plant species used by nesting king rails.

Vegetation at nest site	<u>Percent of nest associated</u>	Mississippi Floodplain (N=67) ^c	Grand Prairie ^{ab} (N=25)
Hart Wright's sedge <i>(Carex hyalinolepis)</i>	39		8
Ricecut grass <i>(Leersia oryzoides)</i>	28		-
Water smartweed <i>(Polygonum coccineum)</i>	22		-
Burreed <i>(Sparganium eurycarpum)</i>	7		-
Flat culm spikerush <i>(Eleocharis macrostachya)</i>	3		-
Spikerush <i>(Eleocharis</i> sp.)	-		12
Softrush <i>(Juncus effuses)</i>	1		40
Giant bulrush <i>(Scirpus heterochaetus)</i>	1		-
Reed canary grass <i>(Phalaris arundinacea)</i>	1		-
Cattail <i>(Typha latifolia)</i>	-		12
Awl-fruited sedge <i>(Carex stipata)</i>	-		12
Joint-grass <i>(Paspalum distichum)</i>	-		8
Barnyard grass <i>(Echinochloa</i> sp.)	-		4
Chess <i>(Bromus secalinus)</i>	-		4

^a After Meanley 1969.^b Natural plants only; cultivated rice excluded for comparison.^c Three nests had 2 dominant species.

TABLE 9. Physical characteristics of king rail nest sites.

Variable (N)	Mean \pm SE	Range	CV
Water depth (mm) (N=67)	51.4 \pm 6.5	0-220	103.1
Water depth of wet sites only (mm) (N=44)	78.2 \pm 7.0	22-220	59.4
Distance to open water (m) (N=67)	6.7 \pm 0.5	1-15	56.4
Stem/culm density (#/m ²) (N=67)	437 \pm 28	225-1950	51.7
Vegetation height (cm) (N=67)	68.7 \pm 1.9	45-121	22.8
Height base of nest bowl above ground/water (mm) (N=67)	86.6 \pm 3.2	22-147	30.0
Inner diameter of nest bowl (cm) (N=67)	21.3 \pm 0.2	18-25	7.4

TABLE 10. Initiation/hatch dates and clutch size of king rail nests at Ted Shanks Wildlife Area, Missouri, 1981-85.

Variable (N)	Mean \pm SD	CV
Initiation date (N=66)	29 May \pm 14.5 days	9.7
Hatch date (N=53)	30 June \pm 15.3 days	8.5
Clutch size (N=55)	10.5 \pm 1.2 eggs	11.1

TABLE 11. Nest success for king rails at Ted Shanks
Wildlife Area, Missouri, 1981-85. Methodology
after Mayfield (1975).

Period (days)	Daily survival rate (\pm SE)	Interval survival rate (\pm SE)
Egg laying (11)	0.973 \pm 0.009	0.737 \pm 0.071
Early incubation (7)	0.992 \pm 0.005	0.943 \pm 0.032
Mid incubation (7)	1.000 \pm 0.000	1.000 \pm 0.000
Late incubation (7)	1.000 \pm 0.000	1.000 \pm 0.000
Span rate (egg laying to hatch) = 0.695 \pm 0.071		

TABLE 12. Logistic regressions for nest success versus continuous factors (water depth, distance to open water, vegetation height, and vegetation stem density).

Variable ^a	Max. Like.	χ^2	P Value	C ^b	Gamma ^c	Tau-a ^d
Water depth		61.19	0.029	0.667	0.399	0.106
Distance to open water		62.75	0.075	0.635	0.287	0.085
Stem density		64.53	0.237	0.559	0.122	0.038
Vegetation height		65.88	0.827	0.514	0.029	0.009

^a N = 67.

^b C = # concordant pairs + 0.5(# ties)/[n(n+1)/2].

^c Gamma = # concordant pairs - # discordant pairs/sum of pairs (- ties).

^d Tau-A = # concordant pairs - # discordant pairs/[n(n+1)/2]

TABLE 13. Final model from stepwise logistic regression for nest success versus continuous nest site characteristics (water depth, distance to open water, vegetation height, and vegetation stem density).

Variable	Parameter Estimate	χ^2	P
Intercept	1.865	10.20	0.0014
Water depth	0.028	6.25	0.0124
Distance to open water	-6.552	5.47	0.0194
C = 0.788	Gamma = 0.575	Tau-a = 0.183	

TABLE 14. Pearson correlation coefficients for continuous habitat factors^a

	Distance to open water	Vegetation height	Stem density
Water depth	-0.371 P = 0.002	0.090 P = 0.467	-0.161 P = 0.192
Distance to open water	-----	-0.026 P = 0.836	0.114 P = 0.360
Vegetation height	-----	-----	0.059 P = 0.634

^a N = 67 nests.

TABLE 15. Log-linear model for nest success and categorical nest site characteristics (habitat type and location within management unit). Notation follows Bishop et al. (1975).

Final model

$$\log P_{ijk} = U + U_1(i) + U_2(j) + U_3(k) + U_{12}(ij) + U_{23}(jk)$$

where i = success, 1=yes 2=no

j = location, 1=interior without drawdown

2=edge/interior with drawdown

k = habitat, 1=marsh 2=seasonally flooded
(moist-soil) 3=ditch

Parameter estimates

$$U = 0.525$$

$$U_1(1) = 0.428$$

$$U_2(1) = -0.262$$

$$U_3(1) = 0.883$$

$$U_3(2) = -0.157$$

$$U_{12}(11) = 1.103$$

$$U_{12}(12) = -1.103$$

$$U_{23}(11) = 1.188$$

$$U_{23}(12) = -0.074$$

$$U_{23}(13) = -1.114$$

Likelihood ratio chi-square for lack of fit

$$\text{Chi-square} = 2.76$$

$$df = 4$$

$$P = 0.598$$

Note: parameter estimates not listed may be calculated because of restriction that estimates must sum to zero over any subscript, ie. $U_{12}(21) = +1.103$, $U_{23}(21) = -1.188$, etc.

Table 16. Two-way contingency table of nest success and nest location within management unit.

Location	Success		
	Yes	No	
Interior w/o drawdown	52	1	53
Edge/Interior with drawdown	2	12	14
	54	13	67

$$\chi^2 = 44.525, P < 0.001$$

$$OR = \text{Odds Ratio} = (Y_{11}Y_{22}) / (Y_{12}Y_{21}) = 312$$

Fig. 7 Timing of king rail nest initiation at Ted
Shanks Wildlife Area, Missouri, 1981-85.

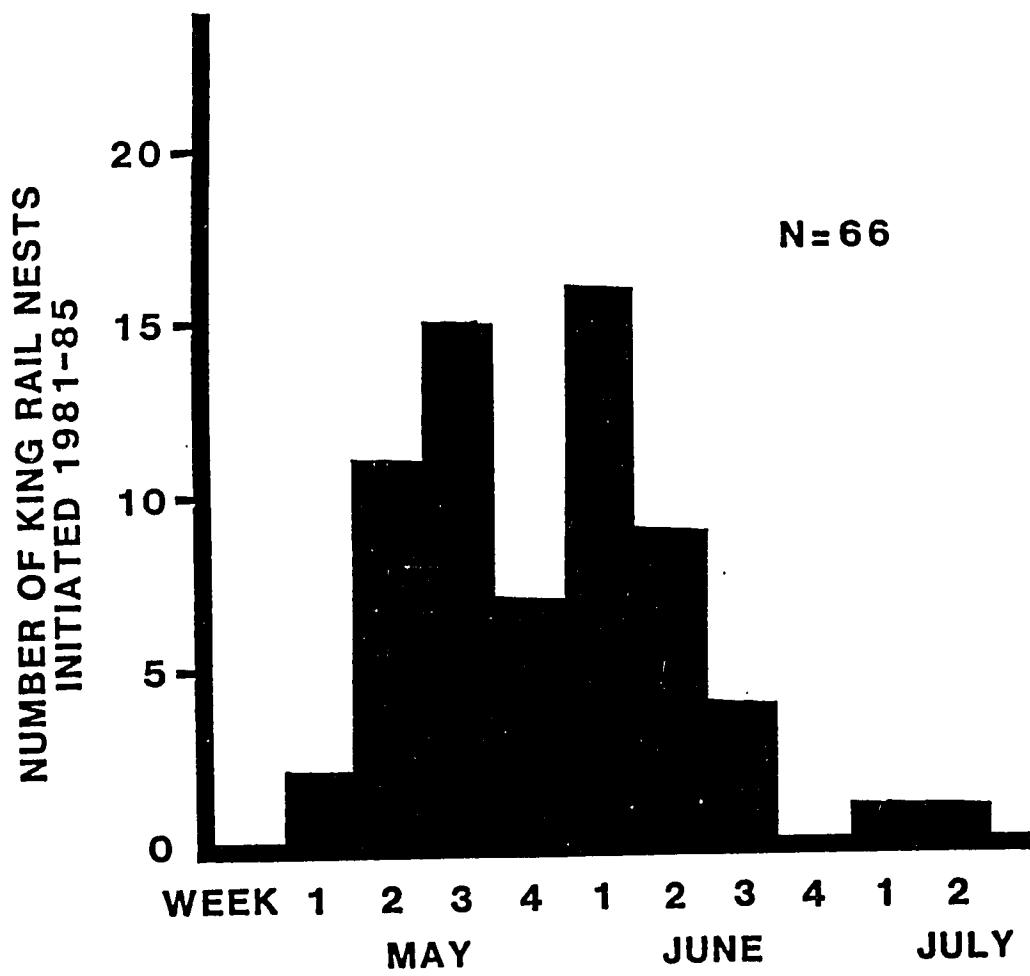


Fig. 8 Box plots showing a comparison of king rail clutch size among North American study sites. Data are from Missouri ($N = 55$, this study), Arkansas ($N = 16$, Meanley 1969), Ohio ($N = 37$, Trautman 1940), and Delaware ($N = 14$, Stone 1937 in Meanley 1969). Vertical lines show extremes, while box represents upper and lower quartiles.

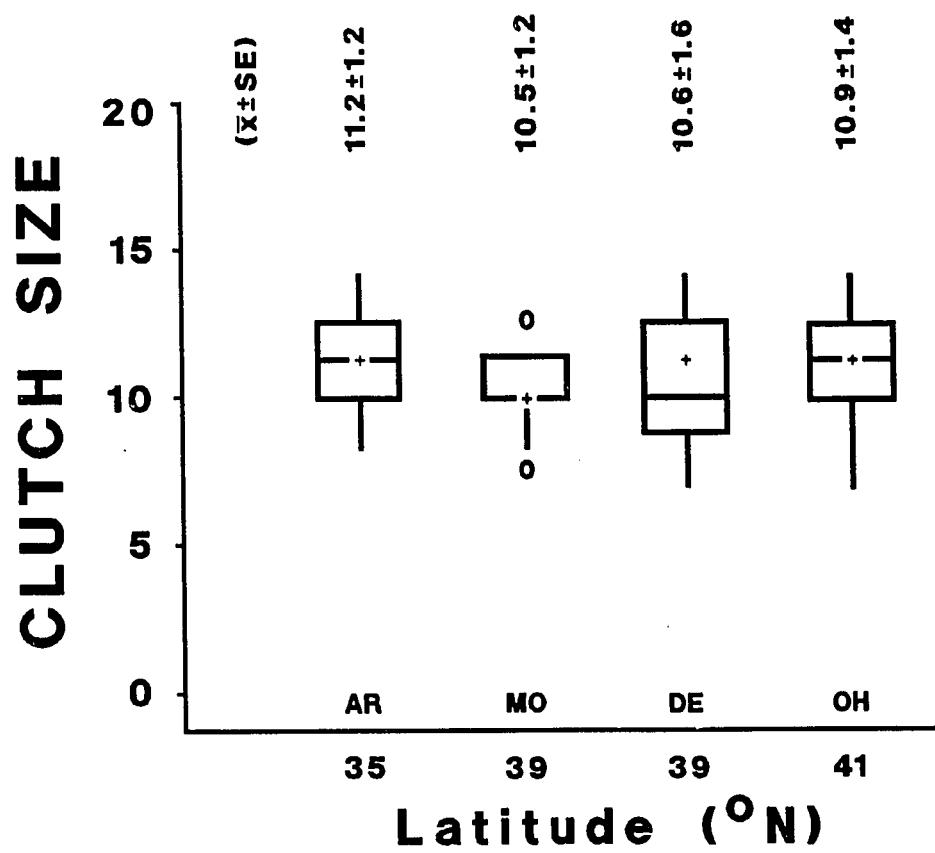
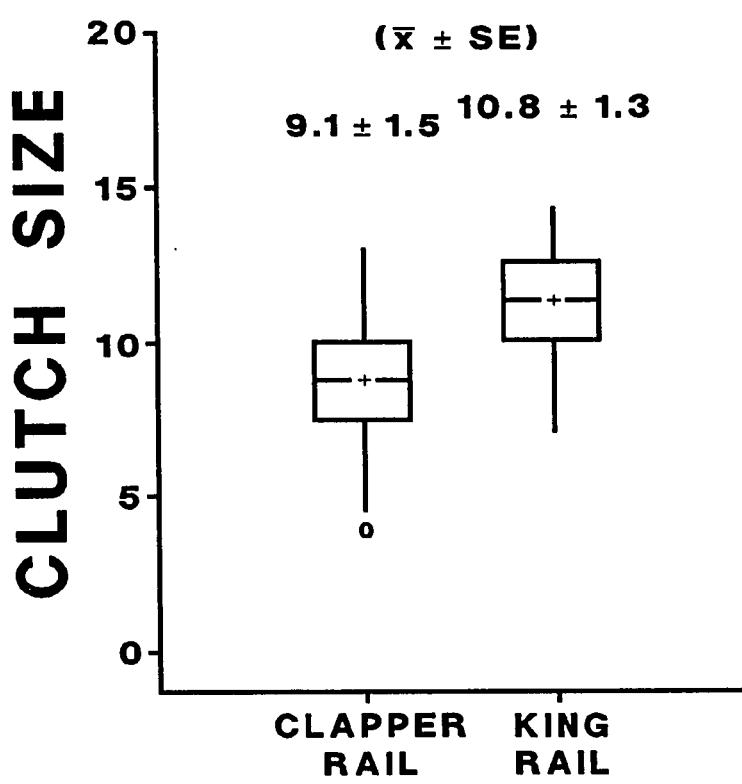


Fig. 9 Box plots showing a comparison of clutch size between clapper rail ($N = 162$) and king rail ($N = 122$). Data are a composite of all major quantitative nesting studies of these species and include North Carolina (Adams and Quay 1958) and Virginia (Stewart and Meanley 1960) for clapper rail and Missouri (this study), Arkansas (Meanley 1969), Ohio (Trautman 1940), and Delaware (Stone 1937 in Meanley 1969) for king rail. Vertical lines show extremes, while box represents upper and lower quartiles.



CHAPTER IV

FORAGING ECOLOGY OF BREEDING KING RAIL

The Mississippi River corridor has historically formed important breeding and migratory habitat for king rails (Rallus elegans) in the central portion of North America (AOU 1983). Major degradations to this ecosystem have occurred in the last century and include constriction of banks that modify flow and flood capacity, dike construction that impacts channel direction, and addition of toxicants through point and non-point pollution. Perhaps the greatest direct threat to king rail habitats has been the large reduction in herbaceous floodplain wetlands through agricultural, urban, and industrial developments. Today, most quality wetland habitats remain on public refuges. In concert with severe habitat modifications, several areas within the Midwest have experienced recent declines in populations of this species, and most states in the region consider the king rail as threatened or endangered (Eddleman et al. 1988). To provide better management strategies for public refuges, an understanding of specific habitat use patterns throughout the breeding and migration periods is needed.

Wetland habitat use by waterbirds can be viewed as a cline across variables of vegetation structure and water depth (Weller and Spatcher 1965). Yet few avian studies

have attempted to document changing habitat use, in relation to these clines, within a dynamic wetland complex (Weller and Fredrickson 1974, Ryan and Renken 1987, Fredrickson and Heitmeyer 1988). Such habitat changes may be noted on a macrohabitat scale (distribution of bird use relative to wetland classes) or a microhabitat scale (water depth or vegetation characteristics of specific sites of bird use). Even fewer studies have attempted to link structural changes of habitat with potential invertebrate prey densities (Voights 1976, Murkin et al. 1982, Nelson and Kadlec 1984). To better understand king rail habitat use, water depth and vegetation height, density, and composition were recorded between 1982-85 for a breeding population in northeastern Missouri (Chapter 3). Potential prey numbers and diversity of prey were also documented at king rail foraging sites. King rails are semi-precocial, thus adults not only feed young, but must lead the young to areas of sufficient food (Faaborg 1988). Such behavior should manifest itself in differences among nesting and brooding periods in habitat characteristics and potential prey composition and densities at foraging sites. It has been proposed that clutch size in semi-precocial birds was primarily limited by the ability of parents to feed their young (Lack 1947, Williams 1966, Hogstedt 1980). Of semi-precocial birds, only the family Rallidae has clutch sizes that approach those of precocial birds, such as galliforms and anatids, that do not feed their young (Winkler and Walters 1983).

Because king rails have large clutch sizes even among the Rallidae (Ripley 1977, Chapter 3), this species should be a good choice to investigate patterns of micro-habitat use across the breeding period.

STUDY SITE AND METHODS

The study site was located within the 1015 ha block of fields, marshes, and seasonally flooded wetlands on the Ted Shanks Wildlife Area (WA) in northeastern Missouri ($39^{\circ} 30'N$, $91^{\circ}W$). This block of herbaceous habitats is but a portion of the 4,480 ha refuge which lies at the confluence of the Mississippi and Salt rivers. Extensive clearing for agriculture occurred in the early and mid-twentieth century, however, wetland restoration activities in the last 15 years have recreated floodplain wetland conditions.

Marsh, ditch, and seasonally flooded units were systematically searched for king rails between 1 April and 15 October from 1982-85. Several investigators searched vegetation for flushing rails between 0700 to 1000 hrs or between 1700 to 2000 hrs in an attempt to gather data more reflective of foraging location (Sayre and Rundle 1984). Once a specific flush site was located, water depth, vegetation height, plant species composition, and stem density (recorded as stems/[20 cm x 20 cm] and converted to stems/ m^2 before analyses) were recorded. Data were not collected if the bird appeared to be moving away from the

observer, had potentially been flushed from another area, or a specific flush site was not clearly identified. To compare habitat use among migrating (data presented previously in comparison to other migratory rail habitat usage, Chapter 3) and breeding periods, data were compartmentalized into 6 categories: spring migration (before any nesting activites on the area [Chapter 3]), nesting/incubation (from date of first egg laid to hatch for breeding adults [Chapter 3]), young brood (adults with chicks 1-3 weeks of age, total natal down on chicks [Meanley and Meanley 1958]), old brood (adults with chicks 4-8 weeks of age, increasing juvenal body plumage on chicks [Meanley and Meanley 1958]), separate young (chicks 7-10 weeks of age that have separated from adults and other brood members), and fall migration (adults and juveniles from 15 August to 12 October). A seventh category was recorded for hiding areas in association with foraging pools during the young brood period.

To gather data yielding the percent of foraging activity relative to time of day, 102 brood days were observed for the 4-year period. Known broods on specific foraging sites were checked in 7 2-hr periods (0600-2000 hrs) for foraging or non-foraging activities. If any of the chicks or either adult were foraging within a 5-minute observation period, the brood was considered foraging. Activity patterns of foraging king rail chicks were documented for 264 brood days (based on brood sitings where

at least one adult was seen foraging). Broods were aged by plumage or known hatching date (Chapter 3) and recorded as hiding, fed by adults or foraging for themselves.

Potential animal prey densities were sampled at specific foraging sites. Sites with dense vegetation association were assumed to be foraging areas during the specific time of day for sampling, whereas, potential prey were collected at specific foraging locations in open habitats. Potential prey were collected by two methods. During spring migration and nesting/incubation periods, deeper water levels allowed collection of sweep net samples. Nitex inserts were placed in the 40 cm x (water depth) net and the sweep consisted of a straight 1 m distance, yielding a $4 \times 10^{-2} \text{ m}^3$ volume at 10 cm water depth. Core samples were taken at all periods. The core consisted of a 10 cm diameter with a 5 cm height, yielding a $3.93 \times 10^{-4} \text{ m}^3$ volume (Reid 1983). Location of sampling site (water, water-mud interface, or mud substrate) was recorded. Net inserts or benthic cores were immediately placed in zip-lock bags and returned to the laboratory. Samples were cleaned, sorted and organisms were identified to genus or family using standard keys (Pennak 1978, Merritt and Cummins 1984). For purposes of analyses, most of the organisms were grouped to order, and all samples were converted to organisms/ m^3 . All chironomids and corixids were excluded from analyses because they were too small for king rail prey items (Meanley 1969). Regurgitated pellets were gathered from

nest sites just after hatch (representing prey from the nesting and incubation period, N = 23) and in the area of 1 week old brood usage (N = 11). These were examined in the laboratory for prey composition.

RESULTS

Habitat characteristics of foraging sites

Habitat characteristics were collected from 307 king rail foraging sites and 44 diurnal hiding sites in association with foraging areas. Water depth at sites differed ($F = 86.6$, 6 df, $P < 0.0001$) among migration and breeding periods (Fig. 10). Water depth at foraging sites was greatest during spring migration and least during the brood periods (Table 17). All hiding sites (data collected during the young brood period) were dry. Vegetation height at king rail foraging sites also differed ($F = 108.8$, 6 df, $P < 0.0001$) among migration and breeding periods (Fig. 11). Vegetation height was greatest during fall migration and least (where present) during the brood periods for foraging sites (Table 18). Hiding sites had taller vegetation (LSD, $P < 0.05$) than all foraging sites. Vegetation stem density at foraging sites differed ($F = 68.8$, 6 df, $P < 0.0001$) among migration and breeding periods (Fig. 12). Stem density at foraging sites was greatest during both migration periods and the nesting period and least during the brood periods (Table 19). Hiding sites had denser vegetation (LSD, $P < 0.05$) than all foraging sites. When all data for

foraging sites and hiding sites were compared for correlation of variables, water and vegetation height (Pearson correlation coefficient = 0.278, $P < 0.0001$) and vegetation height and stem density (Pearson correlation coefficient = 0.520, $P < 0.0001$) were highly correlated. Water depth and vegetation stem density were not correlated (Pearson correlation coefficient = 0.836, $P > 0.118$). When hiding sites data were excluded from the analyses, but all foraging sites were analyzed, not only was vegetation height correlated to both water depth and vegetation stem density ($P < 0.0001$), but water depth and vegetation stem density were also correlated.

During the spring and fall migrations and during the nesting/incubation period, foraging sites almost are exclusively located in vegetated areas (100% for the migration periods and 81% for the nesting period). Perennial vegetation dominates sites of the spring migration period (100%), nesting/incubation period (98%), and fall migration period (72%). Moist-soil plants (versus robust emergents) dominate both migration periods and the nesting period (ranging between 67-70% of flush sites in all periods). Ricecut grass (Leersia oryzoides) is the dominant plant at sites during spring migration and nesting (45% and 41% respectively), whereas barnyard grass (Echinochloa spp.) is the dominant plant in fall migration (32%). Burreed (Sparganium eurycarpum) is also important in both spring migration (16%) and nesting/incubation period (13%), while

cattail (Typha spp.) and blunt culm spikerush (Eleocharis macrostachya) are also important during that latter period (17% and 15% respectively). Foraging sites used during the brood periods consisted of unvegetated swales and mudflats and were unlike foraging sites during the migration and nesting periods. Percent of sites unvegetated during the brood and juvenile periods ranged from 100% of sites open during the old brood period or 95% of sites unvegetated during the young brood period to 86% of sites open during use by separate juveniles. Of the eight vegetated sites in the young brood and separate young periods, 75% of the sites were associated with moist-soil plants. Associated vegetation during the separate young period was 50% annual growth, whereas all the associated vegetation was perennial growth, where present, during the young brood period.

Adults foraged in the vegetated fringe of moist-soil impoundments (Fredrickson and Taylor 1982) as the wetlands were dewatered, but broods failed to forage in large, open mudflat areas exposed by major drawdowns. Brood habitat use was restricted to smaller drying swales, present throughout the wetland complex.

Foraging activity patterns

Because broods foraged at open swale or mudflat sites, certain activity patterns were documented during these periods. Although broods were not marked, nest location (Chapter 3), number of young, and foraging site location

suggested that thirty-four separate broods were observed in 102 independent surveys. Diurnal foraging activity was concentrated between 0600-0800 hrs and 1800-2000 hrs, and was least between 1200-1600 hrs (Fig. 13). A crepuscular pattern of activity was suggested for diurnal foraging king rail broods. Despite many attempts to observe rails at night at locations where diurnal foraging was common, only a single chick was seen foraging between 2200-2300 hrs on a single occasion. On six occasions broods were located at night in hiding sites associated with swales used for diurnal foraging.

Based on 264 brood sightings (of forty-six presumed broods, Chapter 3) where at least 1 adult was seen foraging, activity patterns of foraging king rail chicks were documented. Youngest broods (1-3 weeks of age) would often hide in nearby vegetation or stand along the edge of vegetation. When prey was captured by an adult, several of the brood would rush toward the adult and beg. If an adult was foraging alone in an area of a known brood, the brood was considered hiding. Other activities of the young consisted of waiting for the adult to feed, begging for food and being fed by an adult (all 3 activities considered "fed by adults") or foraging on their own. The pattern of foraging displayed by different aged broods suggests that 1-3 week old chicks rely heavily on adults to feed them (Table 20). Some 63% of observations of 4-6 week old broods are foraging, whereas 7-9 week old broods forage almost

exclusively for their own food. The activity patterns are different among age groups (Likelihood ratio $\chi^2 = 157$, 4 df, $P < 0.001$).

Observations of foraging broods and separate juveniles suggested two foraging patterns. Most broods appeared at a drying swale and stayed in the vicinity of that site until the pool (or puddles) was almost completely dry. Some of the broods and several of the young appeared to develop a specific foraging route among several small pools. Location of these individuals could be predicted at given sites at specific times of the morning or late afternoon. Most young broods (1-3 weeks of age) were associated with 2 foraging adults, but old broods were generally associated with only 1 adult.

Prey association at foraging sites

Core samples ($N = 310$) were collected at king rail foraging sites during all migration and breeding periods, but sweep net samples ($N = 51$) could only be collected during spring migration and nesting/incubation periods because very shallow water levels were present at other periods. To test if the presence of potential prey was independent of king rail foraging periods, a contingency table was constructed and data from cores with and without prey were compared (Table 21). The presence of prey was found not to be independent of period (Likelihood ratio $\chi^2 = 76.3$, 5 df, $P < 0.001$). The chances of encountering any prey was greater in the brood periods, whereas variation in

prey density from the migration periods and nesting/incubation period suggested that potential food resources had a patchy distribution. The uncertainty coefficient suggests a 20% better estimate of presence if the period is identified.

An ANOVA was conducted on untransformed data to test for specific differences of various prey items utilized among the migration and breeding periods. Because of several samples with no prey, an ANOVA with a $\log(x+1)$ transformation of data was also conducted. This transformation is common for most invertebrate analyses (Allan 1984). In both analyses, residuals plotted against periods were not randomly scattered around a mean of zero (non-random pattern). These analyses indicated ANOVA using all data and $\log(x+1)$ transformed data were inappropriate. Because the presence of prey was not independent of king rail migration and breeding periods, an ANOVA was conducted on $\log(x+1)$ transformed data in which all zero samples had been deleted. The plot of residuals against periods was much improved from the previous analyses and the random scattering around a mean of zero suggested a normal distribution. Thus ANOVA comparisons among king rail breeding and migration periods for potential prey were appropriate when data were transformed as $\log(x+1)$ and excluding all zero samples.

An examination of total potential prey densities among periods (Appendix 1) reveals little difference among spring

migration, nesting/incubation, or fall migration, but differences were present (LSD, $P < 0.05$) among these periods and each brood period (Table 22). Likewise, all the brood periods were different from each other (LSD, $P < 0.05$). Prey densities based on net collections were lower than densities in core samples, but prey densities were not different between the two periods for net collections. Total potential prey densities showed the greatest range during the old brood period where animal prey ranged from zero to over 330,000 organisms/ m^3 .

Total macroinvertebrate densities revealed a somewhat similar pattern in relation to total animal prey, except that the separate young period was not different (LSD, $P > 0.05$) from the migration or nesting periods (Table 23). Even though peak levels of nearly 100,000 invertebrates/ m^3 occurred during the separate young period, transformed log data were not different from levels that peaked at just over 10,000 invertebrates/ m^3 in spring migration. Total invertebrate densities for young and old broods were not different (LSD, $P > 0.05$) and represented the peak concentrations of potential prey. Twelve orders (representing 34 families) of invertebrates and four orders of vertebrates were collected at foraging sites. Vertebrate organisms consisted of 3 orders of larval or small fish (Clupeiformes - shad; Cypriniformes - minnows, catfish, and carp; Cyprinodontiformes - mosquito fish) and 1 order of frogs (Anura - Rana tadpoles). Diversity of prey (at the

order level) was not different (LSD, $P > 0.05$) from the migration or nesting periods (Table 24). Likewise the range of taxa was low (maximum of 2 orders/core) for these periods compared to all other periods. The old brood, young brood, and separate young periods had the greatest diversity (2.8, 1.9, and 1.6 orders/core, respectively). The net samples had relatively high diversity, but the volume per sample from nets was greater than the densities based on cores.

In analyses of dominate prey, large freshwater oligochaetes (of the families Lumbriculidae or Lumbricidae) were the most abundant during a single period (Table 25), but densities differed among periods ($F = 4.3$, $P < 0.009$). No freshwater worms were present in core or net samples during spring migration or nesting/incubation periods. Samples from the old brood period ranged to densities near 300,000 organisms/m³. Oligochaete densities were not different for young and old brood periods (LSD and HSD, $P > 0.05$), nor were oligochaete densities different for young brood and separate juvenile periods (LSD, $P > 0.05$). Densities of freshwater oligochaetes were different (LSD, $P < 0.05$) between fall migration and all other periods, except separate young.

Total leech densities at king rail foraging sites differed ($F = 16.8$, $P < 0.001$) among periods (Table 26) and displayed a generally similar pattern to oligochaete distribution among periods. Leeches were most abundant during old and young brood periods and when young had

recently separated from adults. No difference (LSD, $P > 0.05$) in leech densities existed for nesting, young brood, separate young, and fall migration periods.

Differences in crayfish densities existed among periods where the crustaceans were collected ($F = 161.3$, $P < 0.001$). Total crayfish were most abundant during the two brood periods and secondarily in net samples from spring migration and nesting periods (Table 27).

Although pulmonate snail densities differed ($F = 107.0$, $P < 0.001$) among periods (Table 28), the pattern of densities relative to king rail breeding periods differed from the patterns of other prey organisms. Pulmonate snail densities in core samples did not differ (LSD and HSD, $P > 0.05$) for spring and fall migrations and nesting periods. Snail densities also were not different during spring or fall migrations and separate young periods. Snail densities were similar during the old brood and separate young periods, but the young brood period had greater densities (ranging $> 99,000/m^3$) of snails than any other period (LSD, $P < 0.05$).

Aquatic beetle (chiefly of the families Dytiscidae and Hydrophilidae, but also including Haliplidae, Gyrinidae and Elmidae) densities differed ($F = 123.7$, $P < 0.001$) among periods (Table 29), with the greatest densities during the young and old brood periods. Densities of aquatic beetles were similar for spring and fall migration, nesting, and separate young periods ($P > 0.05$). Semi-aquatic beetle (of

the families Staphylinidae, Carabidae, and Chrysomelidae) densities did not differ ($F = 0.7$, $P > 0.6$) among periods (Table 30). No differences in beetle densities existed (LSD and HSD, $P > 0.05$) from core samples among all periods.

Larval fish (chiefly carp and gizzard shad) and small adult fish (chiefly mosquito fish) were the only common vertebrate prey item sampled and their densities differed ($F = 27.1$, $P < 0.001$) among king rail migration and breeding periods (Table 31). Densities of fish during the old brood period did not differ (LSD and HSD, $P > 0.05$) from densities in the young brood or separate young periods, but did differ (LSD, $P < 0.05$) from fish densities in all other periods. During the old brood period, fish densities in the drying swales reached levels over 100,000 individuals/m³.

In addition to comparing potential prey across king rail migration and breeding periods, items from core samples were compared across specific substrate locations (water, water-mud interface, or mud). Only core samples from early and late brood periods ($N = 176$) were analyzed, because viable sample sizes were available from all three categories. As in the comparison for periods, because of non-normal data distribution, a $\log(x+1)$ data transformation that excluded all zero samples was performed before ANOVA tests. Total potential prey differed ($F = 6.8$, $P < 0.002$) among locations (Table 32). Prey densities were greater (LSD and HSD, $P < 0.05$) at sites with water than sites with mud or the interface between mud and water. No difference

(LSD and HSD, $P > 0.05$) existed between total prey densities for mud and interface sites. No difference ($F = 0.05$, $P > 0.95$) existed for total macroinvertebrate densities among locations (Table 33). Although prey densities at sites with water ranged as high as 330,000 invertebrates/ m^3 , no difference (LSD and HSD, $P > 0.05$) was detected among locations. Differences existed ($F = 6.6$, $P < 0.002$) among diversity at the order level for potential prey among the locations (Table 34). Diversity at locations with water or water-mud interface locations was not different (LSD and HSD, $P > 0.05$) and taxa/core was high (2.9 and 2.1 respectively). Likewise no difference existed between prey diversities at interface or mud locations (LSD and HSD, $P > 0.05$). The number of taxa/core differed (LSD and HSD, $P < 0.05$) between water and mud locations.

Total freshwater oligochaete densities differed greatly ($F = 8.0$, $P < 0.001$) among locations (Table 35). High densities of oligochaetes were present in flooded sites. Numbers were almost twice the high extreme of oligochaete densities at interface or mud locations. Although densities of oligochaetes in water differed (LSD and HSD, $P < 0.05$) from densities at the interface or in mud, densities in the latter two locations were similar (LSD and HSD, $P > 0.05$). Densities of leeches were similar ($F = 0.5$, $P > 0.59$) among locations (Table 36). Although leeches had a greater mean and range of densities in water, all locations were similar (LSD and HSD, $P > 0.05$).

Pulmonate snail densities differed ($F = 4.3$, $P < 0.02$) among locations (Table 37). Densities of snails at locations with water or at interface between mud and water were greater than at mud sites (LSD, $P < 0.05$). A high range of snail densities existed at water sites (nearly 100,000 snails/m³), but the water-mud interface also held high densities ($\bar{x} = 8000$ snails/m³).

Coleopteran densities showed differing patterns in distribution. Aquatic beetles were concentrated at sites with water and at the interface between water and mud, whereas semi-aquatic beetles were concentrated at the water-mud interface and at mud sites. However, when data were transformed and zero samples excluded, no difference existed for either total aquatic beetles ($F = 0.5$, $P > 0.59$) and locations (Table 38) or total semi-aquatic beetles ($F = 0.9$, $P > 0.41$) and locations (Table 39).

Total fish densities differed ($F = 3.0$, $P < 0.091$) among locations (Table 40). As might be expected, fish were in greater densities in water or at the water-mud interface than in mud (LSD and HSD, $P < 0.05$).

Regurgitated pellet analysis

Pellets from the nesting/incubation period ($N = 23$) and the first 5 days of the young brood period ($N = 11$) all contained only 1 prey item, the exoskeletons of burrowing crayfish, Procambarus blendingii.

DISCUSSION

Many waterbirds, including grebes, loons, rails and bitterns, are semi-precocial species that require the adults to feed the young, at least for a short period. Perhaps more importantly, the adults must lead young to areas with sufficient food availability. These brood foraging sites must contain food resources that are energetically economical to obtain, either for the adults during the early stages of brooding or for the adults and young during the later stages of brooding.

King rails display dramatic shifts in foraging habitat among migration and breeding periods. Sites used during spring migration and nesting/incubation are located in dense vegetation where water is relatively deep (2.5-20 cm), but broods tend to forage in open mudflats with very shallow water (saturated soil to 7.5 cm water depth). Brood foraging sites are closely associated with drier sites that have dense, tall vegetation in which the broods hide during mid-day. Sites used during fall migration have relatively deep water (1.0-24.5 cm) and include dense, tall vegetation. Brood foraging areas include mosaics of drying swales, not large expanses of exposed mudflats. The lack of dense vegetation associated with the larger mudflats may explain in part the lack of brood usage. The use of drying freshwater sites by foraging king rails may be similar to use of tidal exposed mudflats by clapper rails (R.

longirostris) (Meanley 1985), except that the foraging pattern related to time of day for the latter species would be more regulated by tidal action.

The feeding of young by king rail adults may be critical because of the rapid growth in anatomical structures which are important to foraging and digestion. Culmen length increases by a factor $\times 2.5$, tarsal length increases by a factor $\times 2.6$, and total body weight increases by a factor $\times 4-6$ between 1 day-old chicks and chicks 30 days-old (Meanley and Meanley 1958). Between 1 day-old and 60 days-old, total body weight increases by a factor $\times 15-20$ and culmen length increases by a factor $\times 3-5$. Tarsal length, however, only increases approximately 10% between 30 and 60 days of growth (Meanley and Meanley 1958). The short tarsus and culmen of young king rail chicks greatly limits use of potential foraging sites. Increased foraging behavior by chicks between weeks 4 and 8 of age may in part be related to the rapid growth of the tarsus which enables juveniles to enter both saturated and flooded foraging sites. Diurnal variation in feeding times and rates, as seen in other waterbirds (Kushlan 1976b), may be controlled by predation risk (although chiefly nocturnal mammals occur here) and heat stress on the open mudflats.

King rails are chiefly animal predators (Meanley 1956) that exploit aquatic and semi-aquatic macroinvertebrates. The protein-rich diets which invertebrates provide are important for rapid growth rates of young waterbirds (Krapu

and Swanson 1977, Krapu and Reinecke in press). Not only are specific amino acids and micronutrients from animal prey important for developing young, but gastropods and crayfish may also be valuable as a source of calcium. Young chicks need calcium for bone and feather development, while hens need to replenish calcium reserves after egg laying.

Potential prey were present at 81-88% of sampled brood or juvenile foraging sites, whereas, potential prey were present at only 30-36% of sampled sites during spring migration or nesting/incubation periods. Potential prey were present at 52% of sampled foraging sites during the fall migration periods. Differences among periods indicate brood sites yield a more predictable prey base, whereas, the nesting and migration periods have patchy food resources at foraging sites. In addition to greater predictability of prey, brood sites had greater densities of potential prey. Higher densities of total prey, freshwater oligochaetes, total fish, and numbers of different taxa were present during the two brood periods and the period of separate young than the migration and nesting periods. The old brood period had greater densities of these same variables than the young brood or separate juvenile periods. The two brood periods had higher densities of total invertebrates, crayfish (at least from core samples), and aquatic beetles than the other periods. The young brood period had higher densities of pulmonate snails than other periods, whereas, the old brood period and separate young period had

significantly greater densities of snails than the migration or nesting periods. Net samples during spring migration were dominated by snails and crayfish, whereas net samples from the nesting/incubation period were dominated by snails, aquatic beetles, and crayfish.

Although crayfish were not abundant in core samples of any period, burrowing crayfish were a dominant organism in the net samples of spring migration and nesting/incubation periods. Crayfish captured during these early periods are large adults, whereas only small young-of-year were captured during the brood periods. Likewise, exoskeletons of crayfish were the only prey remains found in the analyses of regurgitated pellets from either the nesting/incubation period or the first 5 days after hatch for young. Although a bias for hard exoskeletons in pellets is expected, as compared to soft bodied oligochaetes or larval insects, crayfish are probably the most important prey item before brood feeding. The core sampler probably did not adequately sample crayfish in the environment.

The pattern of prey exploitation by migratory and breeding king rails undoubtedly involves shifts among potential prey types. Adults, which are experienced foragers with completely developed bills and tarsi, feed at sites with low density, patchy distributed potential prey, but individual prey items are large (such as crayfish). Adults with broods and separated juveniles feed at sites with high density, predictable potential prey, such as at

small, drying swales. The individual prey items at these brood sites are, however, small and soft bodied (oligochaetes, leeches, beetles). The size range of prey increases with age of chicks for many birds (Best 1977), and older king rail chicks and juveniles may be able to feed on a wide diversity of prey ranging from leeches to small fish.

Within the brood periods, when prey is more predictable, differences existed among prey densities at water, water-mud interface, and mud substrates. Water sites had higher total prey and freshwater oligochaetes than either other location. Sites with water also had greater diversity of prey (taxa-order/core), density of snails, and density of fish than mud sites.

Seasonal variations in prey types were observed for king rail food habits in the Grand Prairie of Arkansas (Meanley 1956). Crayfish were the most important type from March to May (61% volume, 81% occurrence), whereas aquatic beetles (19% volume, 31% occurrence), semi-aquatic beetles (11% volume, 87% occurrence), and fish (8% volume, 19% occurrence) were all important items from June to August (Meanley 1956). Percent volume and percent occurrence of crayfish and snails present in rail esophagi dropped during the later period, whereas prey such as aquatic beetles, semi-aquatic beetles, aquatic bugs, fish, and frogs all increased. Crayfish and aquatic insect fragments were also found in regurgitated pellets from king rails in Arkansas and Maryland (Meanley 1962). In a ranked comparison, the

three most common potential prey items at king rail foraging sites during spring migration or nesting periods in Missouri were also the three dominant prey items in esophagi of collected king rails during March-May in Arkansas.

Important prey from June-August esophagi samples (Meanley 1956) included fish, aquatic beetles, and semi-aquatic beetles, and these items were also all present in concentrated densities during rail brood periods in Missouri. Annelids were not recorded in Arkansas food habits (Meanley 1956), but freshwater oligochaetes and leeches were among the most abundant potential prey at brood foraging sites in Missouri. Postmortem digestion may exclude soft bodied annelids from discovery if esophagi samples are not preserved immediately after bird collection. Aquatic coleoptera, especially hydrophilids and dytiscids, have also been recorded as important prey for the Virginia rail (*R. limicola*) (Horak 1970). This smaller congener of the king rail, however, generally breeds in more semi-permanent wetlands at higher latitudes. Grasshoppers and crickets have also been reported as food items for king rails (Meanley 1969) and may be consumed at drier sites during mid-day.

Several questions related to king rail foraging need further investigation. The relationship of feeding frequency and size or weight of prey needs elucidation across the breeding period. The relationship of prey density at a specific swale to brood arrival and departure

needs to be quantified. Does a specific threshold exist for prey density where a brood will abandon a foraging site? Although both adults forage with a young brood, where is the second adult during later stages of brooding? Renesting activity seems doubtful, at least in the immediate wetland complex (Chapter 3). Alternative adult behaviors include brood abandonment to gain reserves for molt and migration, or testing of other potential foraging sites in the complex for the brood. Several questions related to survival and macrohabitat use may be quantified through telemetry techniques, but a large population in quality wetland habitat is needed.

The shift in foraging site characteristics observed for migrating, breeding and young king rails suggests that a complex of wetland habitats is necessary for population survival. Densely vegetated sites are necessary for migration and nesting periods, whereas drying swales are most important to brood foraging. Public refuges should protect the natural drying process of small depressions during the king rail brood period.

Table 17. Water depth (mm) at king rail foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	97.0 \pm 5.8	25-200	42	49	A	A
Nesting/ incubation	85.0 \pm 4.8	25-141	39	46	B	AB
Early brood	26.6 \pm 2.1	0-75	72	85	C	C
Late brood	21.7 \pm 2.1	0-56	80	68	C	C
Separate young	31.1 \pm 3.6	0-68	61	28	C	C
Fall migration	76.5 \pm 8.9	10-245	65	31	B	B
Hide	0	0	-	44	D	D

^a General linear ANOVA model: $F = 86.60$, 6 df, N = 351,
 $P < 0.0001$.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 18. Vegetation height (cm) at king rail foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	50.6 \pm 1.8	31-84	24	49	A	A
Nesting/ incubation	68.2 \pm 3.5	42-126	35	46	B	AB
Early brood	2.7 \pm 1.9	0-152	656	85	C	C
Late brood	0	0	-	68	C	C
Separate young	10.6 \pm 5.2	0-112	262	28	C	C
Fall migration	88.1 \pm 10.6	0-195	67	31	D	BD
Hide	106.0 \pm 7.6	44-208	47	44	E	D

^a General linear ANOVA model: $F = 108.83$, 6 df, N = 351, $P < 0.0001$.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 19. Vegetation density (number of stems/m²) at king foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	293.4 \pm 29.2	50-1000	70	49	A	A
Nesting/ incubation	297.3 \pm 29.2	75-875	67	46	A	A
Early brood	9.7 \pm 5.9	0-400	562	85	B	B
Late brood	0	0	-	68	B	B
Separate young	33.0 \pm 17.5	0-400	281	28	B	B
Fall migration	248.4 \pm 36.7	0-750	82	31	A	A
Hide	406.3 \pm 30.8	125-1250	50	44	C	C

^a General linear ANOVA model: $F = 68.83$, 6 df, $N = 351$, $P < 0.0001$.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$)

Table 20. Activity patterns of foraging king rail chicks^{ab}.

Age (weeks)	<u>Percent sitings for activity</u>		
	Hiding	Fed by adults	Foraging
1-3 (N = 80) ^c	24	70	6
4-6 (N = 120)	3	34	63
7-9 (N = 64)	-	3	97

^a Based on brood sitings where at least one adult was seen foraging.

^b Statistics for table of age by activity - Likelihood ratio $\chi^2 = 157$, 4 df, $P < 0.001$, Cramer's V = 0.498,

Uncertainty Coefficient (activity given age) = 0.325.

^c N for each age group is equal to the number of foraging sitings for that specific age category. Total N = 264.

Table 21. Contingency table for presence of prey by periods at king rail foraging sites^a.

Period	Prey Presence	Frequency	Percent within period
Spring migration	No Prey	28	70
	Prey	12	30
Nesting/ incubation	No Prey	25	64
	Prey	14	36
Early brood	No Prey	14	18
	Prey	66	82
Late brood	No Prey	11	12
	Prey	83	88
Separate young	No Prey	6	19
	Prey	26	81
Fall migration	No Prey	12	48
	Prey	13	52

^a Table statistics: Likelihood Ratio $\chi^2 = 76.3$, 5 df, $P < 0.001$, Cramer's V = 0.499, Uncertainty Coefficient (presence given period) = 0.199, Total N = 310.

Table 22. Total potential prey (individuals/m³) at king rail foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	1910 \pm 530	0-10,184	175	40	A	A
Nesting/ incubation	1893 \pm 501	0-12,730	165	39	A	A
Early brood	34,053 \pm 3490	0-112,024	92	80	B	BC
Late brood	59,433 \pm 6815	0-346,256	112	96	C	B
Separate young	20,925 \pm 5062	0-122,208	137	32	D	CD
Fall migration	4379 \pm 1335	0-28,006	152	25	A	AD
Spring migration (net data)	260 \pm 54	0-1075	112	29	E	E
Nesting/ incubation (net data)	281 \pm 69	0-1125	115	22	E	E

^a Based on core samples, unless sweep net data indicated.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data transformations that excluded all zero total prey samples.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 23. Total macroinvertebrates (individuals/m³) at king rail foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	1846 \pm 524	0-10,184	179	40	A	AB
Nesting/ incubation	1828 \pm 494	0-12,730	169	39	A	AB
Early brood	30,457 \pm 3470	0-112,024	102	80	B	BC
Late brood	52,723 \pm 6486	0-328,434	121	96	B	C
Separate young	16,788 \pm 4185	0-99,294	141	32	A	A
Fall migration	4175 \pm 1330	0-28,006	159	25	A	AB
Spring migration (net data)	256 \pm 54	0-1075	114	29	C	D
Nesting/ incubation (net data)	278 \pm 69	0-1125	116	22	C	D

^a Based on core samples, unless sweep net data indicated.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data

^d transformations that excluded all zero total prey samples.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 24. Diversity of potential prey items (taxon-order/core or net sample) at king rail foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	0.45 \pm 0.12	0-2	167	40	A	AB
Nesting/ incubation	0.79 \pm 0.13	0-2	147	39	A	A
Early brood	1.93 \pm 0.14	0-5	67	80	B	AB
Late brood	2.77 \pm 0.17	0-6	60	96	C	C
Separate young	1.58 \pm 0.28	0-6	74	32	BC	AC
Fall migration	0.80 \pm 0.17	0-2	108	25	A	AB
Spring migration (net data)	2.10 \pm 0.28	0-5	71	29	BC	AC
Nesting/ incubation (net data)	2.18 \pm 0.35	0-5	74	22	BC	BC

^a Based on core samples, unless sweep data indicated.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data

^d transformations that excluded all zero total prey samples.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 25. Total freshwater oligochaetes (individuals/m³) at king rail foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	0	0	-	40	A	A
Nesting/ incubation	0	0	-	39	A	A
Early brood	8434 \pm 2507	0-106,932	267	80	BC	BC
Late brood	27,104 \pm 5635	0-280,060	204	96	B	B
Separate young	3739 \pm 1657	0-40,726	251	32	CD	BC
Fall migration	1120 \pm 659	0-12,730	294	25	D	C
Spring migration (net data)	0	0	-	29	A	A
Nesting/ incubation (net data)	0	0	-	22	A	A

^a Based on core samples, unless sweep net data indicated.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data transformations that excluded zero samples. General linear ANOVA model: $F = 4.27$, 3 df, $P < 0.009$.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 26. Total leeches (individuals/m³) at king rail foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	0	0	-	40	A	A
Nesting/ incubation	65 \pm 65	0-2546	624	39	B	B
Early brood	1782 \pm 563	0-35,644	282	80	BC	B
Late brood	4429 \pm 830	0-35,644	184	96	CD	B
Separate young	2069 \pm 1179	0-35,644	323	32	BD	B
Fall migration	102 \pm 102	0-2546	500	25	B	B
Spring migration (net data)	0	0	-	29	A	A
Nesting/ incubation (net data)	1 \pm 1	0-25	469	22	A	A

^a Based on core samples, unless sweep net data indicated.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data transformations that excluded all zero samples. General linear ANOVA model: $F = 16.76$, 5 df, $P < 0.001$.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 27. Total crayfish (individuals/m³) at king rail foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	0	0	-	40	A	A
Nesting/ incubation	0	0	-	39	A	A
Early brood	477 \pm 182	0-10,184	340	80	B	B
Late brood	212 \pm 187	0-17,822	865	96	B	B
Separate young	0	0	-	32	A	A
Fall migration	0	0	-	25	A	A
Spring migration (net data)	25 \pm 6	0-100	122	29	C	C
Nesting/ incubation (net data)	22 \pm 6	0-100	135	22	C	C

^a Based on core samples, unless sweep net data indicated.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data transformations that excluded all zero samples. General

^d linear ANOVA model: $F = 161.33$, 3 df, $P < 0.001$.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 28. Total snails (individuals/m³) at king rail foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	955 \pm 361	0-10,184	239	40	AB	AB
Nesting/ incubation	849 \pm 286	0-7638	210	39	A	A
Early brood	10,725 \pm 2197	0-99,294	183	80	C	C
Late brood	5251 \pm 990	0-40,736	185	96	D	CD
Separate young	3819 \pm 1357	0-35,644	201	32	BD	BCD
Fall migration	306 \pm 224	0-5092	366	25	AB	AD
Spring migration (net data)	200 \pm 49	0-1025	132	29	E	E
Nesting/ incubation (net data)	195 \pm 55	0-975	133	22	E	E

^a Based on core samples, unless sweep net data indicated.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data transformations that excluded zero samples. General linear ANOVA model: $F = 107.02$, 7 df, $P < 0.001$.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 29. Total aquatic beetles (individuals/m³) at king rail foraging sites^a.

Period	Mean ± SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	191 ± 107	0-2546	356	40	A	A
Nesting/ incubation	392 ± 176	0-5092	281	39	A	A
Early brood	3628 ± 902	0-40,736	222	80	B	B
Late brood	4349 ± 744	0-35,644	167	96	B	B
Separate young	1830 ± 669	0-15,276	207	32	A	AB
Fall migration	407 ± 241	0-5092	295	25	A	AB
Spring migration (net data)	9 ± 4	0-100	227	29	C	C
Nesting/ incubation (net data)	27 ± 10	0-150	167	22	C	C

^a Based on core samples, unless sweep net data indicated. Beetles chiefly of the families Dytiscidae and Hydrophilidae, but also including Haliplidae, Gyrinidae and Elmidae.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data transformations that excluded zero samples. General

^d linear ANOVA model: $F = 123.74$, 7 df, $P < 0.001$.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 30. Total semi-aquatic beetles (individuals/m³) at king rail foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	382 \pm 282	0-10,184	467	40	A	A
Nesting/ incubation	391 \pm 239	0-7638	381	39	A	A
Early brood	2260 \pm 710	0-30,552	291	80	A	A
Late brood	2970 \pm 739	0-30,552	244	96	A	A
Separate young	1910 \pm 800	0-15,276	237	32	A	A
Fall migration	815 \pm 636	0-15,276	390	25	A	A
Spring migration (net data)	0	0	-	29	B	B
Nesting/ incubation (net data)	0	0	-	22	B	B

^a Based on core samples, unless sweep net data indicated. Beetles of the families Staphylinidae, Carabidae, and Chrysomelidae.

^b LSD = T-tests, Least Significant Difference ($P < 0,05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data transformations that exclude zero samples. General linear ANOVA model: $F = 0.72$, 5 df, $P > 0.60$.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 31. Total fish (individuals/m³) at king rail
foraging sites^a.

Period	Mean \pm SE	Range	CV	N	LSD ^{bc}	HSD ^d
Spring migration	64 \pm 64	0-2546	632	40	A	A
Nesting/ incubation	65 \pm 65	0-2546	624	39	A	A
Early brood	3596 \pm 958	0-40,736	238	80	AB	A
Late brood	6789 \pm 1488	0-109,478	215	96	B	A
Separate young	4058 \pm 1371	0-33,098	191	32	AB	A
Fall migration	204 \pm 204	0-5092	500	25	A	A
Spring migration (net data)	4 \pm 3	0-50	313	29	C	B
Nesting/ incubation (net data)	2 \pm 2	0-50	469	22	C	B

^a Based on core samples, unless sweep net data indicated.

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data transformations that excluded all zero samples. General

^d linear ANOVA model: $F = 27.09$, 7 df, $P < 0.001$.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$)

Table 32. Total potential prey (individuals/m³) at king rail brood foraging sites^a.

Location	Mean \pm SE	Range	CV	LSD ^{bc}	HSD ^d
Water (N = 91)	65,664 \pm 6993	0-346,256	102	A	A
Water/mud interface (N = 42)	30,734 \pm 4466	0-106,932	94	B	B
Mud (N = 43)	27,059 \pm 4341	0-122,208	105	B	B

^a Based on core samples from early and late brood periods (Total N = 176).

^b LSD = T-tests, Least Significant Difference (P < 0.05).

^c Different capital letters indicate significant differences. Both tests conducted on log(x+1) data transformations that excluded all zero total prey samples.

^d General linear ANOVA model: F = 6.83, 2 df, P < 0.002.
^d HSD = Tukey-Kramer Studentized Range Test (P < 0.05).

Table 33. Total macroinvertebrates (individuals/m³) at king rail brood foraging sites^a.

Location	Mean \pm SE	Range	CV	LSD ^{bc}	HSD ^d
Water (N = 91)	55,655 \pm 6810	0-328,434	115	A	A
Water/mud interface (N = 42)	28,188 \pm 4198	0-106,932	97	A	A
Mud (N = 43)	26,940 \pm 4336	0-122,208	106	A	A

^a Based on core samples from early and late brood periods (Total N = 176).

^b LSD = T-tests, Least Significant Difference (P < 0.05).

^c Different capital letters indicate significant differences. Both tests conducted on log(x+1) data transformations that excluded all zero samples. General linear ANOVA model: F = 0.05, 2 df, P > 0.95.

^d HSD = Tukey-Kramer Studentized Range Test (P < 0.05).

Table 34. Diversity (taxon-order/core) at king rail brood foraging sites^a.

Location	Mean \pm SE	Range	CV	LSD ^{bc}	HSD ^d
Water (N = 91)	2.85 \pm 0.16	0-6	54	A	A
Water/mud interface (N = 42)	2.07 \pm 0.24	0-5	76	AB	AB
Mud (N = 43)	1.72 \pm 0.18	0-4	70	B	B

^a Based on core samples from early and late brood periods (Total N = 176).

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data transformations that excluded all zero samples. General

^d linear ANOVA model: $F = 6.60$, 2 df, $P < 0.002$.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 35. Total freshwater oligochaetes (individuals/m³)
at king rail brood foraging sites^a.

Location	Mean \pm SE	Range	CV	LSD ^{bc}	HSD ^d
Water (N = 91)	27,139 \pm 5903	0-280,060	208	A	A
Water/mud interface (N = 42)	6668 \pm 3059	0-106,932	297	B	B
Mud (N = 43)	12,256 \pm 3979	0-122,208	213	B	B

^a Based on core samples from early and late brood periods (Total N = 176).

^b LSD = T-tests, Least Significant Difference ($P < 0.05$).

^c Different capital letters indicate significant differences. Both tests conducted on $\log(x+1)$ data transformations that excluded all zero samples. General

^d linear ANOVA model: $F = 8.04$, 2 df, $P < 0.001$.

^d HSD = Tukey-Kramer Studentized Range Test ($P < 0.05$).

Table 36. Total leeches (individuals/m³) at king rail brood foraging sites^a.

Location	Mean \pm SE	Range	CV	LSD ^{bc}	HSD ^d
Water (N = 91)	5064 \pm 907	0-35,644	171	A	A
Water/mud interface (N = 42)	1031 \pm 484	0-15,276	304	A	A
Mud (N = 43)	1480 \pm 668	0-22,914	296	A	A

^a Based on core samples from early and late brood periods (Total N = 176).

^b LSD = T-tests, Least Significant Difference (P < 0.05).

^c Different capital letters indicate significant differences. Both tests conducted on log(x+1) data transformations that excluded all zero samples. General linear ANOVA model: F = 0.53, 2 df, P > 0.59.

^d HSD = Tukey-Kramer Studentized Range Test (P < 0.05).

Table 37. Total snails (individuals/m³) at king rail brood foraging sites^a.

Location	Mean \pm SE	Range	CV	LSD ^{bc}	HSD ^d
Water (N = 91)	9149 \pm 1883	0-99,294	196	A	A
Water/mud interface (N = 42)	8244 \pm 2177	0-63,650	171	A	AB
Mud (N = 43)	4263 \pm 1256	0-38,190	193	B	B

^a Based on core samples from early and late brood periods (Total N = 176).

^b LSD = T-tests, Least Significant Difference (P < 0.05).

^c Different capital letters indicate significant differences. Both tests conducted on log(x+1) data transformations that excluded all zero samples. General

^d linear ANOVA model: F = 4.28, 2 df, P < 0.019.

^d HSD = Tukey-Kramer Studentized Range Test (P < 0.05).

Table 38. Total aquatic beetles (individuals/m³) at king rail brood foraging sites^a.

Location	Mean \pm SE	Range	CV	LSD ^{bc}	HSD ^d
Water (N = 91)	5763 \pm 958	0-40,736	159	A	A
Water/mud interface (N = 42)	4001 \pm 997	0-28,006	162	A	A
Mud (N = 43)	355 \pm 262	0-10,184	484	A	A

^a Based on core samples from early and late brood periods (Total N = 176).

^b LSD = T-tests, Least Significant Difference (P < 0.05).

^c Different capital letters indicate significant differences. Both tests conducted on log(x+1) data transformations that excluded all zero samples. General linear ANOVA model: F = 0.53, 2 df, P > 0.59.

^d HSD = Tukey-Kramer Studentized Range Test (P < 0.05).

Table 39. Total semi-aquatic beetles (individuals/m³) at king rail brood foraging sites^a.

Location	Mean \pm SE	Range	CV	LSD ^{bc}	HSD ^d
Water (N = 91)	224 \pm 224	0-20,368	954	A	A
Water/mud interface (N = 42)	2970 \pm 1062	0-28,006	232	A	A
Mud (N = 43)	7460 \pm 1545	0-30,552	136	A	A

^a Based on core samples from early and late brood periods (Total N = 176).

^b LSD = T-tests, Least Significant Difference (P < 0.05).

^c Different capital letters indicate significant differences. Both tests conducted on log(x+1) data transformations that excluded all zero samples. General linear ANOVA model: F = 0.92, 2 df, P > 0.41.

^d HSD = Tukey-Kramer Studentized Range Test (P < 0.05).

Table 40. Total fish (individuals/m³) at king rail brood foraging sites^a.

Location	Mean \pm SE	Range	CV	LSD ^{bc}	HSD ^d
Water (N = 91)	8981 \pm 1638	0-109,478	174	A	A
Water/mud interface (N = 42)	2910 \pm 1021	0-35,644	227	A	A
Mud (N = 43)	0	0	-	B	B

^a Based on core samples from early and late brood periods (Total N = 176).

^b LSD = T-tests, Least Significant Difference (P < 0.05).

^c Different capital letters indicate significant differences. Both tests conducted on log(x+1) data transformations that excluded all zero samples. General

^d linear ANOVA model: F = 2.98, 2 df, P < 0.091.

^d HSD = Tukey-Kramer Studentized Range Test (P < 0.05).

Fig. 10 Water depths (mm) at king rail foraging sites during migrational and breeding periods. Periods include: spring migration, nesting/ incubation, young brood, old brood, separate young, and fall migration.

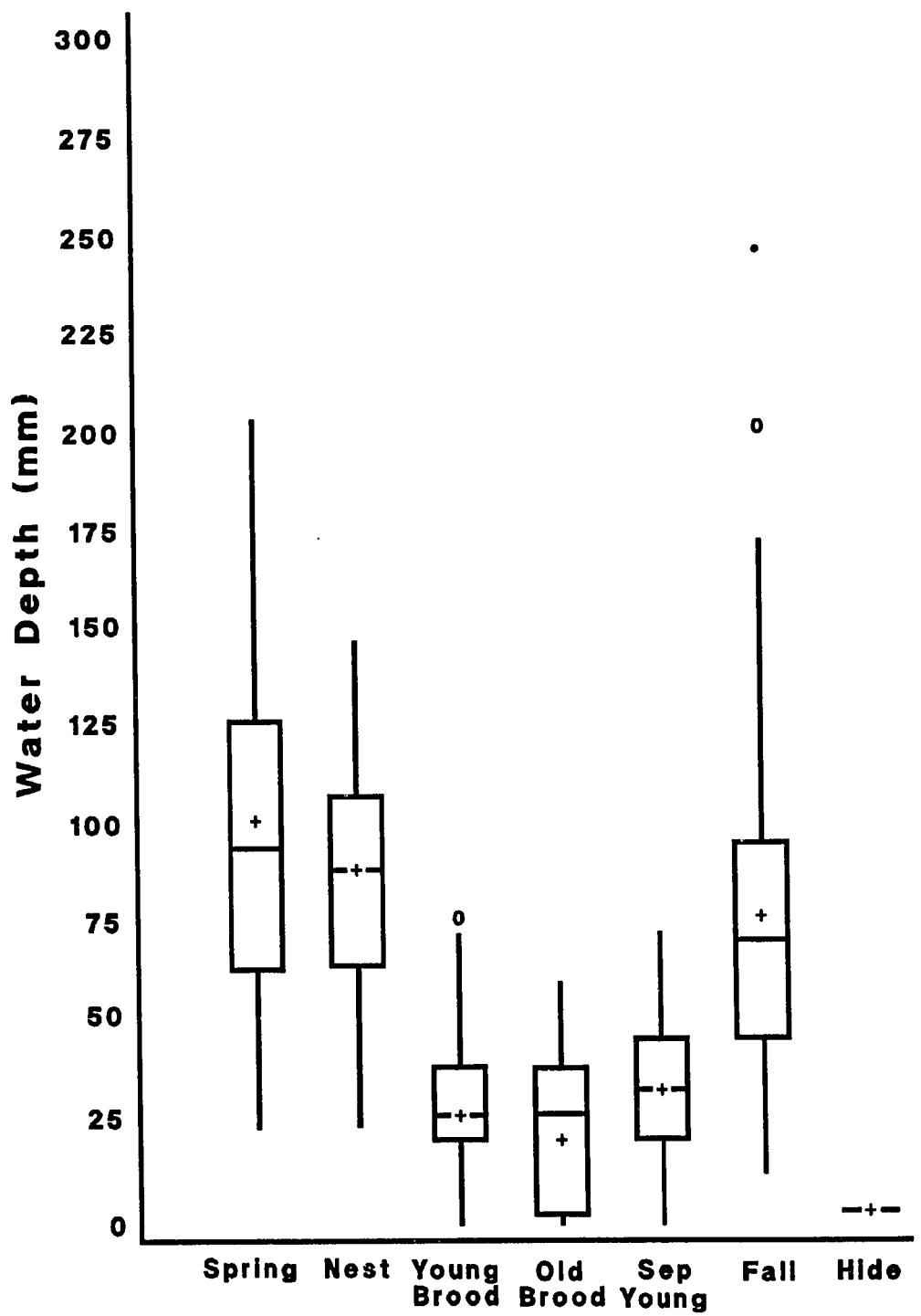


Fig. 11 Vegetation heights (cm) at king rail foraging sites during migrational and breeding periods. Periods include: spring migration, nesting/incubation, young brood, old brood, separate young, and fall migration.

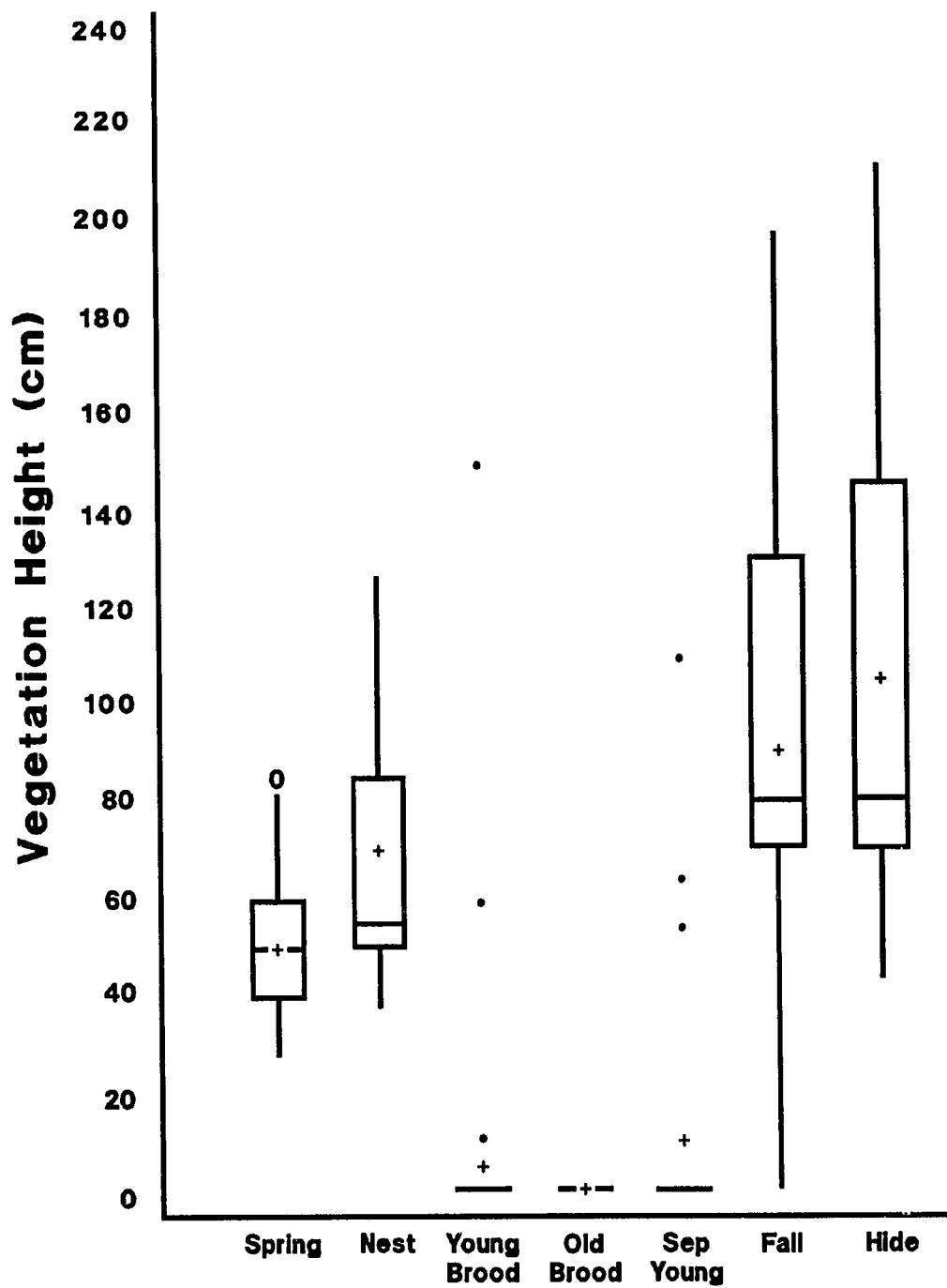
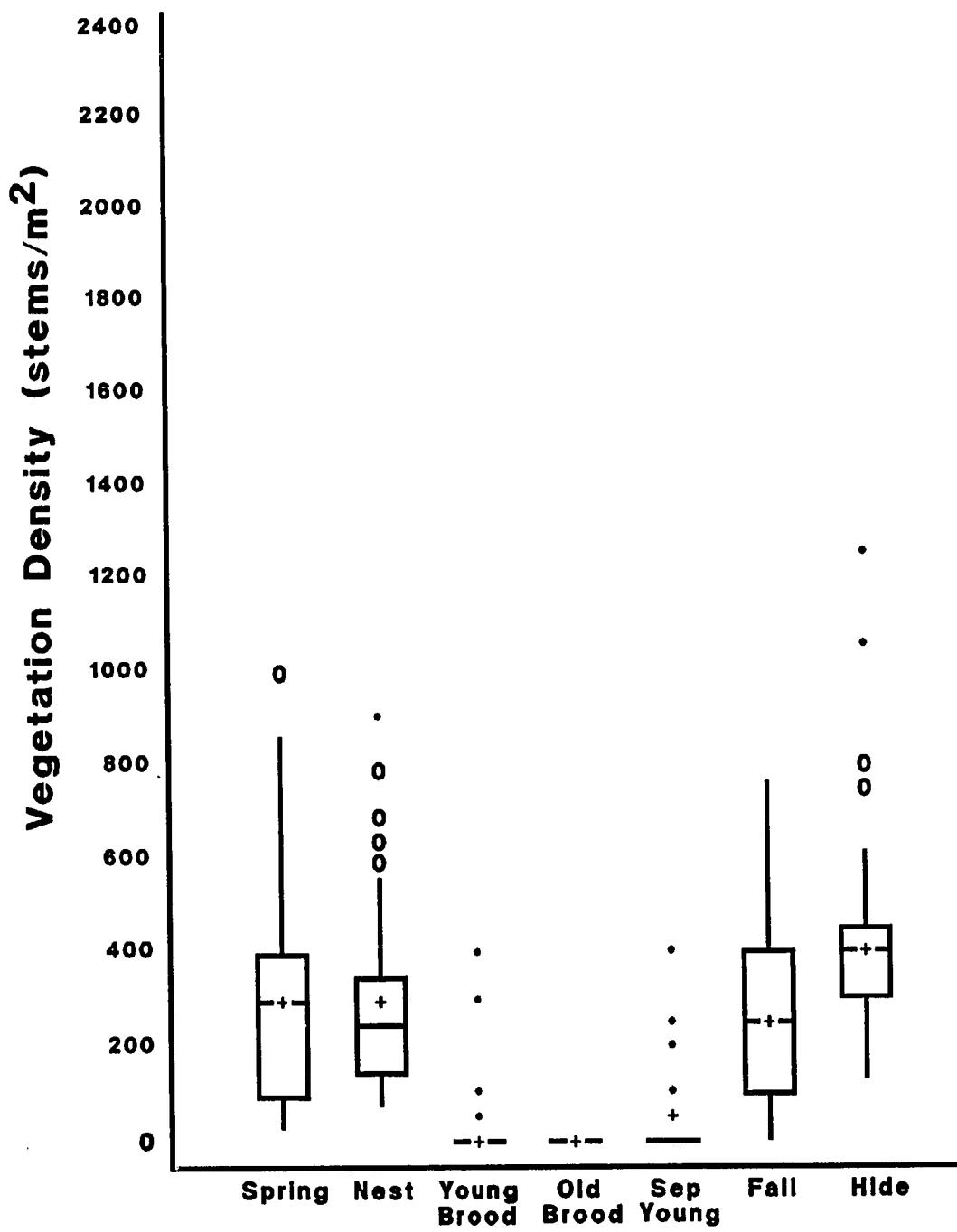
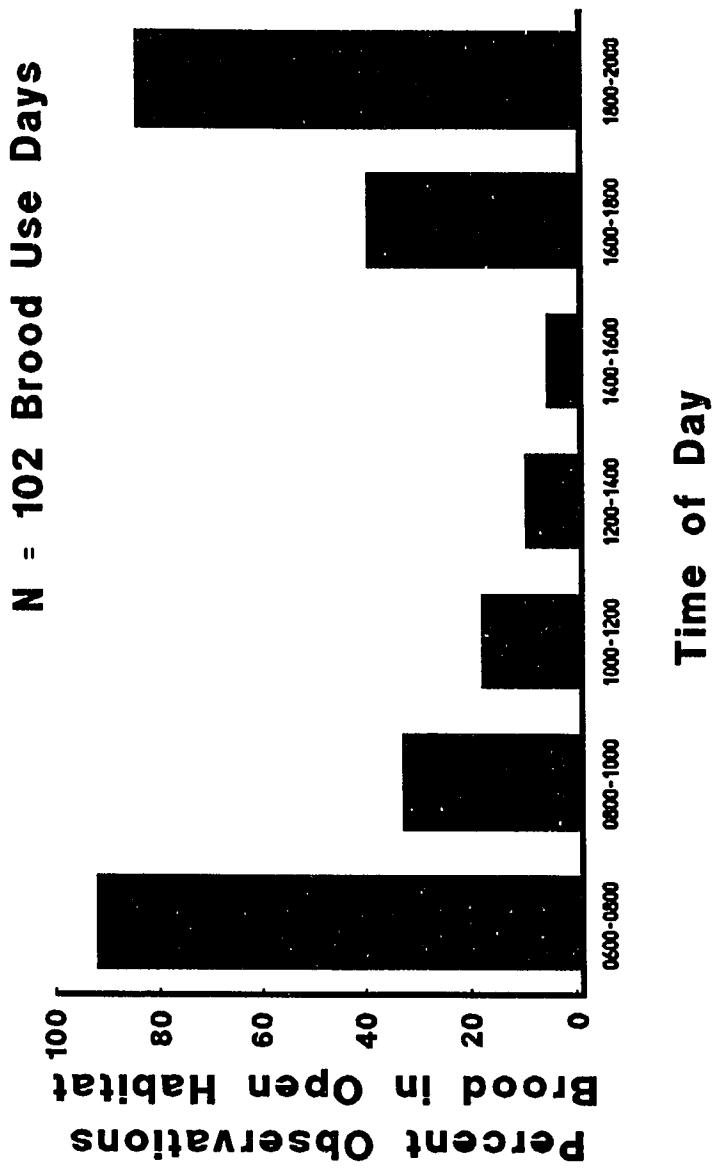


Fig. 12 Vegetation stem density (stems/m²) at king rail foraging sites during migrational and breeding periods. Periods include: spring migration, nesting/incubation, young brood, old brood, separate young, and fall migration.



**Fig. 13 Percent observations brood in open habitat
(N = 102 brood use days).**



CHAPTER V

WADING BIRD RESPONSE TO CONTROLLED DRAWDOWN OF
A MANAGED WETLAND

Early spring flooding historically occurred on the Mississippi River floodplain after snow melt waters and seasonal rains increased watershed runoff (Korschgen 1989, Reid et al. 1989). These vast floodplain wetlands then became nurseries for riverine fishes and invertebrates. As evapotranspiration increased during summer and river water levels fell, many floodplain wetlands became isolated. These isolated wetlands became increasingly smaller and drying water bodies concentrated aquatic organisms. Feeding assemblages of breeding and post-breeding wading birds exploited these seasonally available food resources.

Man's modifications to the large river systems of North America have been great, but the impacts to the Mississippi River floodplains in the last century have been severe. Constriction of the river channel and construction of mainstem levees, revetments and wing dikes have led to dramatic habitat alterations (Nolen 1913, Belt 1975). Forested and herbaceous floodplains alike have been "reclaimed" for agricultural developments, which resulted in losses of seasonal waterbird foraging areas. For much of the river system, especially altered floodplains, dynamic water fluctuations no longer occur. Acquisition of public

refuges and active management have often attempted to simulate some of these seasonal fluctuations. From Minneapolis to Memphis, nearly 0.5 million ha of wetlands are in public ownership throughout the Upper Mississippi Valley (Reid et al. 1989). Many of these areas have the potential to control the rate of dewatering to encourage germination of emergent plants (Fredrickson and Taylor 1982). When the dewatering process or drawdown continues over an extended period, the conditions may more closely simulate the natural drying process that attracts feeding assemblages of waterbirds (Kushlan 1976a). Flocking of waterbirds may occur in response to finding abundant and inconstant food supplies or because of increasing number of prey confrontations to disturbances by other members of the flock (Willard 1977). The patterns of aquatic prey and wading bird responses to water decline remain unknown. To evaluate such patterns, a 38 ha seasonal wetland, in the floodplain of the Mississippi River, was annually drawdown from 1981-85. Selected ecological measures were used to assess the response of wading birds to the changing environment. The experimental design sought to test differences in densities of wading bird prey among years with varying lengths of drawdowns, to test the patterns of wading bird response to drawdowns among years with varying lengths of drawdowns, and to investigate the relationships among aquatic prey and heron species responses.

STUDY AREA AND METHODS

The study area was located on the Ted Shanks Wildlife Area (WA) in northeastern Missouri ($39^{\circ} 30' N$, $91^{\circ} W$), a public wetland managed by the Missouri Department of Conservation. This 4,480 ha area lies at the confluence of the Mississippi and Salt rivers. Although most of the area is forested, a 1,015 ha block of nonforested habitat consists of fields, semi-permanent marshes, and seasonally flooded wetlands. Within the complex of seasonally flooded wetlands is a 38 ha site known as Goose Gap Marsh.

Artificial drawdowns were conducted on this wetland each year from 1981 through 1985 as a mechanism to enhance emergent vegetation for migrant waterbirds (Fredrickson and Taylor 1982). Water drawdowns were initiated between 15-20 June among years. Length of drawdown was measured from initiation of water removal to cessation of water output (when approximately 95% of the wetland was exposed as mudflats). Length of drawdown ranged from 5 to 6 days for 1982 and 1983 to 9-10 days for 1981, 1984 and 1985. Percent water coverage of Goose Gap Marsh and depth of the Mississippi River at Munday's Landing (approximately 1 km from the marsh) were recorded daily, from 15 days prior to drawdown initiation to 15 days after completion of drawdown.

Heron occurrence on the wetland was recorded daily at 0.5-1.5 hr after sunrise (Kushlan 1976a), from 15 days prior to drawdown initiation to 15 days after completion of

drawdown. Heron numbers were determined from 5 fixed observation points. Data were converted to heron numbers/100 ha prior to analyses. Least bittern (Ixobrychus exilis) occurrence was not recorded because of its secretive behavior within smartweed stands.

Ten replicate seine samples were collected 1 day prior to drawdown initiation and each day of drawdown as a quantitative index to potential prey densities. As a means of standardizing seine lengths, stations were flagged 10 m apart on the shoreline in 1981 and reflagged each year. Seine samples were separated by at least 30 m. A weighted seine was pulled by individuals who kept the net 3 m in width and moved as quickly as possible for 10 m. Mesh size opening was no greater than 5 mm. One of the collectors stationed himself 1-2 m from the mudflat/water edge. Organisms were separated by broad taxonomic groups that included large fish (≥ 10 cm length), small fish (< 10 cm length), tadpoles, and crayfish. They were then counted, weighed and replaced in the water column. Wet weight of each taxonomic group was taken to nearest gram. For analyses, potential prey data were converted to organisms (or biomass)/100 m². In reporting results, means of variables are compared.

RESULTS

Aquatic Prey Response to Drawdowns

Water depth and percent of water coverage dropped rapidly in the years 1982 and 1983; whereas, length of drawdown extended 9-10 days during 1981, 1984 and 1985. Patterns of aquatic prey occurrence differed markedly among years with rapid and slow drawdowns. Total biomass and density of total potential prey organisms peaked at days 3-4 after drawdown initiation during years with rapid drawdowns, but during years with slower drawdowns both biomass and numbers of organisms reached higher levels at 7-9 days after drawdown initiation (Figs. 14 and 15).

Large fish captured were principally carp (Cyprinus carpio) and brown bullhead (Ictalurus nebulosus). Other species of large fish collected included gizzard shad (Dorosoma cepedianum), bowfin (Amia calva), bluegill (Lepomis macrochirus), and white crappie (Poxomis annularis). Large fish biomass and density peaked between days 3-5 for rapid drawdowns, whereas little pattern was revealed for slow drawdown years (Figs. 16 and 17). Peaks for mean biomass of large fish were greatest during rapid drawdown years. Small fish captured were principally catfish species, carp, gizzard shad and mosquito fish (Gambusia affinis). Biomass and density of small fish peaked between days 3-5 for rapid drawdowns, whereas little pattern was revealed for years with slow drawdowns (Figs. 18 and 19). Large fish biomass peaked at twice the level of

small fish biomass during rapid drawdown years (Figs. 16 and 18).

Biomass and density of tadpoles (principally Rana catesbeiana) peaked at days 3-5 for rapid drawdown years, whereas peaks were reached at days 8-10 for slow drawdown years (Figs. 20 and 21). Mean peaks of tadpole biomass in slow drawdown years were three times greater than mean peaks in rapid drawdown years. Biomass and density of burrowing crayfish (Procambarus blendingii) peaked at days 3-5 for rapid drawdown years, whereas peaks were reached at days 7-10 for slow drawdown years (Figs. 22 and 23). Mean peaks of crayfish biomass were greater than two times the mean peaks in rapid drawdown years.

Wading Bird Response to Drawdowns

Wading bird use of the wetland differed among years. The numbers of wading bird species using the wetland ranged from 4 to 7 per year. The wading bird species observed on the wetland included great blue heron (Ardea herodias), great egret (Casmerodus albus), snowy egret (Egretta thula), little blue heron (Egretta caerulea), green-backed heron (Butorides striatus), yellow-crowned night-heron (Nycticorax violaceus), and black-crowned night-heron (Nycticorax nycticorax). Total heron use days (calculated from 16 days prior to drawdown and including 18 days during and following drawdown) differed among years, 1981-1985 (Table 41). Greatest total heron use occurred in 1985,

whereas least total heron use occurred in 1983. Not only were total wading bird use days greater for years with slow drawdowns than for years with rapid drawdowns, but patterns of use differed (Figs. 24-29). During rapid drawdowns, total heron occurrence on the wetland increased rapidly until day 4 of drawdown (Figs. 25 and 26). Thereafter use dropped quickly from day 5 after a rapid drawdown. In contrast, heron occurrence during slow drawdowns increased at a slower rate with a peak at days 9-10, when 95% of the wetland was exposed as mudflat (Figs. 24, 27 and 28). Density of wading birds decreased less sharply after slow drawdowns than rapid drawdowns (Fig. 29).

If wading bird use (actual counts) is grouped into one of 4 categories: 0-5 herons, 6-20 herons, 21-40 herons, or > 40 herons, then statistical comparisons between rapid and slow drawdown years are possible. From the day prior to drawdown until 18 days after drawdown initiation, heron use was greater during slow drawdowns than rapid drawdowns ($\chi^2 = 9.72$, $P < 0.05$, 3 df). If only the 10 days after drawdown cessation are compared, slow drawdowns still resulted in greater heron use than rapid drawdowns ($\chi^2 = 8.88$, $P < 0.05$, 3 df).

If wading bird use (actual counts) is grouped into one of 3 categories: 0-40 herons, 41-80 herons, or > 80 herons, then statistical comparisons between heron responses to slow drawdowns during wet and dry years on the Mississippi River are possible. Wading bird use during 1984, when river

levels were at flood stage (≥ 4.3 m) for 89% of the 35 day study, was compared to wading bird use during 1981 and 1985, when river levels never reached flood stage for the period of study. Total heron counts were compared from day 3 after drawdown initiation, when birds began to flock, to day 16 after drawdown initiation, a period of 14 days for each year. Wading bird use was greater during a dry year on the Mississippi River than a wet year ($X^2 = 7.71$, $P < 0.05$, 2 df).

Differences in response patterns also existed among wading bird species (e.g., 1981, Figs. 30-33). Great blue herons and great egrets concentrated with decreasing water levels, but great egrets tended to occur on the site for a longer period after the drawdown was complete (Figs. 30 and 31). Yellow-crowned night-herons, little blue herons and snowy egrets appeared at the completion of drawdowns when water levels were low and mudflat exposure was great (Fig. 32). Yellow-crowned night-herons were present in 4 years, snowy egrets in 3 years, little blue herons in 2 years, whereas black-crowned night-herons only occurred in 1 of 5 years (Table 41). Green-backed herons were present in all 5 years and population densities peaked at or near the end of drawdown. In addition, several green-backed herons continued to forage at small drying pools after the major drawdown was complete (Fig. 33).

Wading Bird Relationships to Potential Prey During Drawdowns

As waters recede, a close relationship exists among several heron species and potential prey (Tables 42, 43 and 44). Ranked correlations of total aquatic prey biomass and numbers are highly significant ($P = 0.0001$) with densities of total herons, great blue herons, and great egrets for all years combined (Table 42). Ranked correlations of crayfish biomass and numbers are highly significant ($P = 0.0001$) with densities of total herons, great blue herons, and great egrets (Table 42) and yield the most predictable relationships ($0.87 < r \text{ values} < 0.92$). The relationship of ranked correlations of tadpole biomass and numbers is also highly significant ($P = 0.0001$) with densities of total herons, great blue herons, and great egrets (Table 42), but less predictable ($0.72 < r \text{ values} < 0.80$) than with either total organisms or crayfish. All other heron species were not rank correlated ($P > 0.05$ or $r < 0.65$) with aquatic prey variables for all years combined.

When aquatic prey variables are compared with heron species in ranked correlations for each individual drawdown year, several relationships are revealed. Densities of total herons, great blue herons, and great egrets are rank correlated in the same relationships in individual years as combined years, so are not further discussed here (Table 42). When yellow-crowned night-herons, black-crowned night-herons, little blue herons, snowy egrets and green-backed herons are compared to aquatic prey, no relationships

are significant for 1982, 1983, and 1984, but several relationships are significant for 1981 and 1985 (Tables 43 and 44). Yellow-crowned night-herons are rank correlated with total biomass, total aquatic organisms, crayfish biomass and crayfish numbers ($P < 0.011$, $0.73 < r < 0.79$) for 1981 and 1985 (Tables 43 and 44). Snowy egrets are rank correlated with total biomass, total aquatic organisms, crayfish biomass, crayfish numbers, and tadpole biomass ($P < 0.014$, $0.71 < r < 0.84$) for 1981, but not for 1985; whereas little blue herons are rank correlated with total biomass, crayfish biomass, crayfish numbers, tadpole biomass, and tadpole numbers ($P < 0.021$, $0.71 < r < 0.87$) for 1985, but not for 1981 (Tables 43 and 44). Green-backed heron densities display significant relationships with aquatic prey for both 1981 and 1985 (Tables 43 and 44), but variables differ between years. Ranked correlations of crayfish biomass and numbers are significant with green-backed heron densities for both years ($P < 0.007$, $0.76 < r < 0.82$). Tadpole biomass and numbers are rank correlated ($P < 0.013$, $0.71 < r$) with green-backed herons in 1981 but not in 1985. In contrast, total prey biomass and total number of organisms are significantly rank correlated ($P < 0.01$, $0.76 < r < 0.91$) with green-backed herons in 1985 but not in 1981 (Tables 43 and 44). Black-crowned night-herons, which were present only in 1981, were not correlated with any aquatic prey variable for that year.

DISCUSSION

Seasonal wetlands that are principally managed for migrant waterfowl can provide critical nutritional resources for breeding wading birds during the drying or drawdown phases of the hydrologic regime. Such management practices today differ markedly from those of fifty years ago when fisheries biologists on the Mississippi River attempted to "salvage" fish from drying floodplain swales and transfer them to the river channel. A broader understanding of the patterns of response for aquatic prey and wading birds to controlled drawdowns will increase the potential for successful management of these floodplain resources.

Tadpole and crayfish densities displayed increasing trends during the drawdown phase, whereas little patterns were displayed for fish densities or biomass, especially during slow drawdowns. Broad patterns of increasing fish biomass with drying Everglades' wetlands have been described (Kushlan 1976a) and may be representative of semi-permanent wetlands that do not dry every year. An alternative hypothesis is that controlled drawdowns allow outlets of escape for fish, especially when drawdowns are rapid and water flow high. Rapid drawdowns may not only reduce available aquatic biomass on a temporal scale, but water movements may push fish and crayfish out of the wetland. Fast mudflat exposure may also increase terrestrial emigration by crayfish or more immediate burrowing activity

on the mudflat. In either case, crayfish densities in swales will decline. For all drawdowns, increasing crayfish biomass was the most important component of total biomass. In contrast, fish energy density (kcal/m^2) was more important to wading bird populations than that of crayfish in drying Everglades wetlands (Kushlan 1986). The significant correlations of tadpole densities and biomass to heron densities in this study may in part be an artifact of the similar rates of increase for tadpoles and crayfish during a drawdown.

Reduced water levels provided a breadth of micro-habitat conditions, so that multiple wading bird species could forage in the same wetland (Kushlan 1976c, Willard 1977, Kushlan 1978). Differences in optimal feeding depths and behavioral specialties in foraging mode lead to segregation of food resources (Willard 1977). Temporal differences in response existed among the heron species. Both great blue herons and great egrets rapidly responded to initiation of drawdowns; however, great blue herons tended to leave the site more quickly after drawdown cessation (Figs. 30 and 31). Social flocking of great egrets may delay rapid site departure. Great blue herons and great egrets made up the greatest proportion of wading birds (> 83% of heron use days per year) during the drawdowns (Table 41). A herony located on Denmark Island in the Mississippi River, 3 km from Goose Gap marsh, contained between 80-200 nests of the two species during this study. Colonial

nesting and social feeding in wading birds are adaptations to enhance the efficiency of exploitation of unpredictable food supplies (Krebs 1974). As large mixed species heronries in the mid-portion of the Mississippi River are rare (J.D. Wilson, pers. comm.), foraging grounds in quality wetland sites may be a limiting factor. The primary selection for natural palustrine wetlands and secondarily for seasonally flooded impoundments, on public waterfowl refuges, has been documented for great blue herons, little blue herons, and green-backed herons in Oklahoma (Heitmeyer 1986).

Green-backed heron densities were greatest at the cessation of drawdown and several individuals continued to forage at small pools for many days. Green-backed herons nested in an aggregation within 4 km of Goose Gap marsh (Kaiser and Reid 1987), but tended to forage as individuals or pairs rather than a flock. In contrast, yellow-crowned night-herons arrived each day as a flock. Little blue-herons, snowy egrets, and black-crowned night-herons were all rare in occurrence, and appeared at the cessation of drawdown. White-plumaged wading birds may be important in attraction of mixed species aggregations to areas of high density prey (Kushlan 1977, Caldwell 1981). Snowy egrets only were present for a few days, suggesting the tendency to leave patches when capture rate declined (Erwin 1985).

Increased foraging efficiency exists for individuals of flocks in areas of renewable food resources (Willard 1977).

How closely patterns of aquatic prey densities during controlled drawdowns simulate patterns of natural drying processes is unknown. Slower drawdowns (9-10 days) produced greater wading bird response, both in total use days and peak densities, than rapid drawdowns (5 days). Although systematic prey response and total heron use was not recorded in 1986, observations also suggest greater wading bird response to drawdowns extending over longer periods. In 1986, partial drawdown extended the length of the complete drawdown of Goose Gap marsh to 19 days, and total heron density exceeded 580 birds/100 ha on day 18 after drawdown initiation.

A single drawdown on a small wetland will not sustain a breeding heron population. Rather, a complex of seasonal wetlands, riverine sloughs and forested wetlands may be necessary for this wading bird community of a Mississippi River floodplain. Conditions in the wetland complex may impact wading bird response to a single drawdown, as occurred in 1984. High river levels provide other ephemeral foraging areas in the Mississippi and Salt river floodplains. Natural palustrine wetlands are preferred by inland wading birds over other aquatic habitats (Kushlan 1976a, Heitmeyer 1986), however, modifications to natural flooding regimes have greatly reduced the area of quality floodplain habitat. Controlled drawdowns on managed wetlands may be most important during locally dry periods. Regional hydrologic patterns determine the timing of wetland

drying. For example, a complex of drying marshes in the Solognots region of southern France is exploited by wintering gray herons (Ardea cinerea) and waterfowl species (Hesse 1972). The wading bird response to drying or controlled drawdown on a given wetland is regulated by drawdown timing, length and condition of the wetland complex. Large scale manipulations of watershed hydrologic regimes may be necessary for waterbird habitat under increasingly competing uses of water by man (Kushlan 1987).

TABLE 41. Heron use days on Goose Gap Marsh for 34 days,
 1981-85. Data for each year are reflective of 16
 days prior to drawdown and 18 days during and
 following drawdown.

Heron species	1981	1982	1983	1984	1985
Total herons	1094	499	462	646	1247
Great blue heron	441	295	262	383	551
Great egret	490	160	156	194	486
Green-backed heron	50	30	38	27	68
Yellow-crowned night-heron	65	14	---	42	102
Black-crowned night-heron	14	---	---	---	---
Little blue heron	30	---	---	---	34
Snowy egret	4	---	6	---	6

TABLE 42. Ranked correlations of wading birds and potential prey for years 1981-85 combined.^a

Ranked variable	Total herons /100 ha	Great blue herons /100 ha	Great egrets /100 ha
Biomass			
Total per 100 m ²	r = 0.895	r = 0.875	r = 0.865
Tadpoles per 100 m ²	r = 0.788	r = 0.732	r = 0.798
Crayfish per 100 m ²	r = 0.914	r = 0.884	r = 0.901
Number			
Total organisms per 100 m ²	r = 0.840	r = 0.834	r = 0.790
Tadpoles per 100 m ²	r = 0.779	r = 0.724	r = 0.796
Crayfish per 100 m ²	r = 0.914	r = 0.879	r = 0.905

^a For all relationships presented, P = 0.0001. For all other ranked correlations of wading bird species and potential prey, r < 0.65 or P > 0.05.

TABLE 43. Ranked correlations of yellow-crowned night-herons, black-crowned night-herons, little blue herons, snowy egrets, and green-backed herons with potential prey for 1981.^a

Ranked variable	Yellow-crowned night-herons /100 ha	Snowy egrets /100 ha	Green-backed herons /100 ha
Biomass			
Total per 100 m ²	r = 0.783 P < 0.005	r = 0.837 P < 0.002	---
Tadpoles per 100 m ²	---	r = 0.724 P < 0.012	r = 0.739 P < 0.010
Crayfish per 100 m ²	r = 0.783 P < 0.005	r = 0.837 P < 0.002	r = 0.761 P < 0.007
Number			
Total organisms per 100 m ²	r = 0.731 P < 0.011	r = 0.717 P < 0.014	---
Tadpoles per 100 m ²	---	---	r = 0.719 P < 0.013
Crayfish per 100 m ²	r = 0.783 P < 0.005	r = 0.837 P < 0.002	r = 0.761 P < 0.007

^a For all other ranked correlations of wading bird species and potential prey, P > 0.05 or r < 0.70. No relationships were significant for black-crowned night-heron or little blue heron.

TABLE 44. Ranked correlations of yellow crowned night-herons, black-crowned night-herons, little blue herons, snowy egrets, and green-backed herons with potential prey for 1985.^a

Ranked variable	Yellow-crowned night-herons /100 ha	Little blue herons /100 ha	Green-backed herons /100 ha
Biomass			
Total per 100 m ²	r = 0.768 P < 0.010	r = 0.867 P < 0.002	r = 0.766 P < 0.010
Tadpoles per 100 m ²	---	r = 0.715 P < 0.021	---
Crayfish per 100 m ²	r = 0.768 P < 0.010	r = 0.867 P < 0.002	r = 0.811 P < 0.005
Number			
Total organisms per 100 m ²	r = 0.768 P < 0.010	---	r = 0.902 P < 0.001
Tadpoles per 100 m ²	---	r = 0.754 P < 0.012	---
Crayfish per 100 m ²	r = 0.768 P < 0.010	r = 0.867 P < 0.002	r = 0.811 P < 0.005

^a For all other ranked correlations of wading bird species and potential prey, P > 0.05 or r < 0.70. No relationships were significant for black-crowned night-heron or snowy egret.

Fig. 14 Plot of total biomass (kg/100 m²) of potential aquatic prey from day prior to drawdown (day 16) to completion of all drawdowns (day 26) for Goose Gap Marsh, 1981-85. Numbers represent values for specific year (Note - 6 observations hidden).

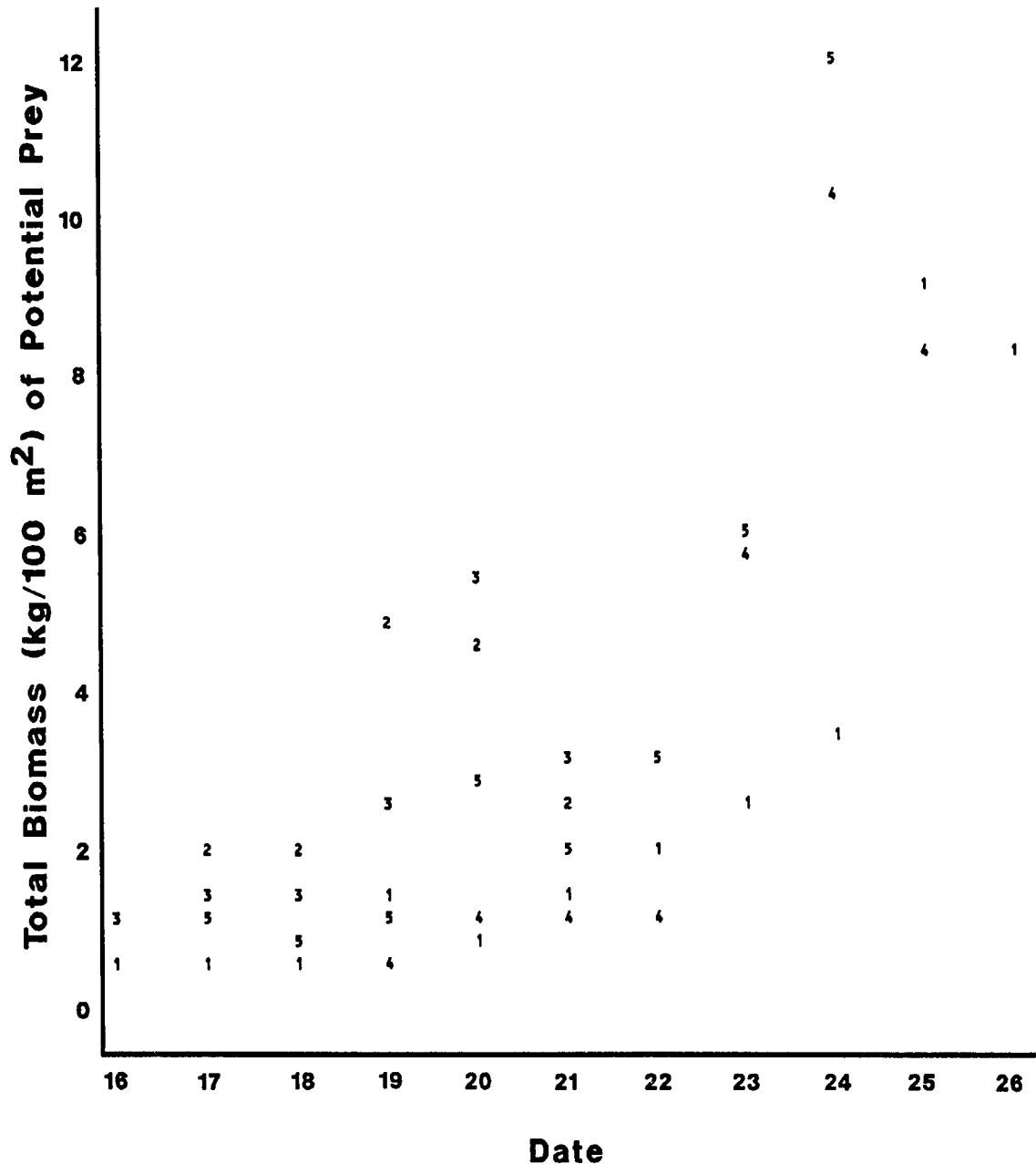


Fig. 15 Plot of total number of organisms/100 m² of potential aquatic prey from day prior to drawdown (day 16) to completion of all drawdowns (day 26) for Goose Gap Marsh, 1981-85. Numbers represent values for specific year (Note - 3 observations hidden).

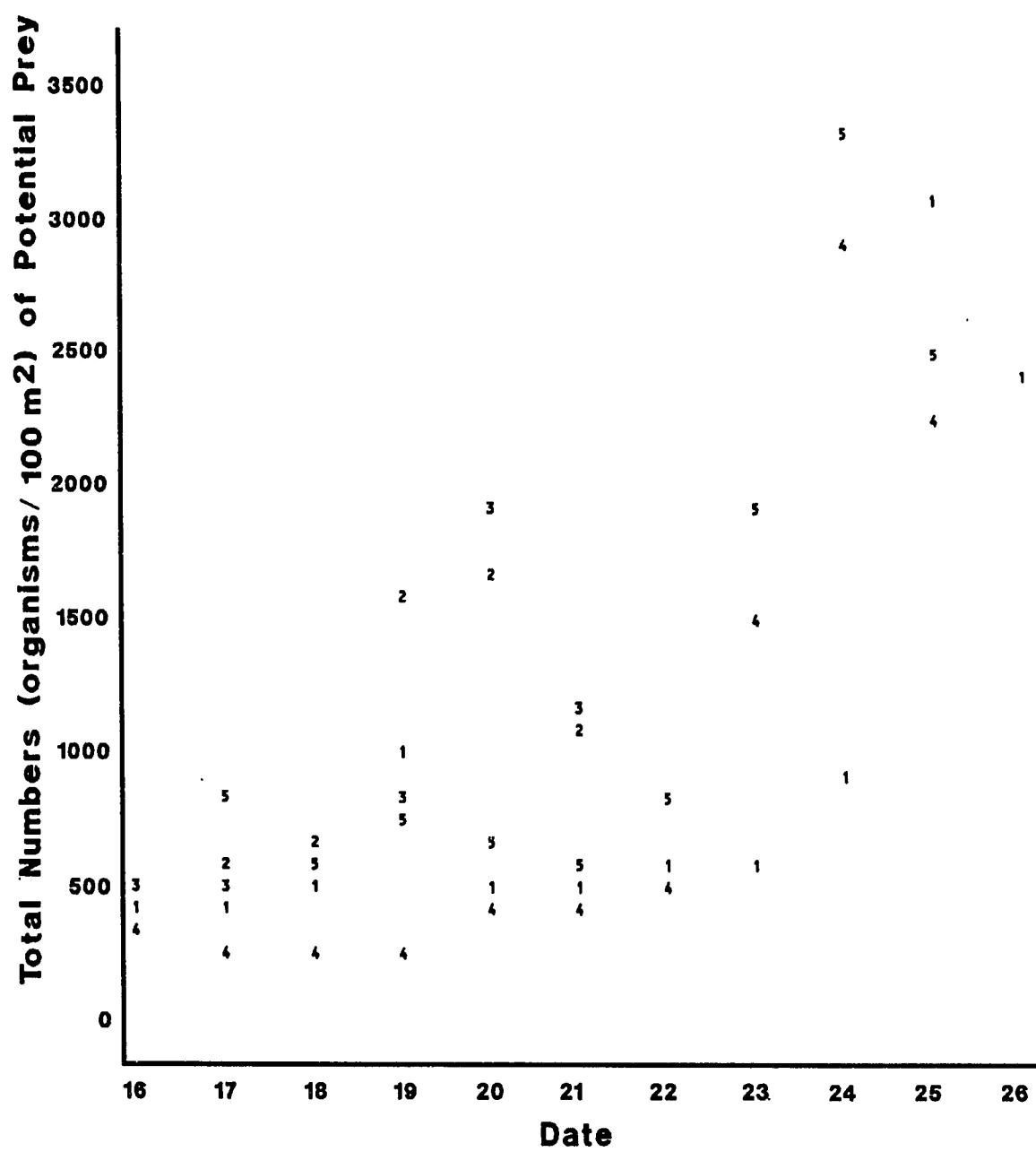


Fig. 16 Plot of large fish biomass ($100 \text{ g}/100 \text{ m}^2$) of potential aquatic prey from day prior to drawdown (day 16) to completion of all drawdowns (day 26) for Goose Gap Marsh, 1981-85. Numbers represent values for specific year (Note - 5 observations hidden).

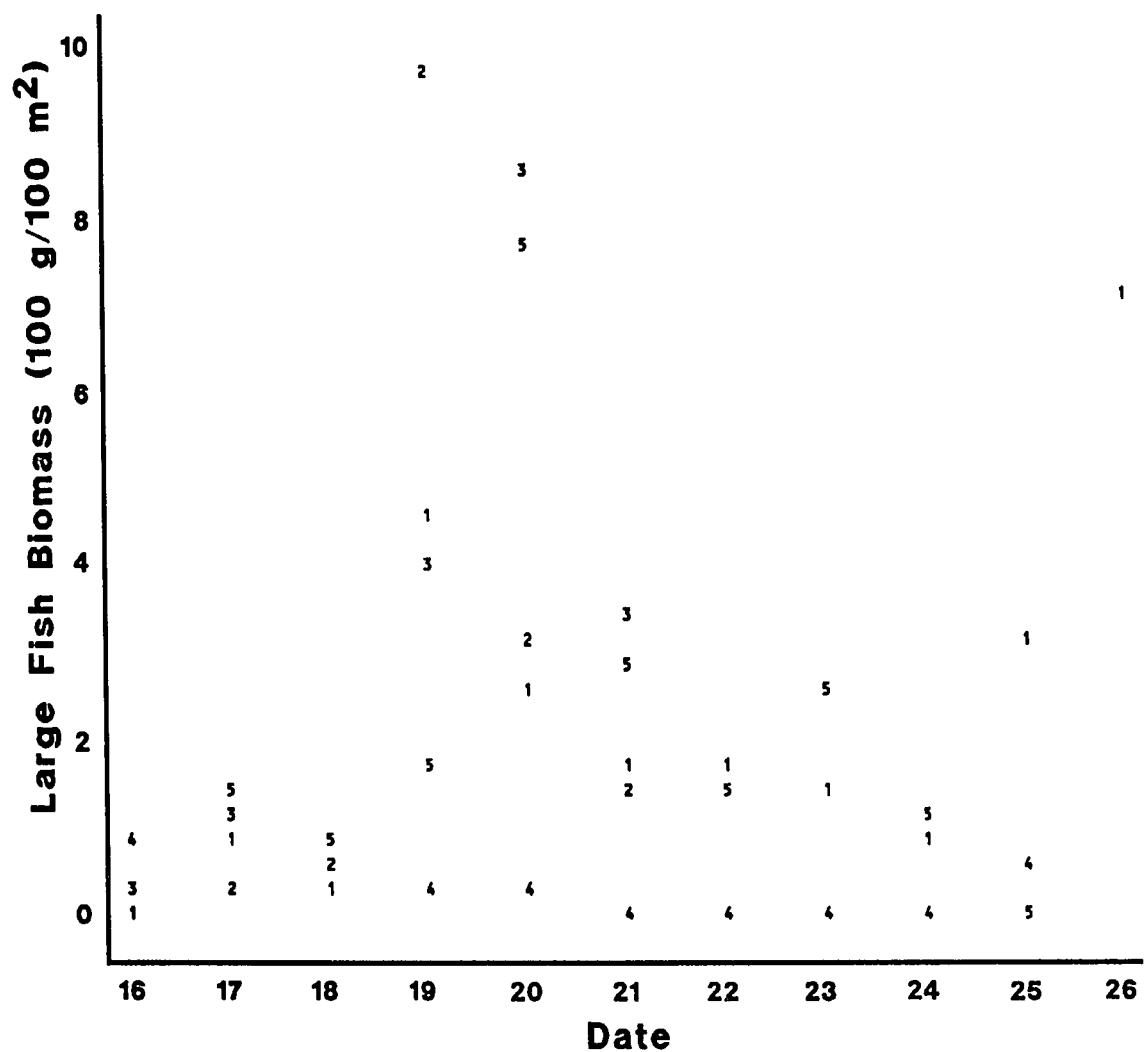


Fig. 17 Plot of large fish numbers/100 m² of potential aquatic prey from day prior to drawdown (day 16) to completion of all drawdowns (day 26) for Goose Gap Marsh, 1981-85. Numbers represent values for specific year (Note - 6 observations hidden).

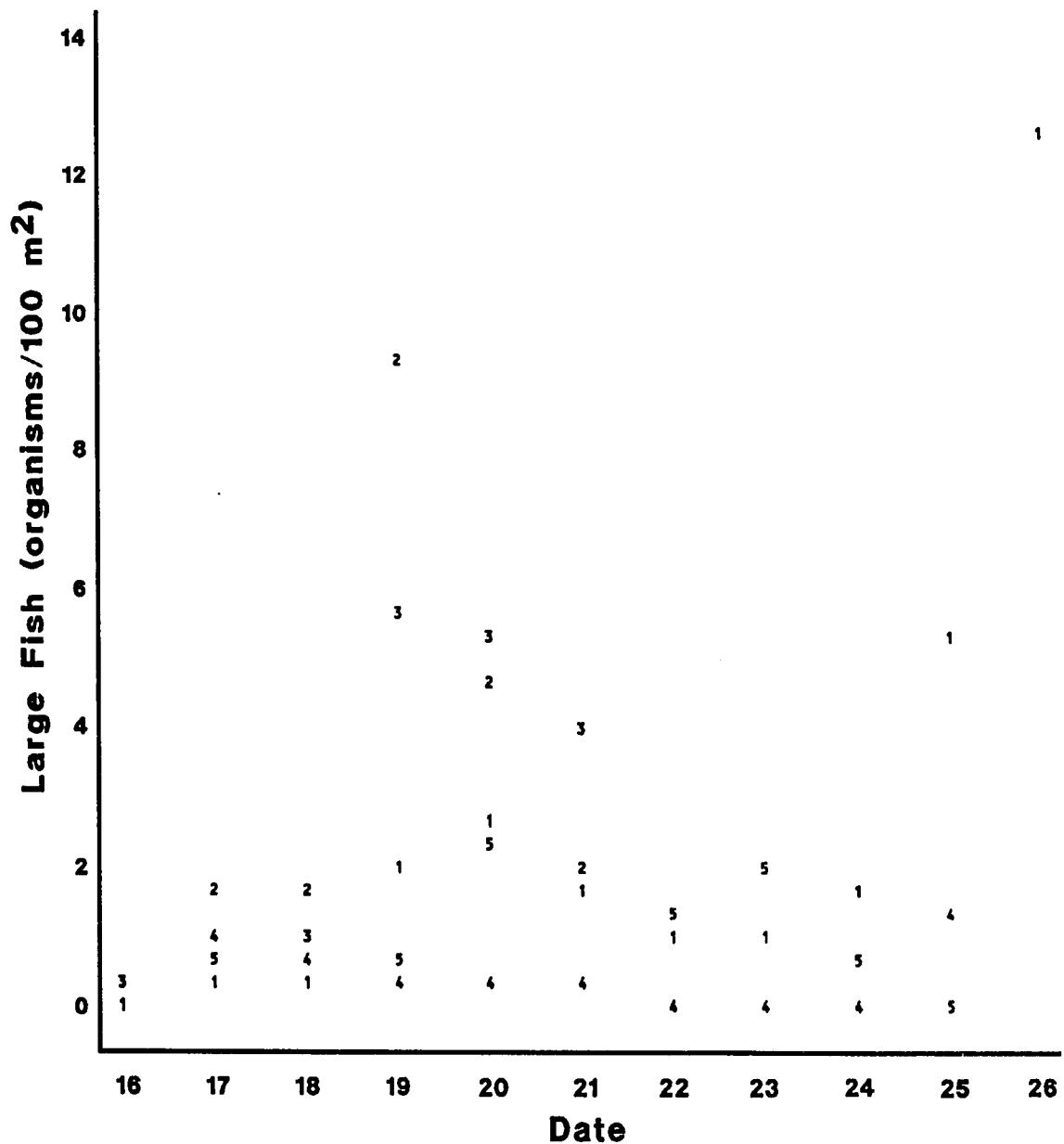


Fig. 18 Plot of small fish biomass ($100 \text{ g}/100 \text{ m}^2$) of potential aquatic prey from day prior to drawdown (day 16) to completion of all drawdowns (day 26) for Goose Gap Marsh, 1981-85. Numbers represent values for specific year (Note - 6 observations hidden).

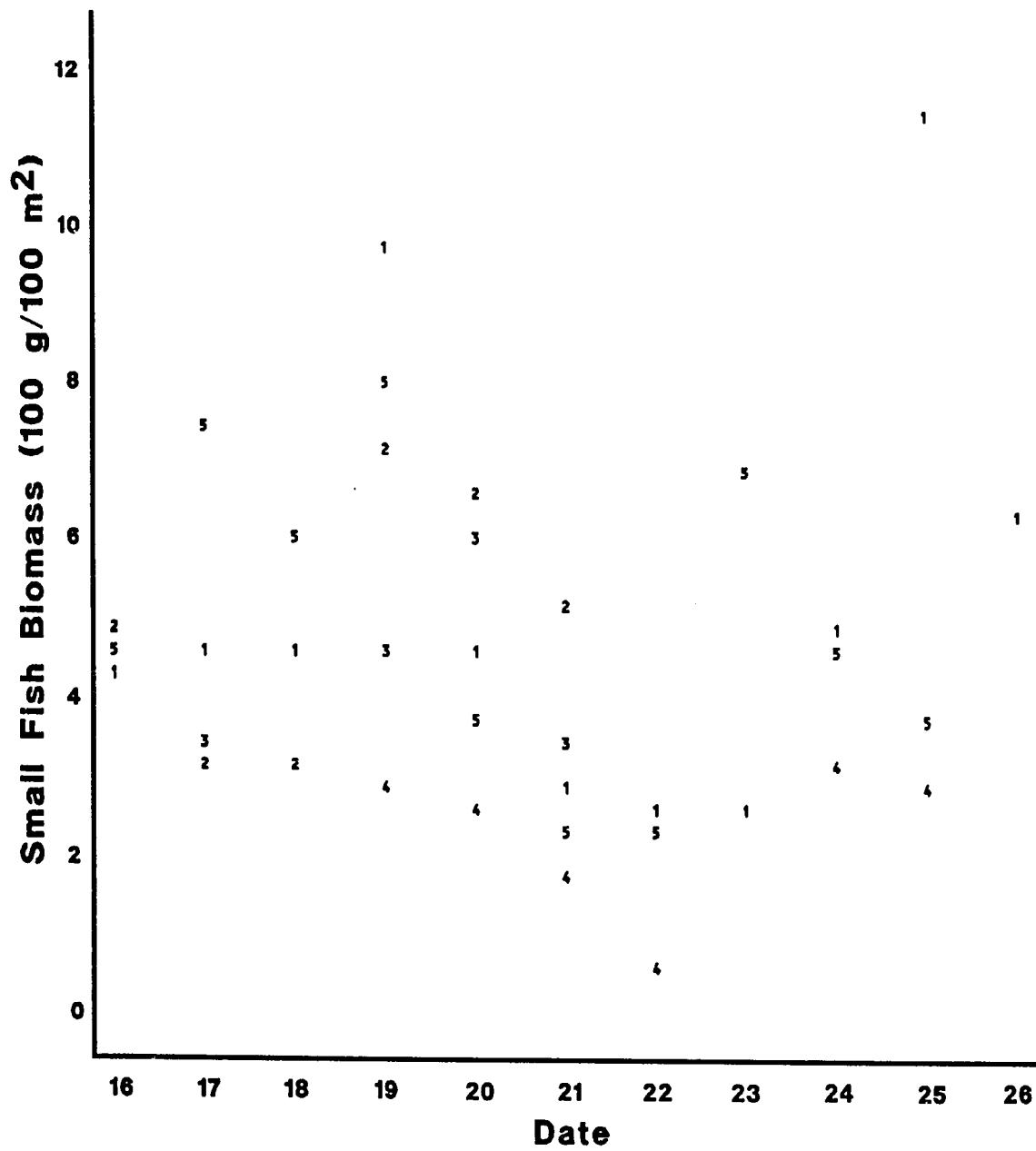


Fig. 19 Plot of small fish numbers/100 m² × 100 of potential aquatic prey from day prior to drawdown (day 16) to completion of all drawdowns (day 26) for Goose Gap Marsh, 1981-85. Numbers represent values for specific year.

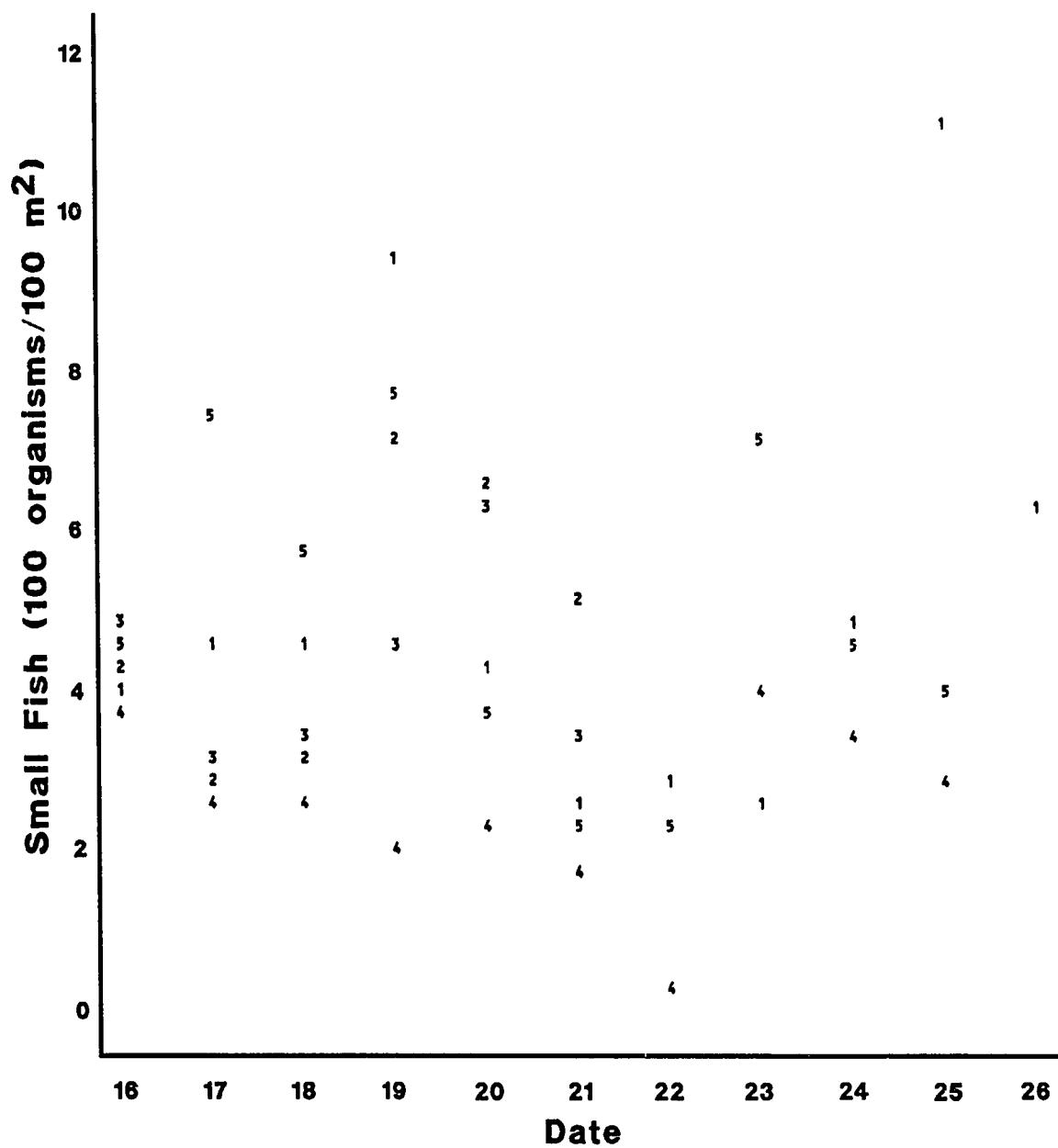


Fig. 20 Plot of tadpole biomass (g/100 m²) of potential aquatic prey from day prior to drawdown (day 16) to completion of all drawdowns (day 26) for Goose Gap Marsh, 1981-85. Numbers represent values for specific year (Note - 11 observations hidden).

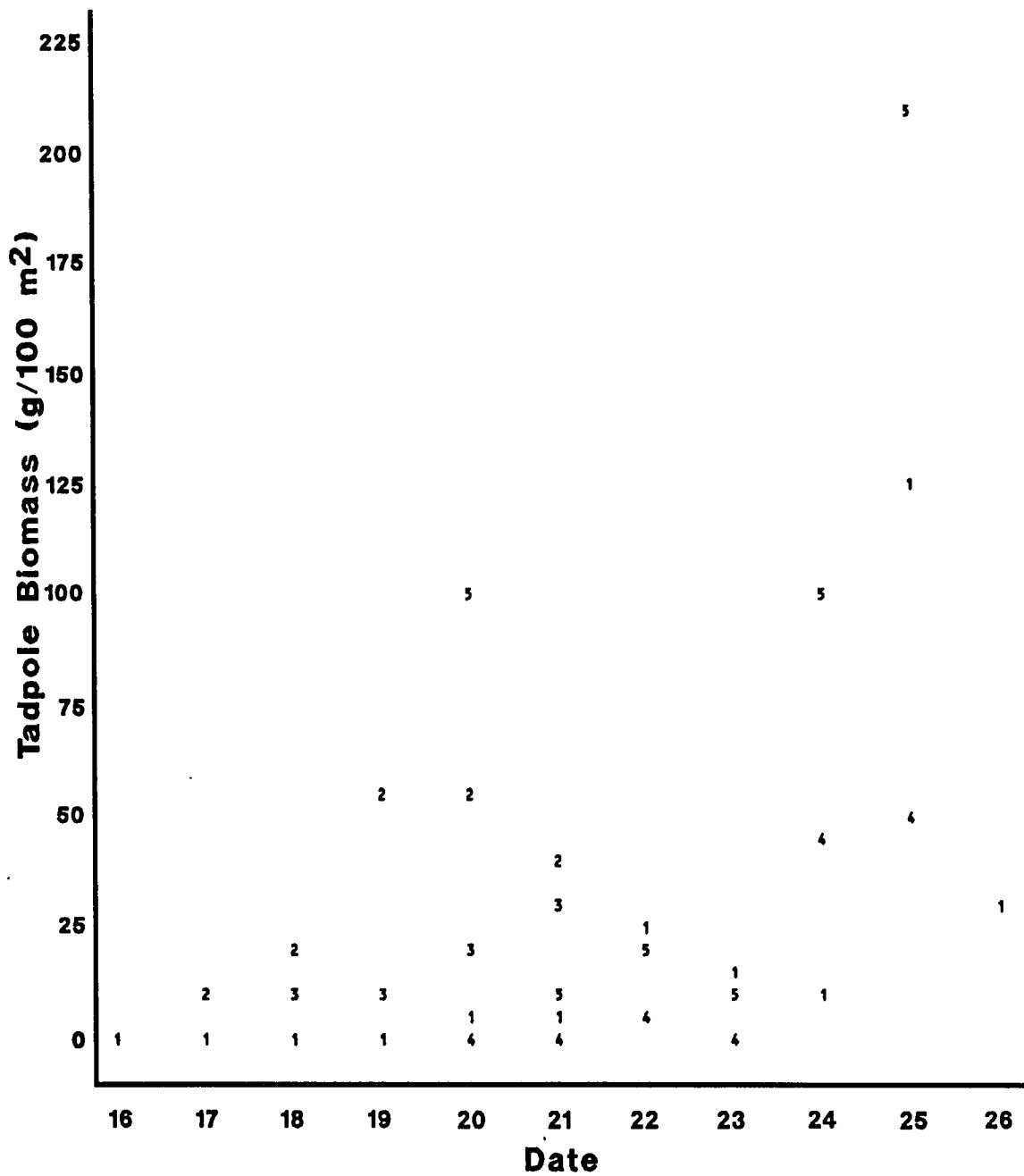


Fig. 21 Plot of tadpole numbers/100 m² of potential aquatic prey from day prior to drawdown (day 16) to completion of all drawdowns (day 26) for Goose Gap Marsh, 1981-85. Numbers represent values for specific year (Note - 14 observations hidden).

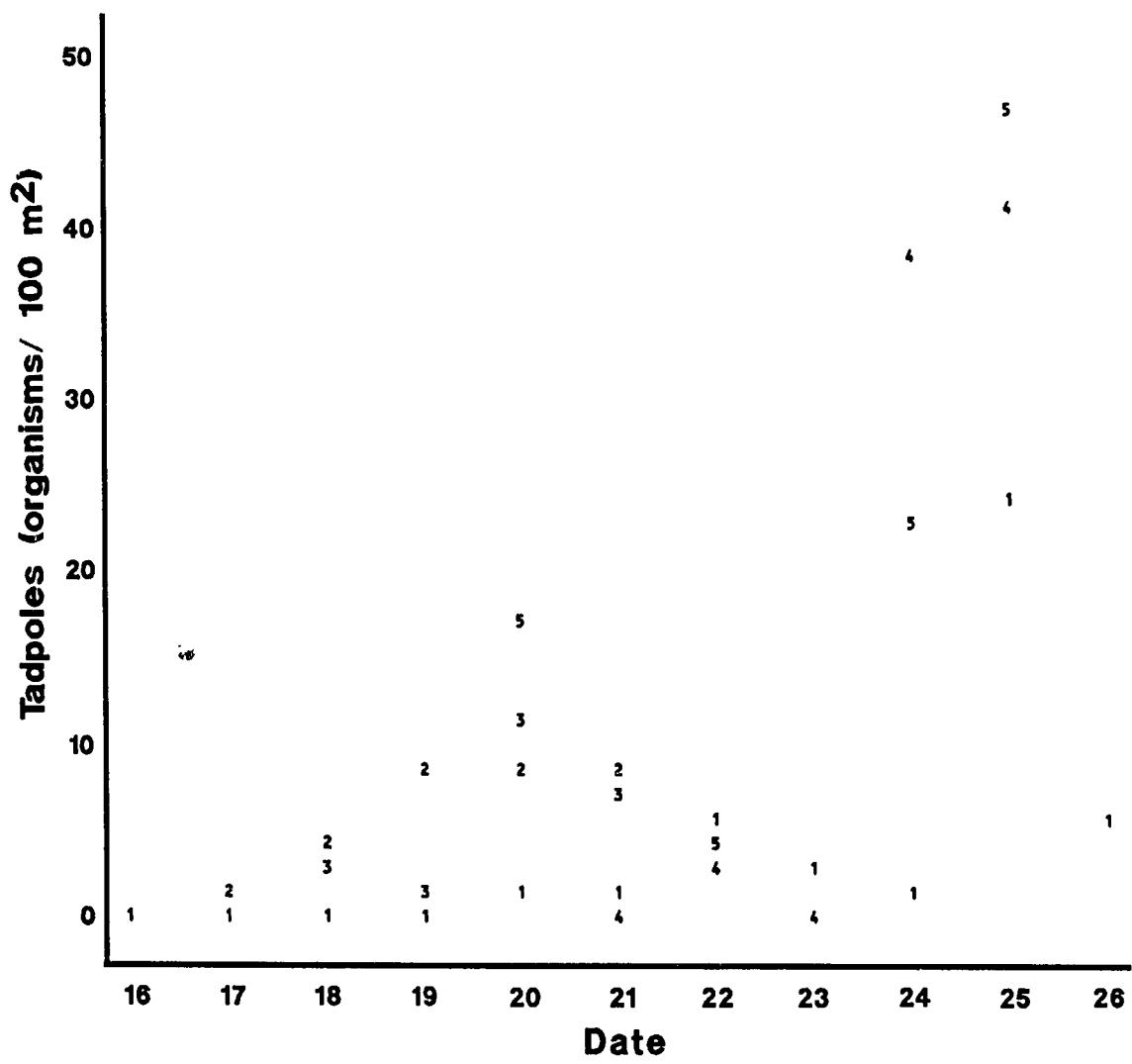


Fig. 22 Plot of crayfish biomass ($\text{kg}/100 \text{ m}^2$) of potential aquatic prey from day prior to drawdown (day 16) to completion of all drawdowns (day 26) for Goose Gap Marsh, 1981-85. Numbers represent values for specific year (Note - 8 observations hidden).

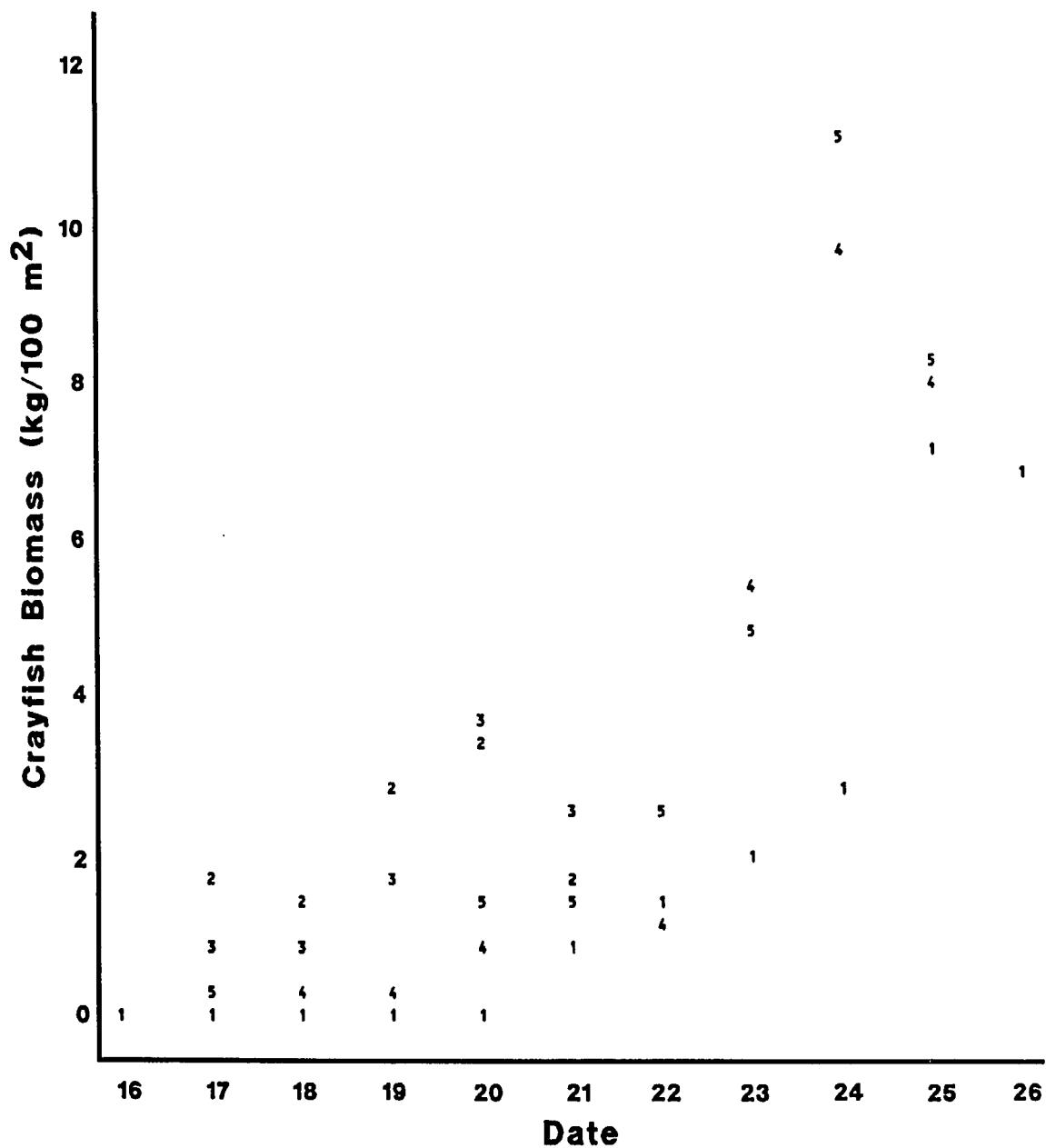


Fig. 23 Plot of crayfish numbers/ 100 m^2 $\times 1,000$ of potential aquatic prey from day prior to drawdown (day 16) to completion of all drawdowns (day 26) for Goose Gap Marsh, 1981-85. Numbers represent values for specific year (Note - 10 observations hidden).

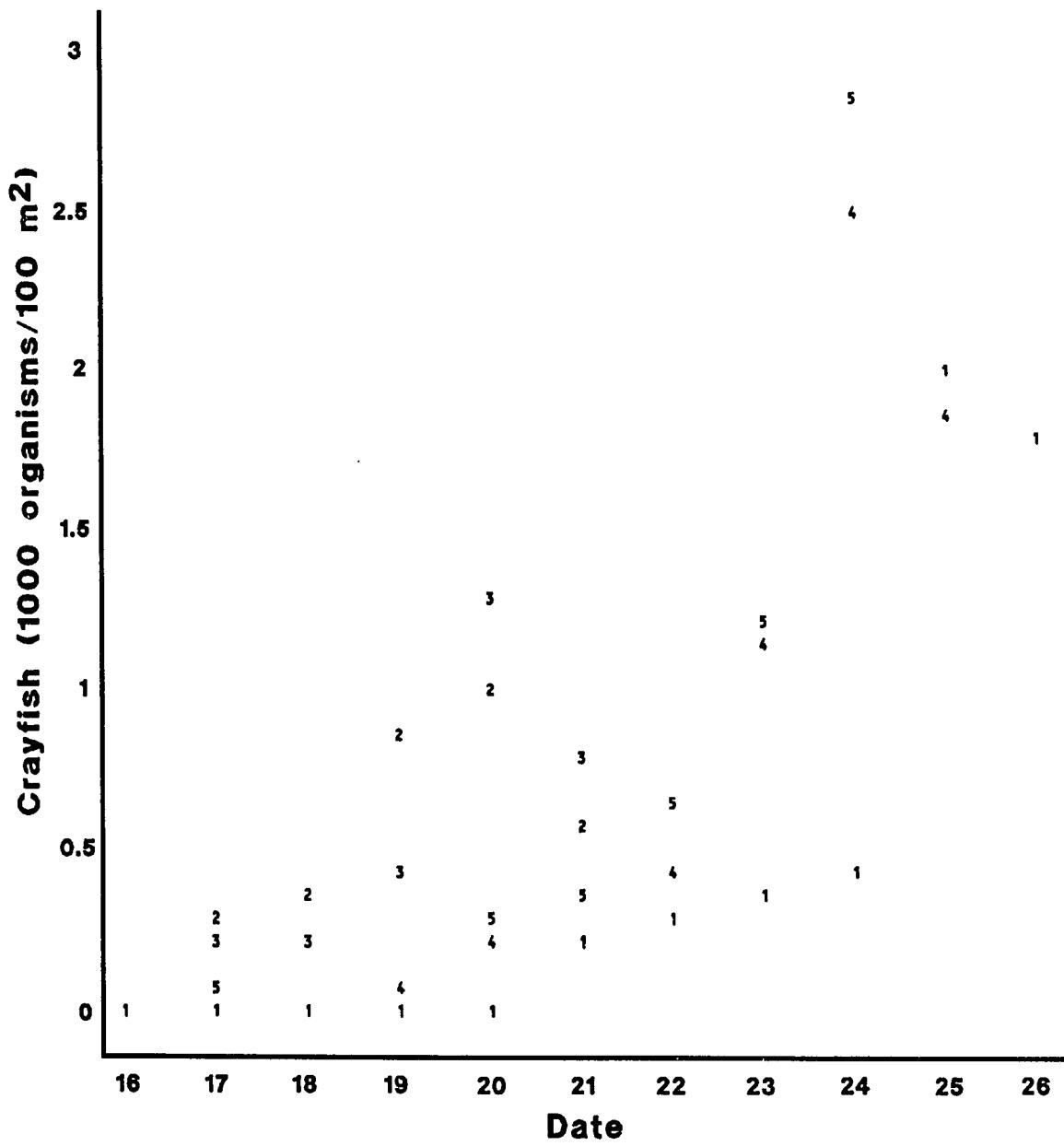


Fig. 24 Total wading bird occurrence (herons/100 ha)
1 day prior (day 16) to drawdown initiation,
during slow drawdown (data displayed as
"J"), and after completion of drawdown (data
displayed as "A") for 1981.

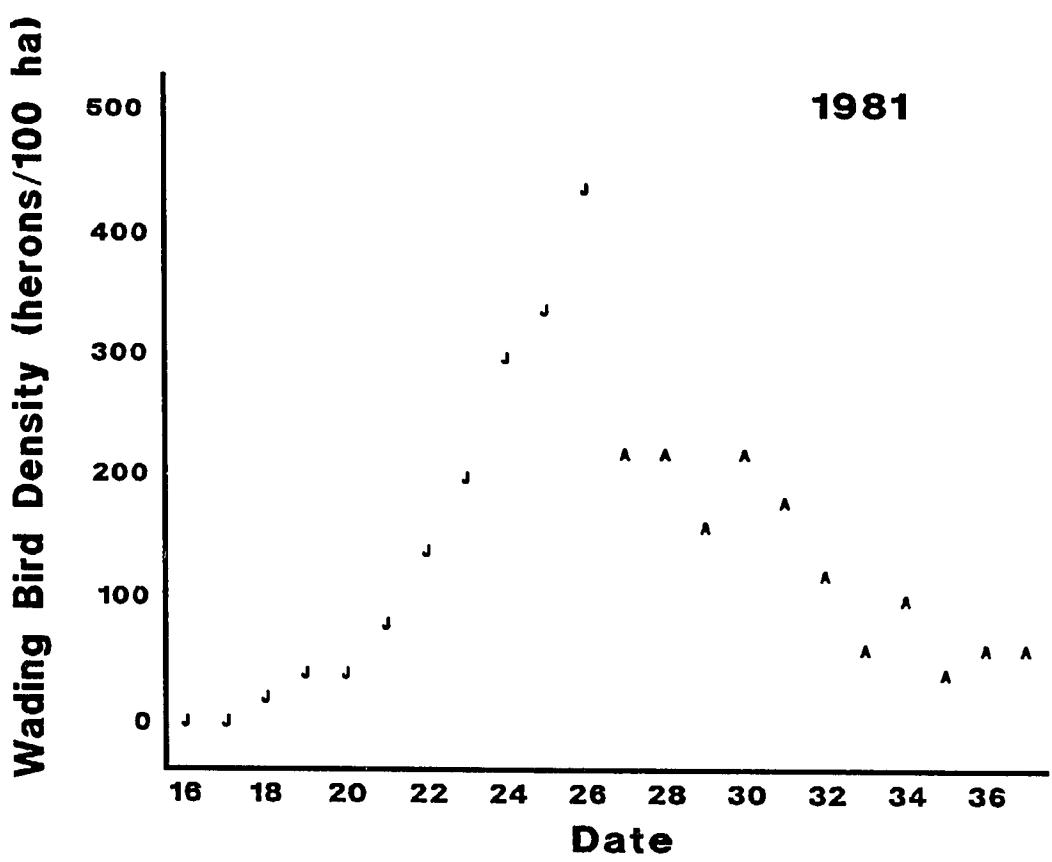


Fig. 25 Total wading bird occurrence (herons/100 ha)
1 day prior (day 16) to drawdown initiation,
during rapid drawdown (data displayed as
"J"), and after completion of drawdown (data
displayed as "A") for 1982.

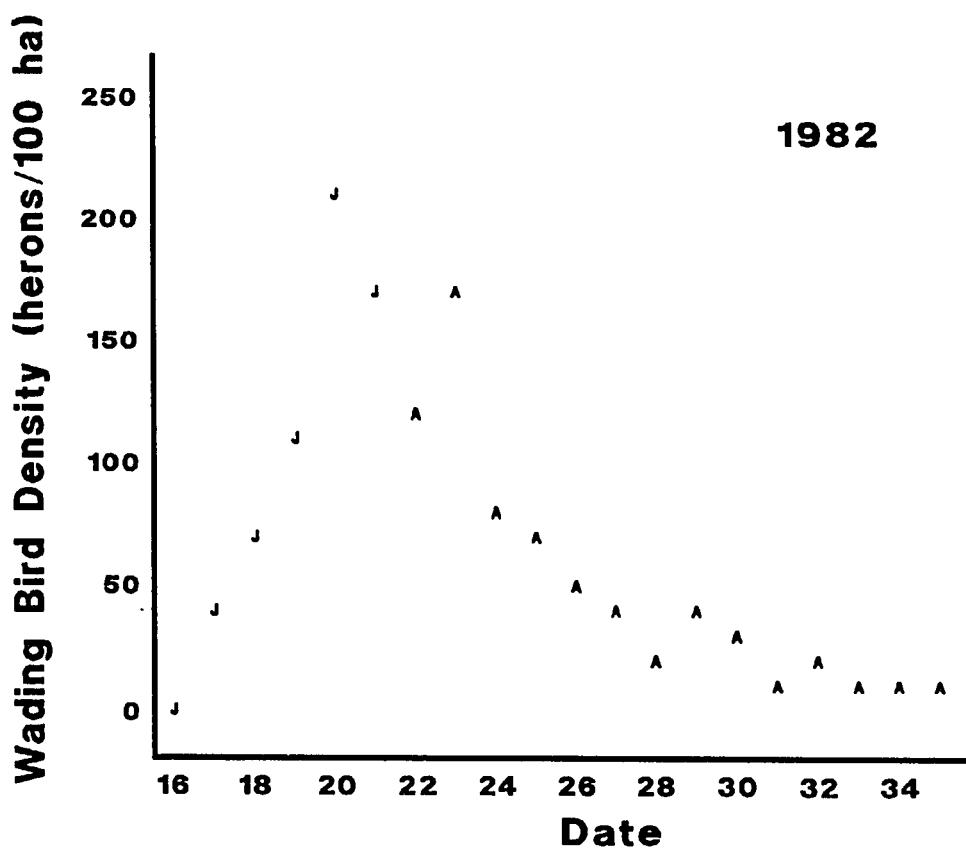


Fig. 26 Total wading bird occurrence (herons/100 ha)
1 day prior (day 16) to drawdown initiation,
during rapid drawdown (data displayed as
"J"), and after completion of drawdown (data
displayed as "A") for 1983.

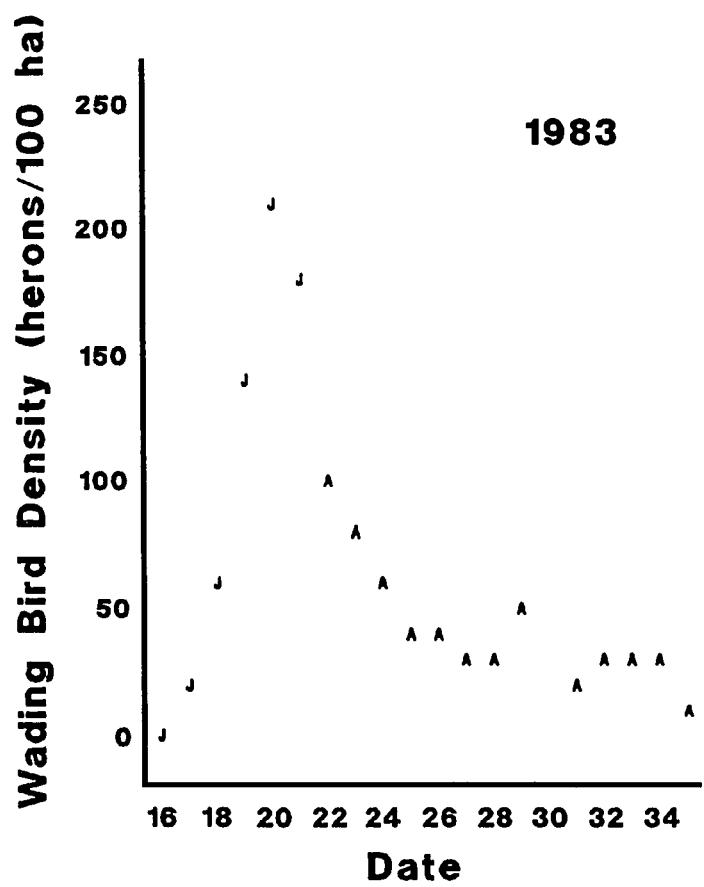


Fig. 27 Total wading bird occurrence (herons/100 ha)
1 day prior (day 16) to drawdown initiation,
during slow drawdown (data displayed as
"J"), and after completion of drawdown (data
displayed as "A") for 1984.

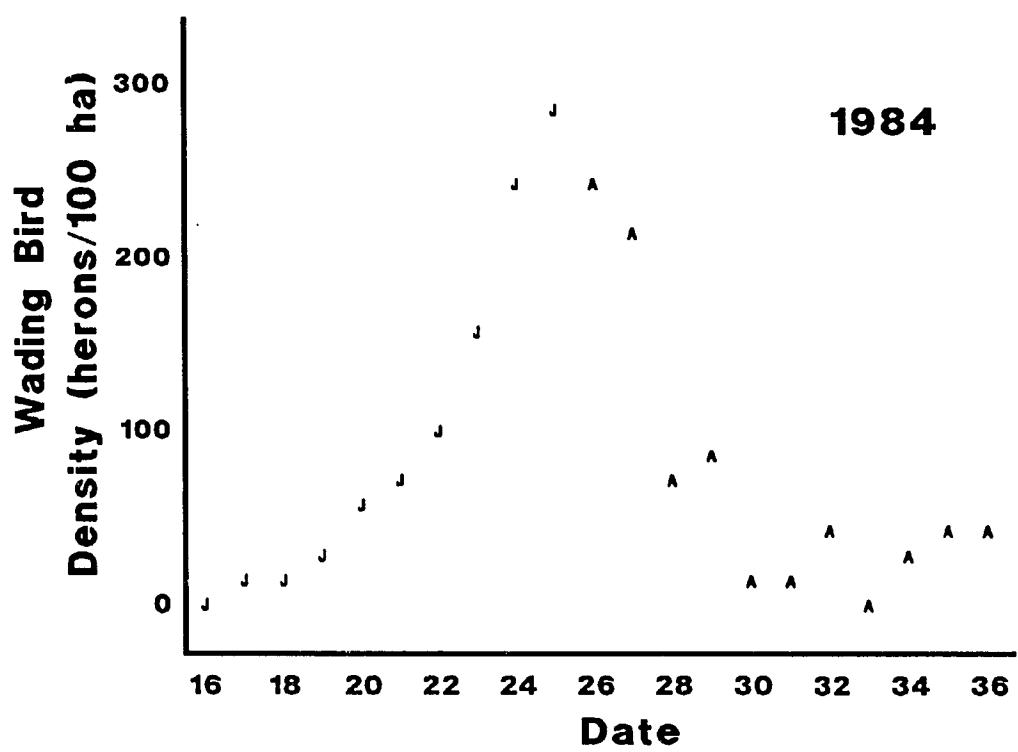


Fig. 28 Total wading bird occurrence (herons/100 ha)
1 day prior (day 16) to drawdown initiation,
during slow drawdown (data displayed as
"J"), and after completion of drawdown (data
displayed as "A") for 1985.

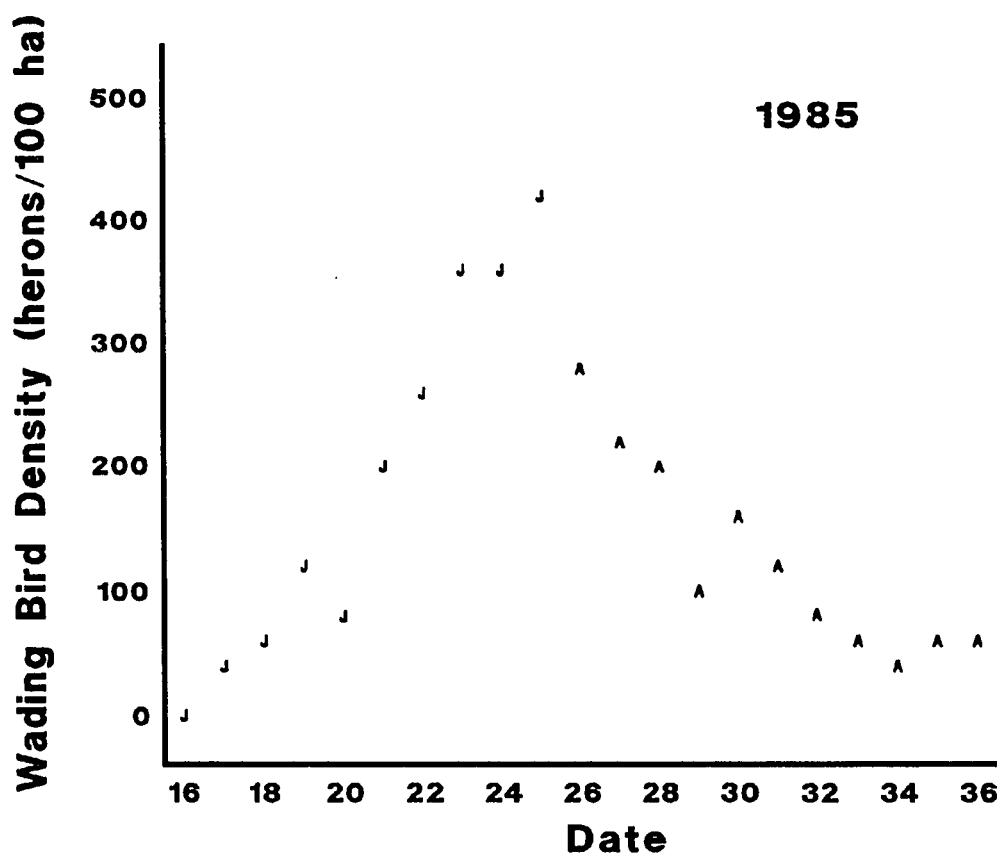


Fig. 29 Comparison of total wading bird occurrence
(herons/100 ha) 1 day prior (day 16) to
drawdown initiation, during drawdown and
after completion of drawdown for a slow
(1-1981) and rapid (2-1982) drawdown regimes.

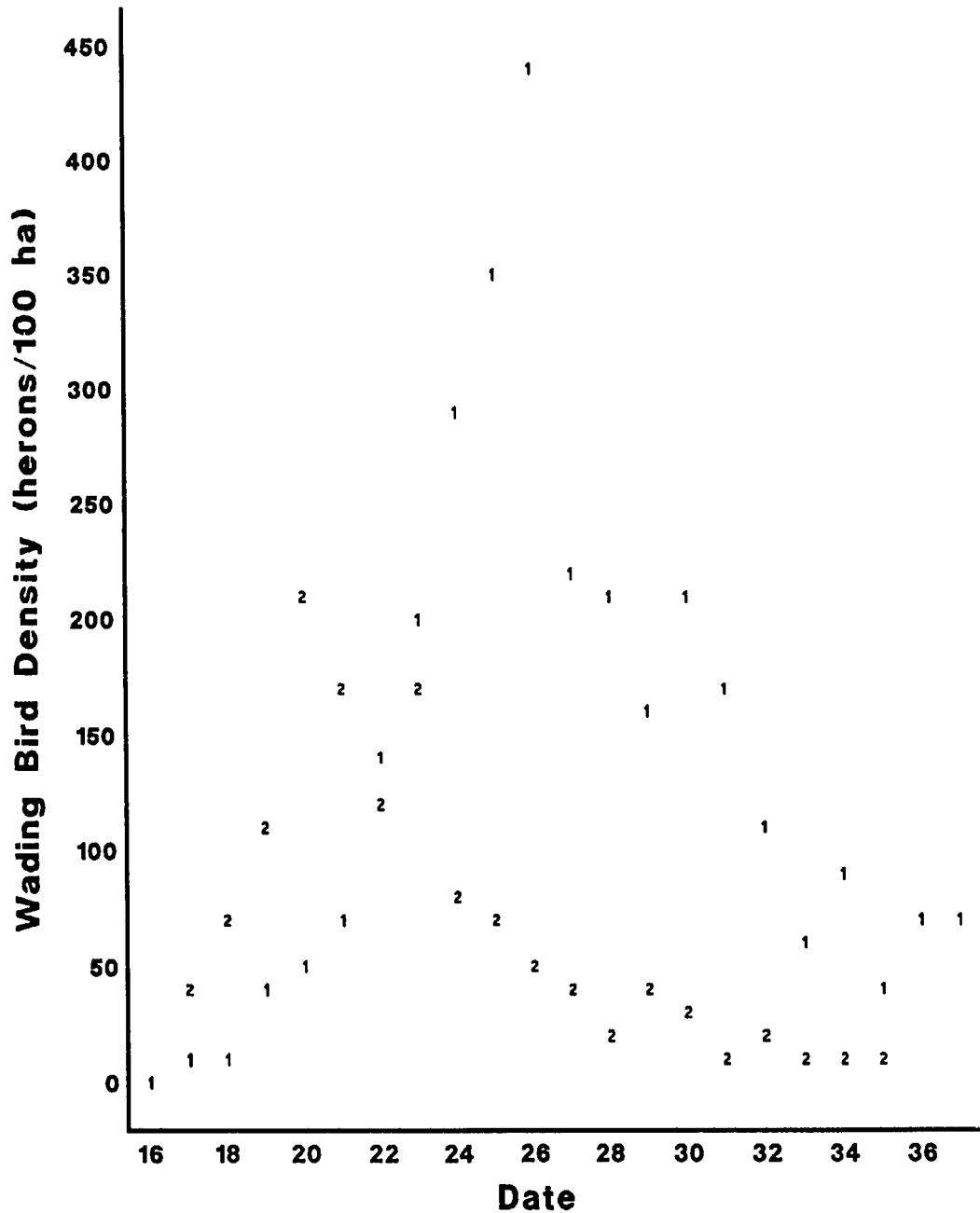


Fig. 30 Great blue heron occurrence (herons/100 ha) 1
day prior (day 16) to drawdown initiation,
during slow drawdown (data displayed as "J"),
and after completion of drawdown (data
displayed as "A") for 1981.

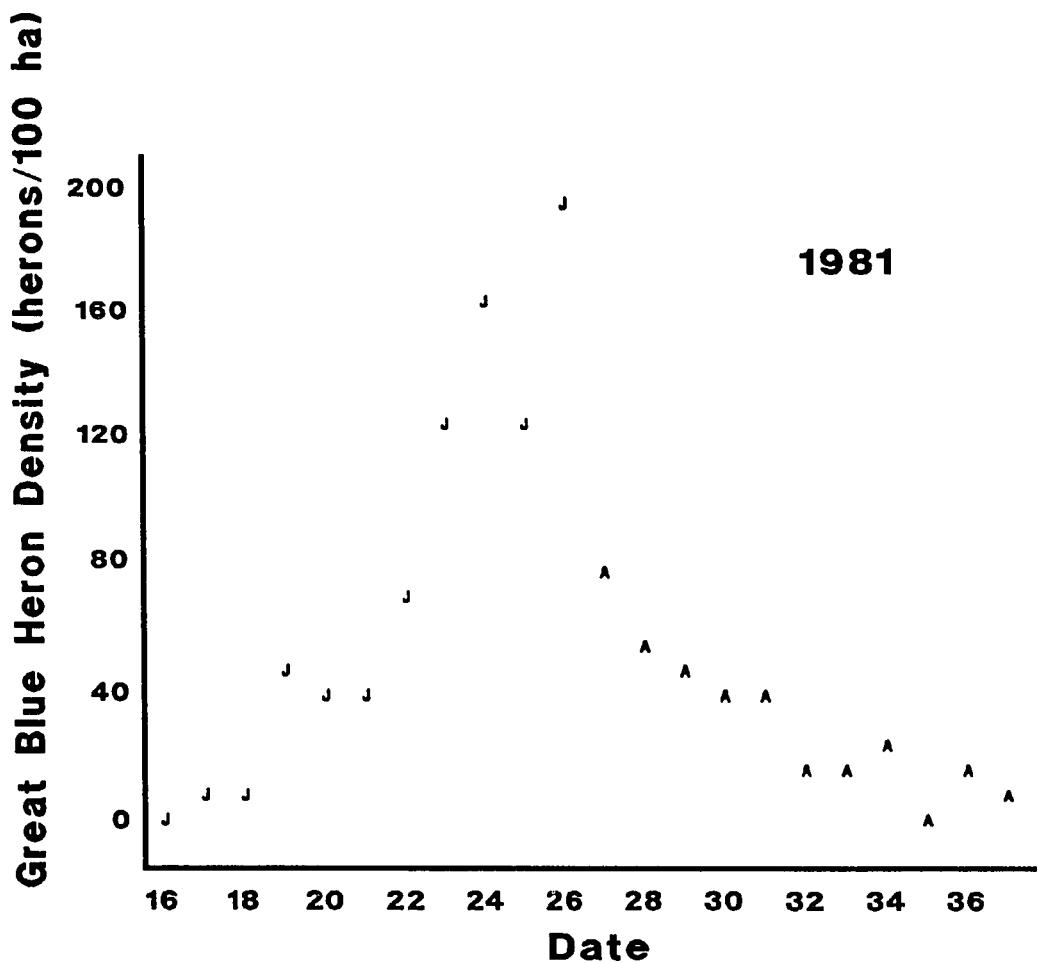


Fig. 31 Great egret occurrence (herons/100 ha) 1 day prior (day 16) to drawdown initiation, during slow drawdown (data displayed as "J"), and after completion of drawdown (data displayed as "A") for 1981.

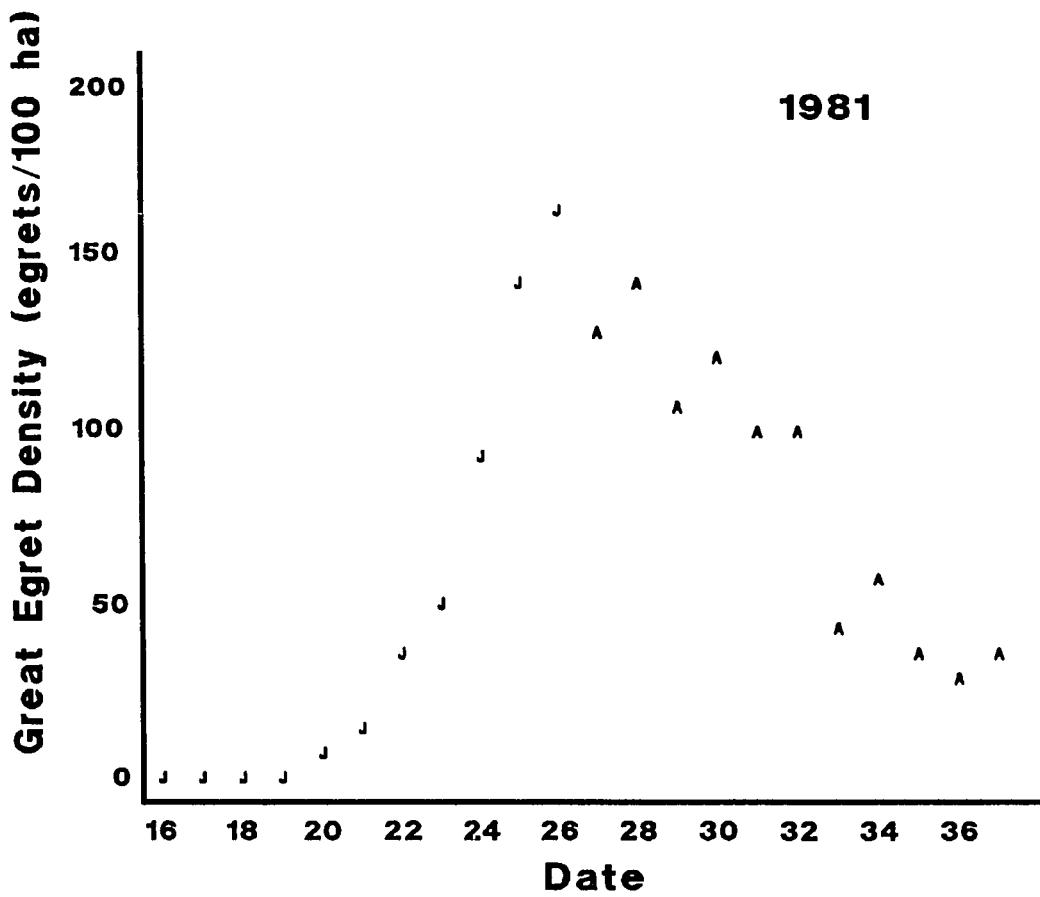


Fig. 32 Yellow-crowned night-heron occurrence
(herons/100 ha) 1 day prior (day 16) to
drawdown initiation, during slow drawdown
(data displayed as "J"), and after completion
of drawdown (data displayed as "A") for 1981.

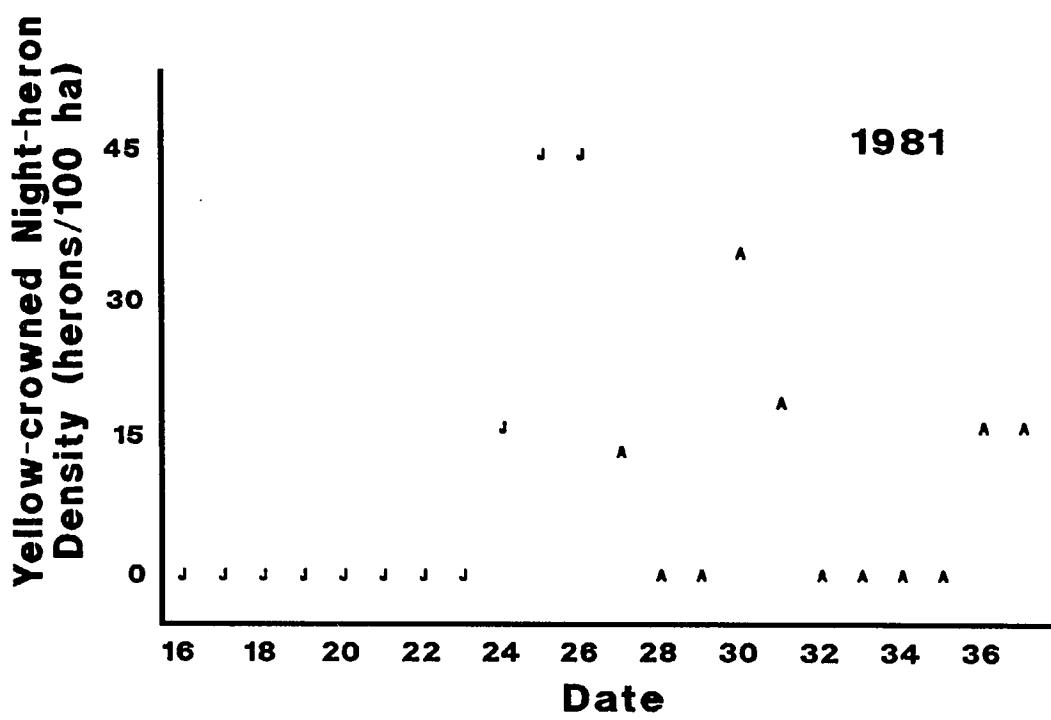
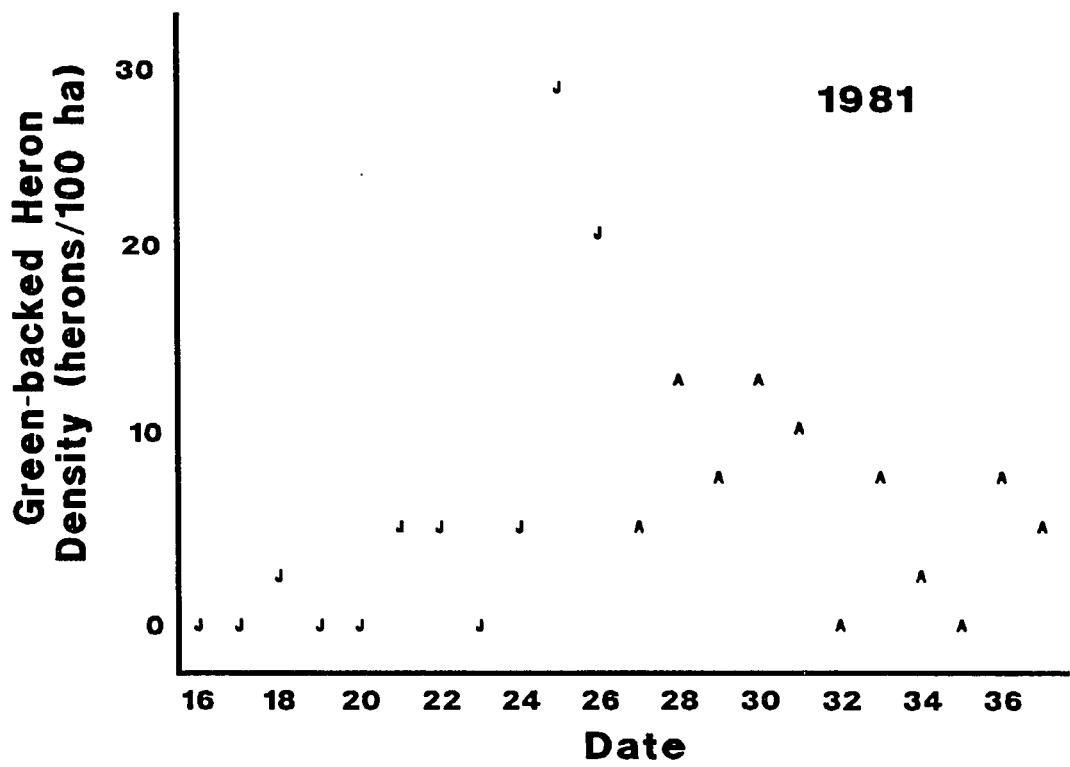


Fig. 33 Green-backed heron occurrence (herons/100 ha)
1 day prior (day 16) to drawdown initiation,
during slow drawdown (data displayed as "J"),
and after completion of drawdown (data
displayed as "A") for 1981.



CHAPTER VI

HABITAT PREFERENCE FOR WATERBIRDS: TED SHANKS WILDLIFE AREA AS A CASE STUDY OF MANAGED FLOODPLAIN WETLANDS

Historically, the hydrologic patterns of the Mississippi River created vast wetlands in the floodplain. This floodplain increased in size along the river's course and in response to watershed inputs and major flooding events. A diversity of temporary, seasonal and semi-permanent water bodies was formed and destroyed in relation to the river's water regime. These dynamic palustrine wetlands are among the most productive of all habitat types in the world (Odum 1979), and many species of waterbirds have adapted life history strategies to exploit these productive wetlands. Unfortunately, man has drastically altered this riverine system over the last 150 years. Channel constriction through wing dikes, revetments and high mainstem levees resulted in higher flood peaks than occurred under pristine conditions despite reduced discharge (Belt 1975). This artificial constriction cut off natural floodplains from the river channel. Under natural flooding conditions, the Mississippi River eroded both banks and bottom, and then spilled into its natural reservoir, the floodplain. Man-made navigational works and channel-constricting levees have forced the Mississippi River out of

its dynamic hydrologic regime that was established at the termination of the last glacial retreat (Belt 1975). As levee districts initiated drainage projects, floodplains were converted to agriculture. Man's modifications to other large river systems of North America are equally devastating to floodplain habitats, as examples from the Illinois and Missouri River systems demonstrate (Havera and Bellrose 1985, Hesse et al. 1989). Intensive agriculture, combined with urban and industrial developments, has eliminated widespread wetland area and only small patches of floodplain wetlands exist today. Many remaining floodplain wetlands lack dynamic water regimes, lack direct input from the river, and are isolated from other wetlands.

Much of the remaining wetland habitat of the Upper Mississippi Valley exists in public ownership, where nearly 0.5 million ha has been acquired between Minneapolis and Memphis (Reid et al. 1989). Although several waterbirds formerly nested in emergent wetlands in the floodplains of the Mississippi River (Widmann 1907, AOU 1983), most species use these habitats when migrating. Migration is an adaptive trait that allows waterbirds to exploit seasonal resources in fluctuating temperate or arctic environments (Weller 1975, Myers et al. 1987). Several species of special concern, such as king rail, least bittern, and American bittern (MDC 1984), now breed in remnant, floodplain wetlands. By gaining insights into the habitat use patterns of waterbirds, implications for water and vegetation management

decisions may be drawn. Two families for which micro-habitat use patterns are poorly known are the Rallidae and Ardeidae. Comparison of general habitat use among species in response to patterns of potential prey densities and duration of water drawdown may elucidate management options to increase foraging opportunities. These data collected from a restored, managed floodplain indicate micro-habitat segregation by the small-sized rails across a cline of water depth. The extremes of micro-habitat preference suggest that neither migrant rails nor migrant bitterns use seasonal wetlands with water depths deeper than 44 cm, and rails do not use water depths deeper than 31 cm during fall migration. These depths provide quantified extremes for habitat use that managers might consider for the deepest portions of managed wetlands for these species.

The importance of saturated soils or very shallow water depths is demonstrated for king rail nest site selection. No nests were constructed over water deeper than 22 cm and most nests were located at much shallower sites ($x < 8$ cm). Nest success was significantly related to water depth and distance to open water among structural characteristics of the habitat. Location of a nest within a management unit appears most important in predicting nest success. King rail nests constructed in borrow ditches, in wetlands during drawdowns, or within 3 m of any managed unit edge were far more likely to be destroyed than nests constructed in the interior of a managed unit that was not drawndown during the

nesting period. Man-impacted wetland area and travel lanes for predators, such as earthen dikes or drying borrow ditches, have been implicated in avian nesting failure in prairie wetlands (Peterson and Cooper 1987). Data from glacial marshes suggest that preservation of marshes in the 20-30 ha size class is most efficient in supporting bird species, but nest success was not specifically measured in that investigation (Brown and Dinsmore 1986). These relationships suggest that small wetland units or units with large shoreline development that yield greater "edge" area may produce greater king rail nest failures than larger block wetlands. Fragmentation of habitats can adversely affect nest success for avian species in forested or herbaceous habitats through increased predation (Wilcove 1985, Burger 1988). In the case of the Ted Shanks Wildlife Area (TSWA), if 4-5 semi-permanent wetlands (15-40 ha in size) with perennial vegetation are flooded shallowly (0-20 cm) and are not artificially drained during the nesting period (peak May-June), these wetlands should support the current king rail nesting population.

Without quality foraging areas, chick survival would be poor for this semi-precocial species. Shifts in micro-habitat use across the king rail breeding period may be one means to select for increased foraging opportunities. Preference for more open mudflat micro-habitats may allow adults and juveniles to forage on concentrated invertebrate prey in drying swales. Because of the importance of animal

prey, water sources should be kept free of toxicants, especially pesticides (Grue et al. 1988). The foraging territory during the brood period is restricted in size because both adult and juvenile rails are flightless. Allowing small depressions to naturally dry during the brood period may more closely mimic floodplain conditions to which king rails responded historically.

Reducing water levels through drawdown provided a breadth of micro-habitat conditions so that seven species of wading birds could forage in the same wetland. Flocking by wading birds is an adaptation to finding abundant, but patchy food resources (Willard 1977, Kushlan 1978). Duration of drawdown determined the creation and longevity of several of these micro-habitats, as is suggested by the differential species' responses after drawdowns began. Long drawdowns, rather than short, rapid drawdowns, may more closely mimic drying floodplain wetlands. Reduced flocking at a specific floodplain wetland during flooding of the Mississippi River suggests the importance of a mosaic or complex of wetland types. For the wading birds using the TSWA the "complex" or functional group of wetlands consists of 16 managed, seasonally flooded or semi-permanent wetlands, forested sloughs and backwaters on the river. During regional drought periods, when riverine wetlands are unavailable, controlled drawdowns of managed wetlands may be most important for breeding populations of wading birds. If several wetland management units are drawdown sequentially,

micro-habitat characteristics can be provided for an array of wading bird species across the entire breeding period. For TSWA, a complex of 5-6 wetlands (10-40 ha in size) drained sequentially between late May to late July could support most of the breeding wading bird populations currently using the area. Natural drying of semi-permanent wetlands in August would provide habitat for post-breeding wading birds.

A series of sequential drawdowns in early to mid-summer can produce desired annual plants for migrant waterfowl (Fredrickson and Taylor 1982) and summer foraging habitat for wading birds. Nesting and foraging habitats for king rails demand more semi-permanent than seasonal water regimes. If preservation of this unique species is a priority, then 4-5 semi-permanent wetlands should not be artificially drained. Natural drying of swales in July and August will provide foraging sites. Restoration of agricultural fields, both on and adjacent to TSWA, to seasonal wetlands will provide more habitat for wading birds, whereas, allowing these fields to convert to shallow, semi-permanent wetlands will provide more habitat for rails and bitterns. These modifications must be weighed against habitat priorities for waterfowl and shorebirds. The TSWA is large enough to provide a complex of herbaceous and forested wetlands within a given refuge system. Man's modifications to the floodplain wetlands of the Mississippi River, and other large river systems of North America, has

greatly reduced the options available for habitat use by migrating and breeding waterbirds. Restoration of wetland complexes in modified floodplains is a necessary management priority for North American waterbirds.

Future Research

Although patterns of micro-habitat use are here described for migrant rails and bitterns, the specific strategies of nutrient acquisition before and during reproduction are unknown. American coots, the largest of North American rallids, store all lipids required for egg production as reserves prior to arrival on breeding grounds (Alisauskas and Ankney 1985). This suggests that the condition of wintering or migrational habitats directly influences whether a coot will nest and the size of her clutch (Alisauskas and Ankney 1985). The patterns of nutrient acquisition for rallids probably represent a cline in strategies, as is seen in waterfowl (Krapu and Reinecke in press), but specific energetic conditions must be documented.

With a pattern for micro-habitat use across migrational and breeding periods now described for king rail, this pattern should be related to the energetic cycle of reproduction. Specific foraging activity patterns of king rails and nutritional value of foods could be compared against energetic patterns of breeding males and females. Timing in the development of foraging could be compared among siblings, among broods, and among individual chick

survival. How size, isolation, and configuration of management units or natural swales impact nesting success or juvenile survival needs further elucidation both for king rails and other waterbirds (Brown and Dinsmore 1986).

Controlled drawdowns in managed floodplain wetlands offer the advantage in experimental design of (relatively) predictable timing and duration of declining water levels. How closely these controlled drawdowns mimic natural drying patterns in floodplains needs further investigation. Comparison of habitat use in isolated floodplain wetlands versus a complex of wetlands should be conducted for breeding and migrant waterbirds.

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APPENDIX

BOX PLOTS OF POTENTIAL PREY AT KING RAIL FORAGING SITES (After Chapter 4)

Figs. 34-51, graphical representation of macroinvertebrate and fish densities at king rail foraging sites during migration, nesting and brooding periods.

Fig. 34 Total potential prey (individuals/m³ x 10,000) at king rail foraging sites during migrational and breeding periods. Periods include: spring migration, nesting/incubation, young brood, old brood, separate young, and fall migration.

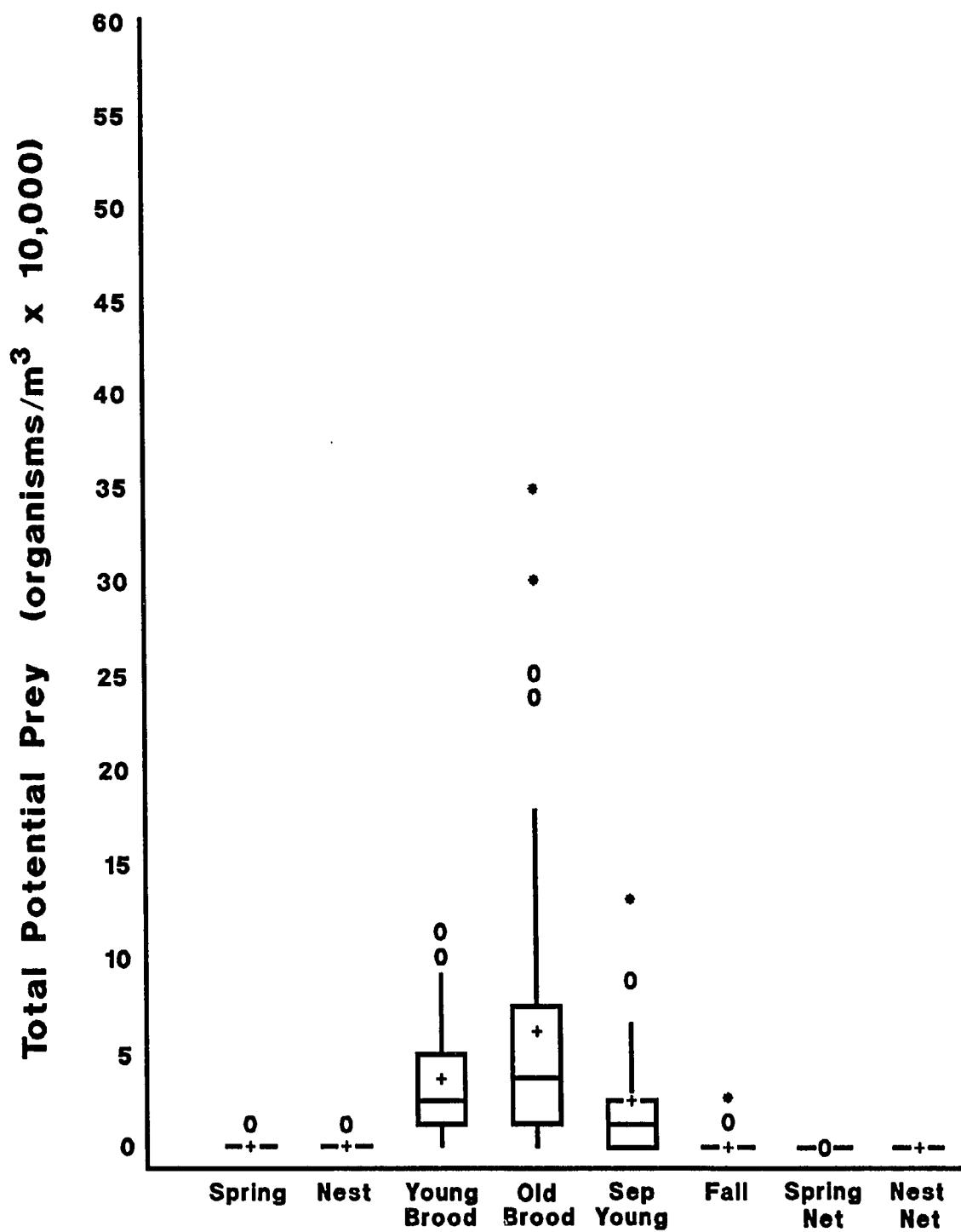


Fig. 35 Total macroinvertebrates (individuals/m³ x 100,000) at king rail foraging sites during migrational and breeding periods. Periods include: spring migration, nesting/incubation, young brood, old brood, separate young, and fall migration.

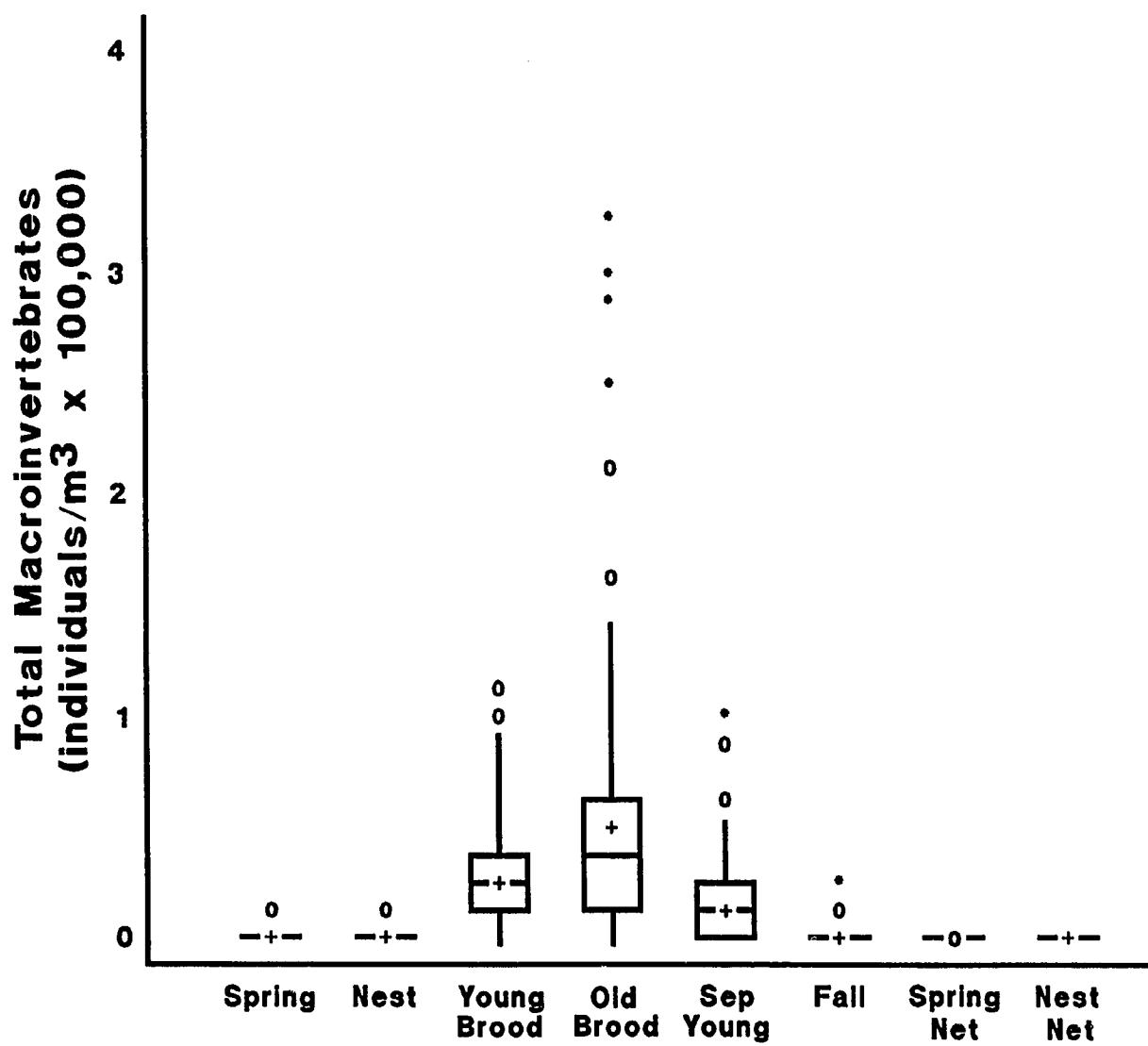


Fig. 36 Diversity of potential prey (taxon at order level/core or net sample) at king rail foraging sites during migrational and breeding periods. Periods include: spring migration, nesting/incubation, young brood, old brood, separate young, and fall migration.

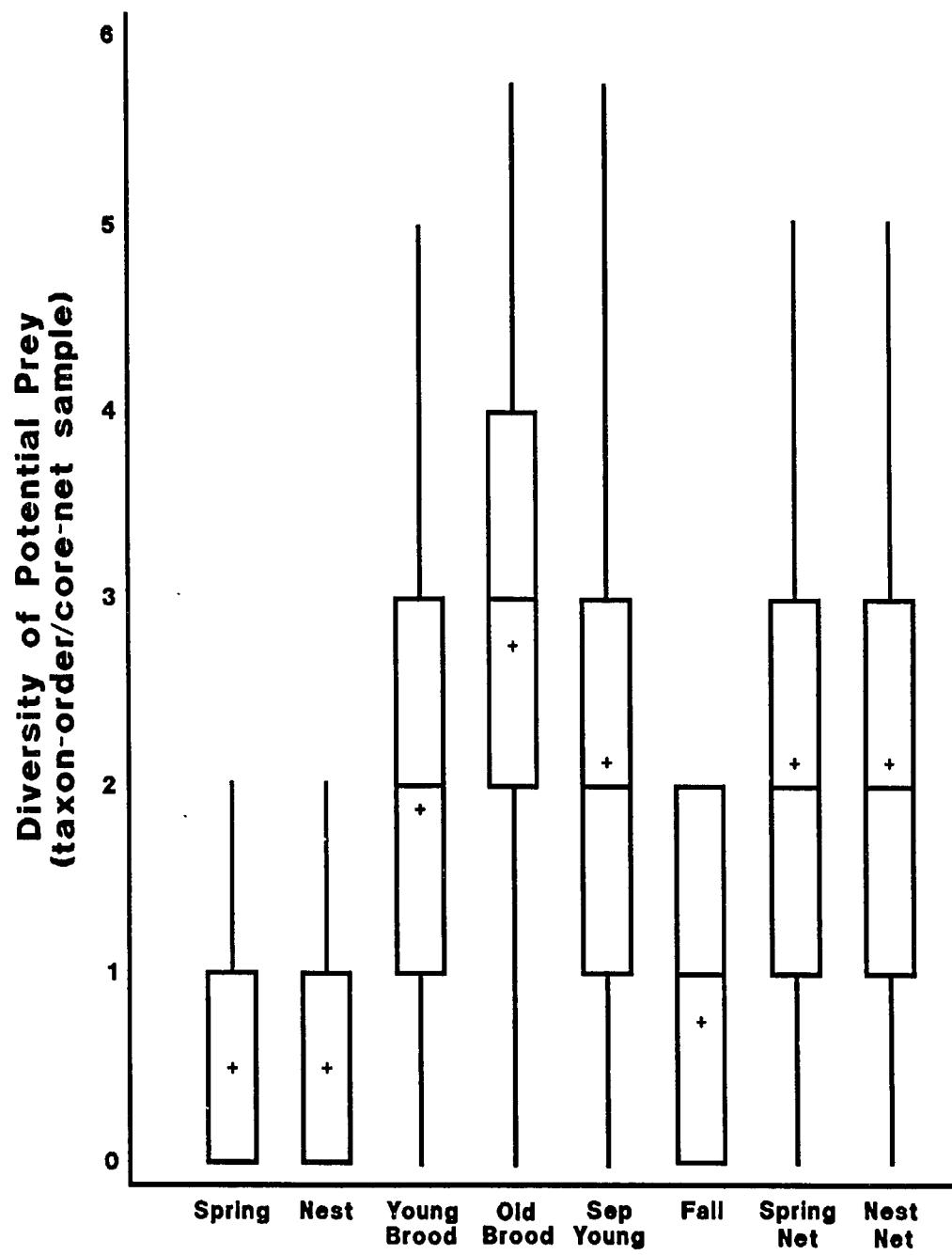


Fig. 37 Total freshwater oligochaetes
(individuals/m³ x 10,000) at king rail
foraging sites during migrational and
breeding periods. Periods include: spring
migration, nesting/incubation, young brood,
old brood, separate young, and fall
migration.

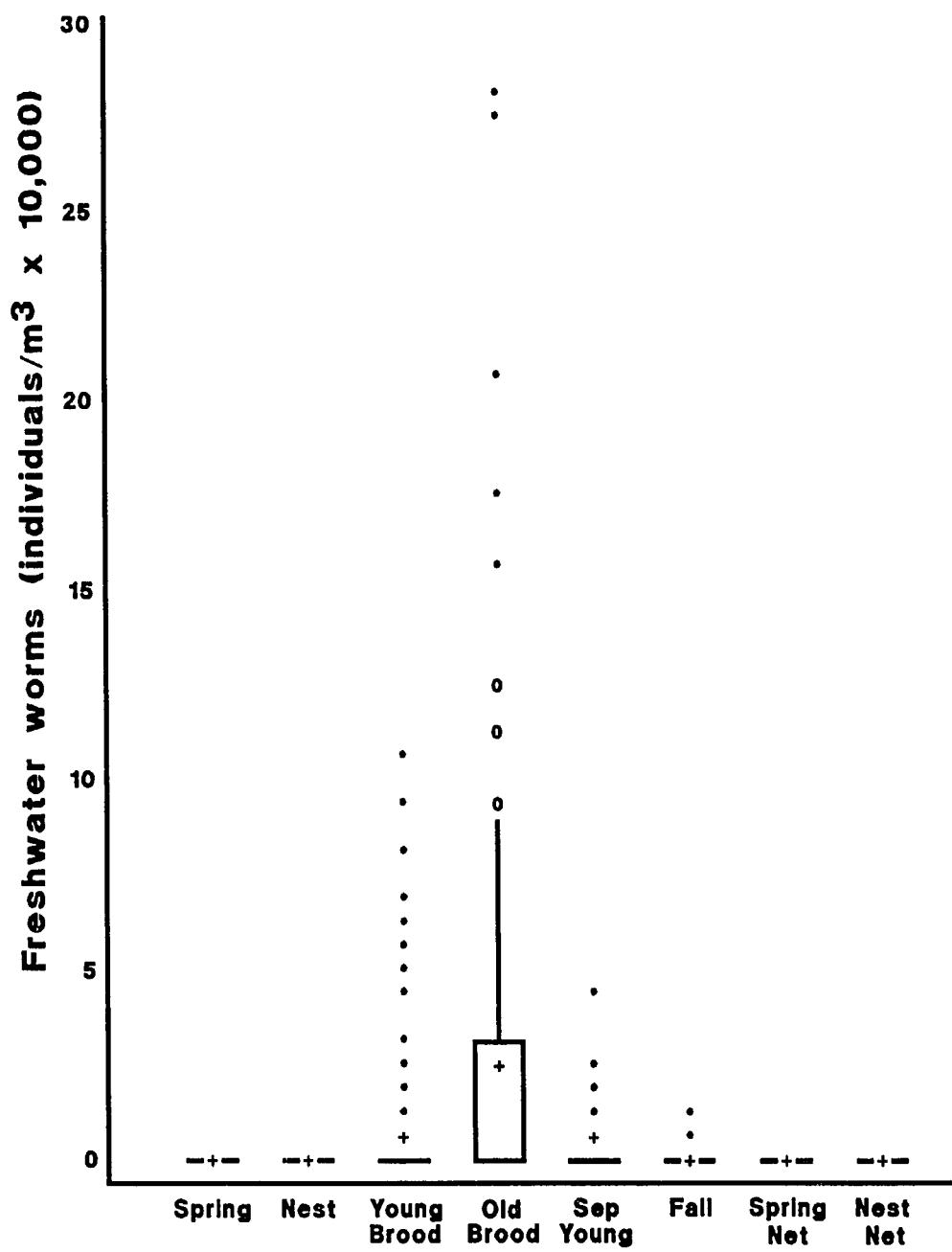


Fig. 38 Total leeches (individuals/m³ x 1,000) at
king rail foraging sites during migrational
and breeding periods. Periods include:
spring migration, nesting/incubation, young
migration.

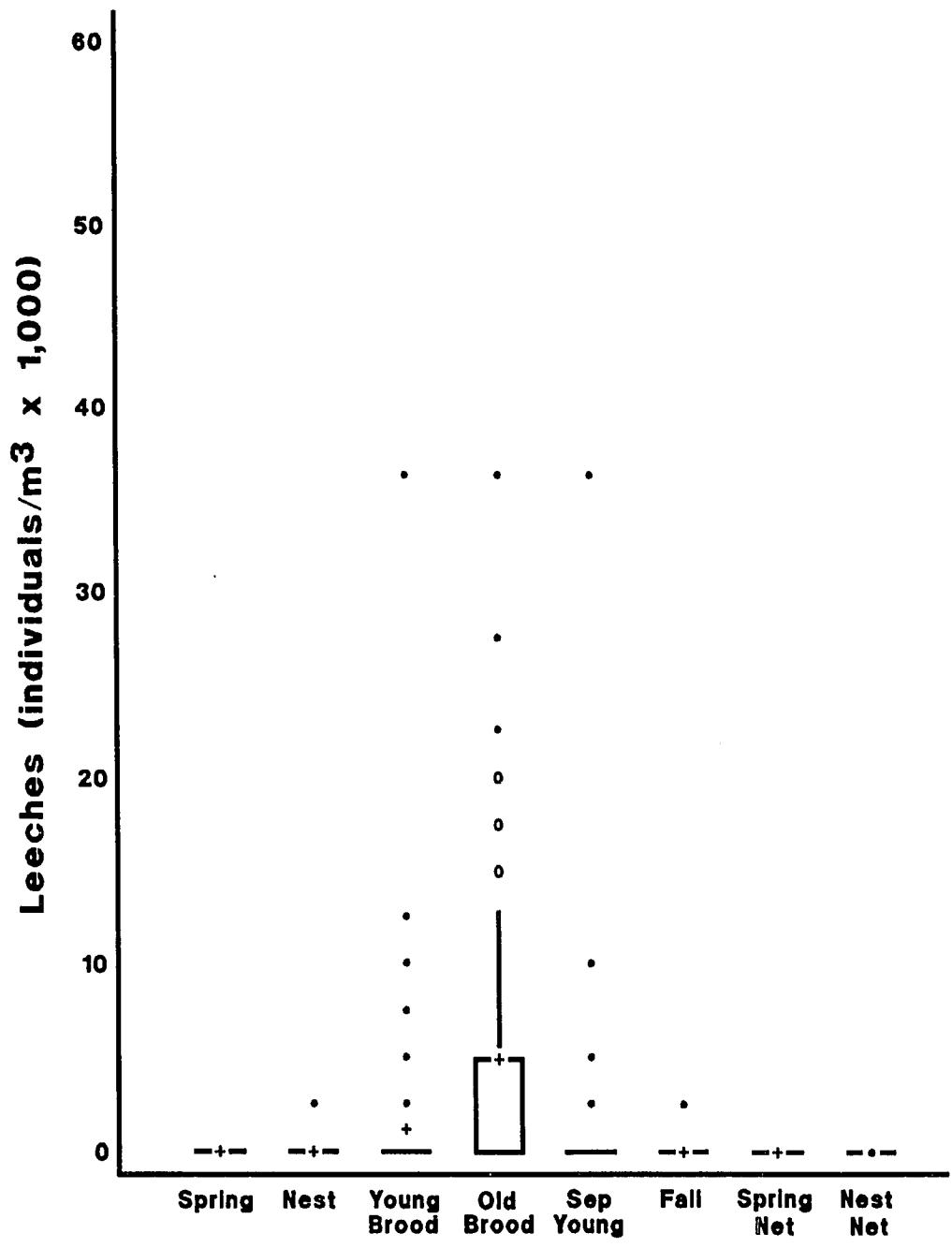


Fig. 39 Total snails (individuals/ m^3 \times 10,000) at king rail foraging sites during migrational and breeding periods. Periods include: spring migration, nesting/incubation, young brood, old brood, separate young, and fall migration.

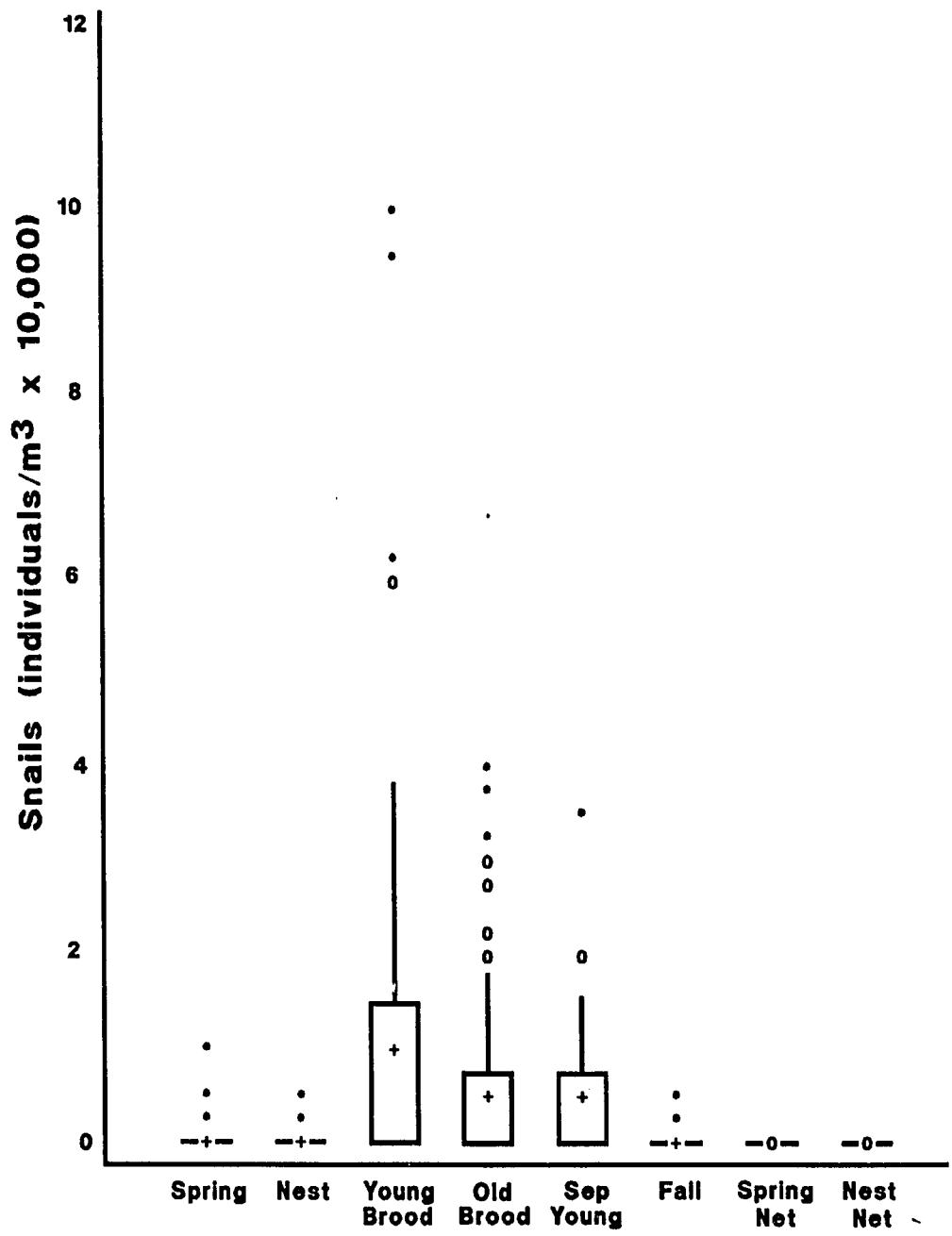


Fig. 40 Total aquatic beetles (individuals/m³ x 10,000) at king rail foraging sites during migrational and breeding periods. Periods include: spring migration, nesting/incubation, young brood, old brood, separate young, and fall migration.

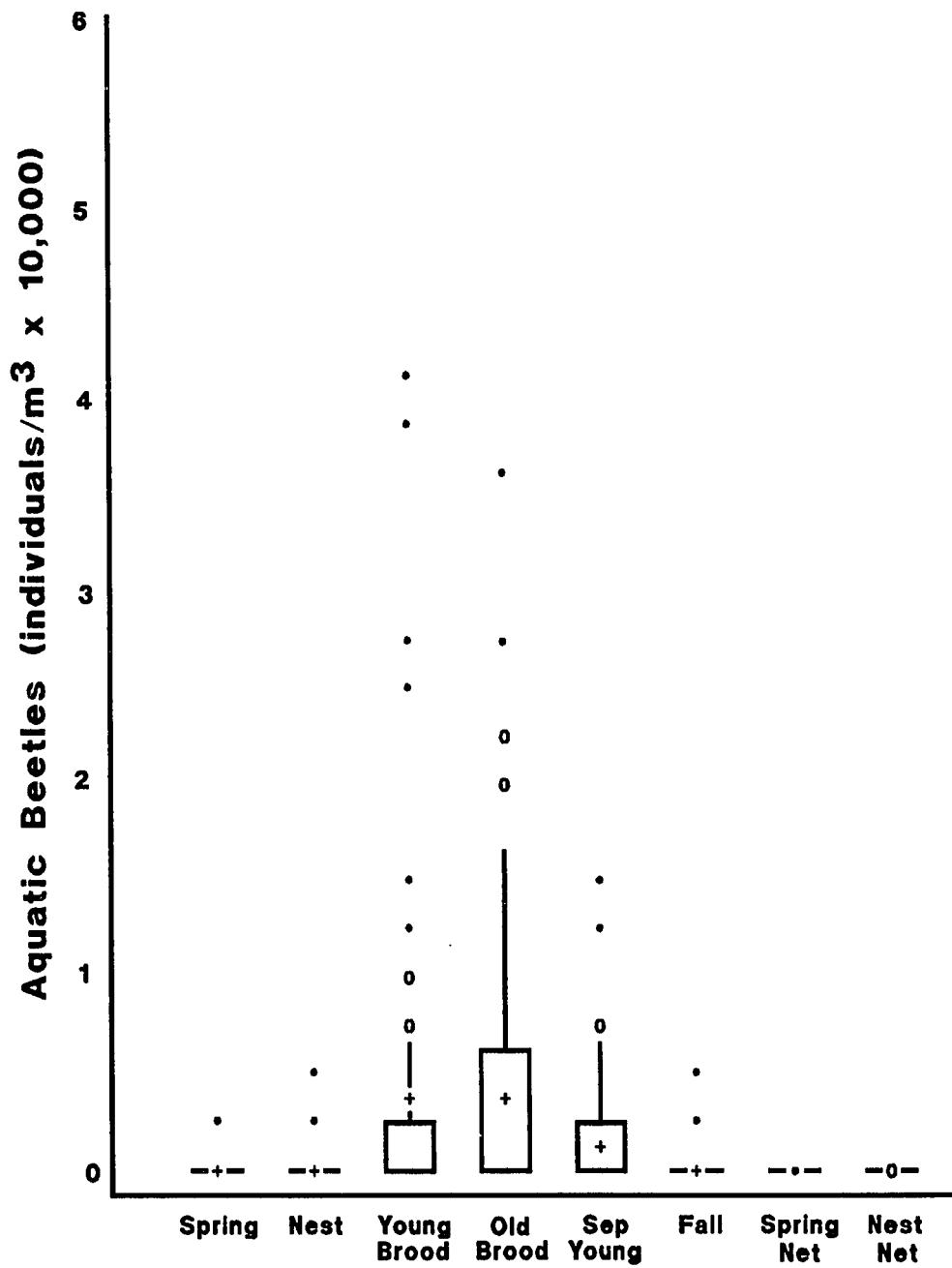


Fig. 41 Total semi-aquatic beetles (individuals/m³ x 10,000) at king rail foraging sites during migrational and breeding periods. Periods include: spring migration, nesting/incubation, young brood, old brood, separate young, and fall migration.

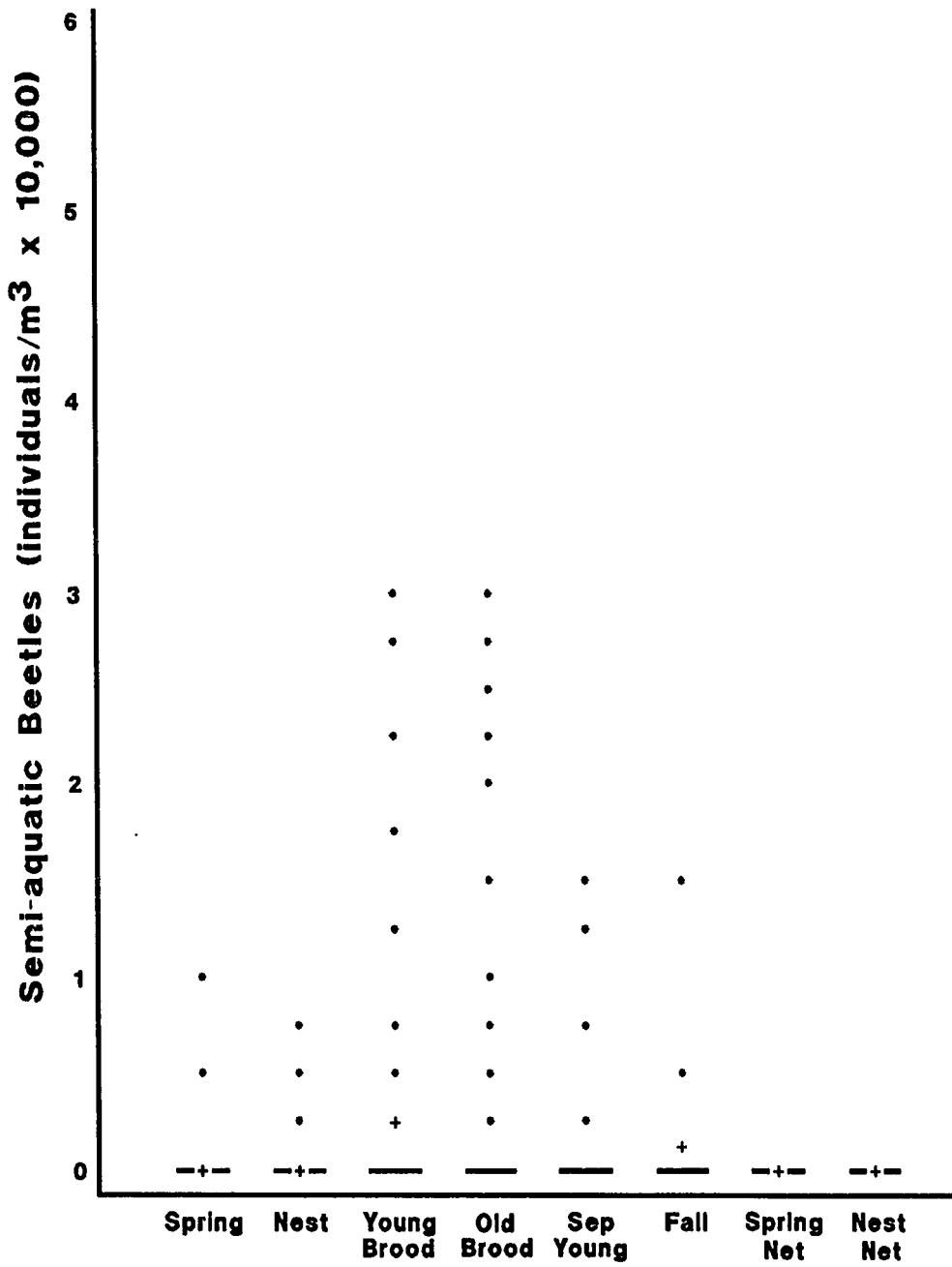


Fig. 42 Total fish (individuals/m³) at king rail
foraging sites during migrational and
breeding periods. Periods include: spring
migration, nesting/incubation, young brood,
old brood, separate young, and fall migration.

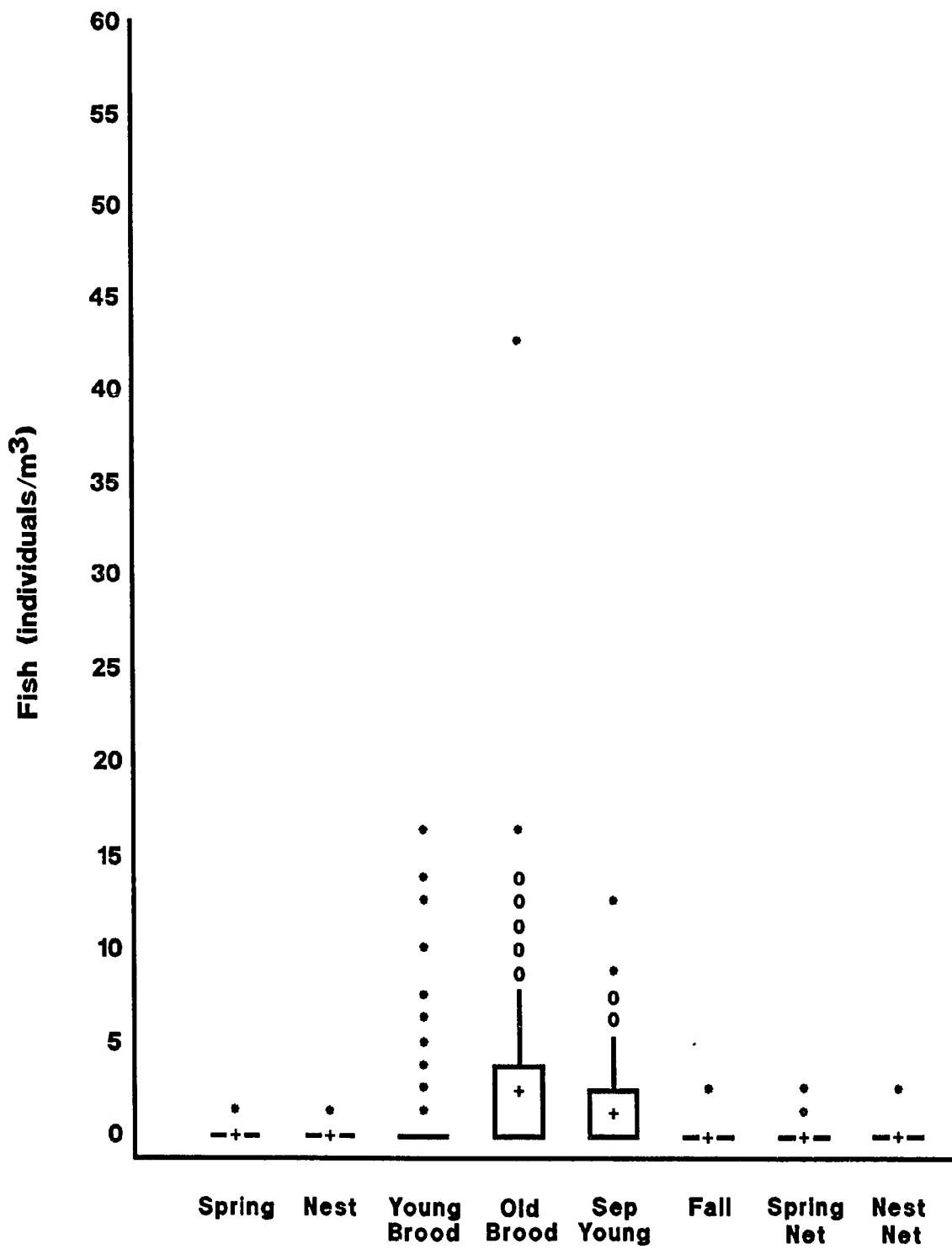


Fig. 43 Total potential prey (individuals/m³ x
1,000) at king rail brood foraging sites.
Foraging locations include: water, water/mud
interface, and mud substrates.

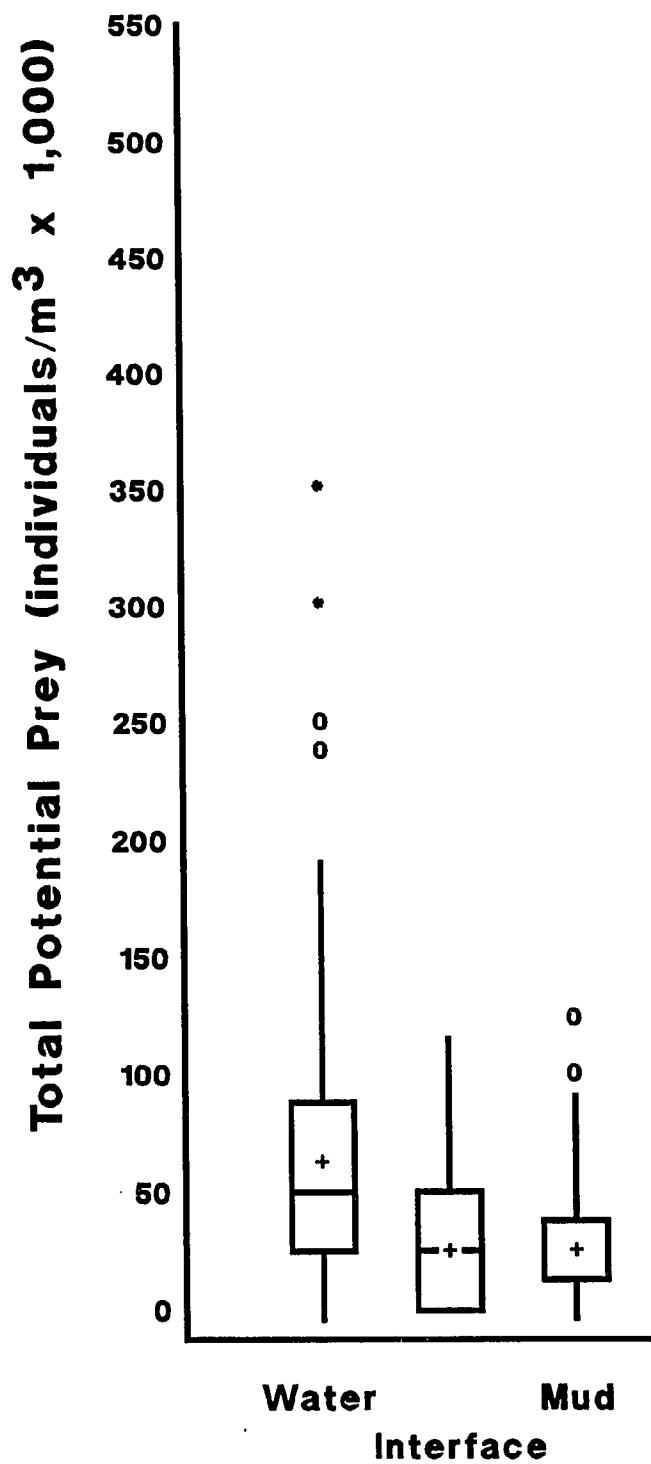


Fig. 44 Total macroinvertebrates (individuals/m³ x 1,000) at king rail brood foraging sites.
Foraging locations include: water, water/mud interface, and mud substrates.

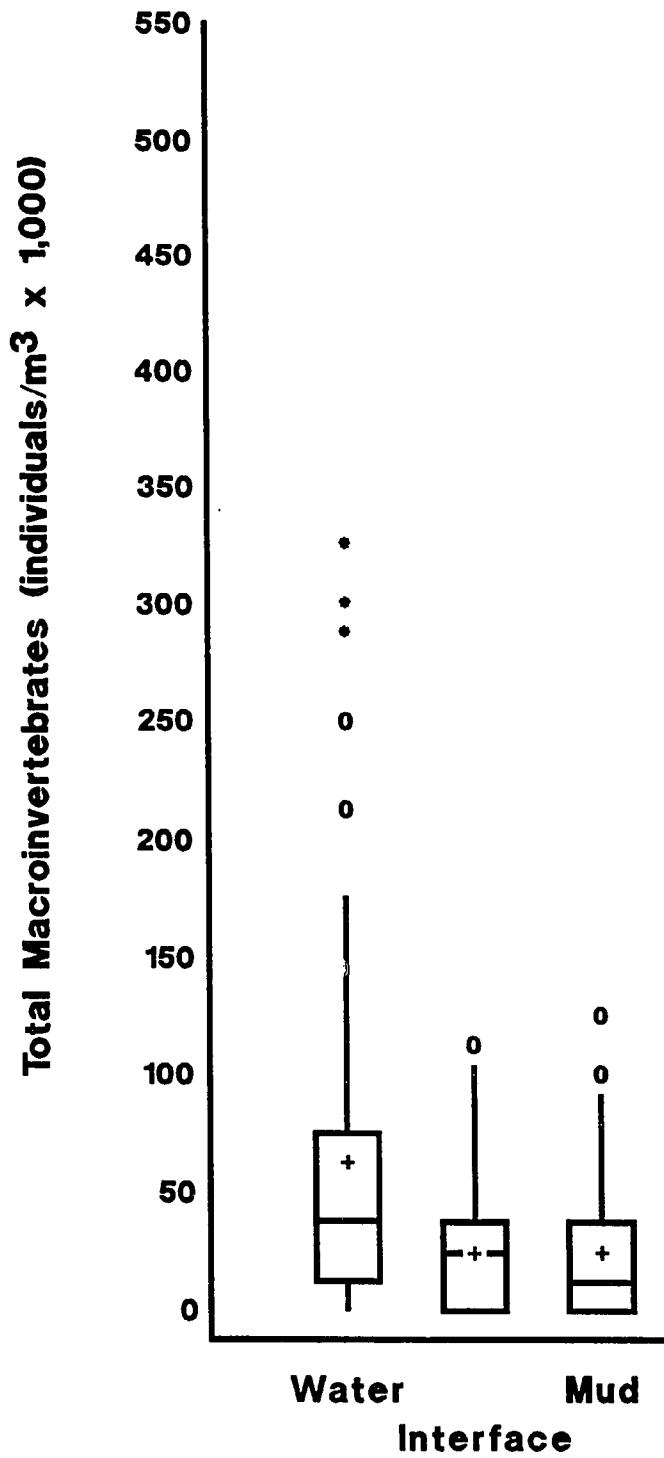


Fig. 45 Diversity (taxon at order level/core) at king rail brood foraging sites. Foraging locations include: water, water/mud interface, and mud substrates.

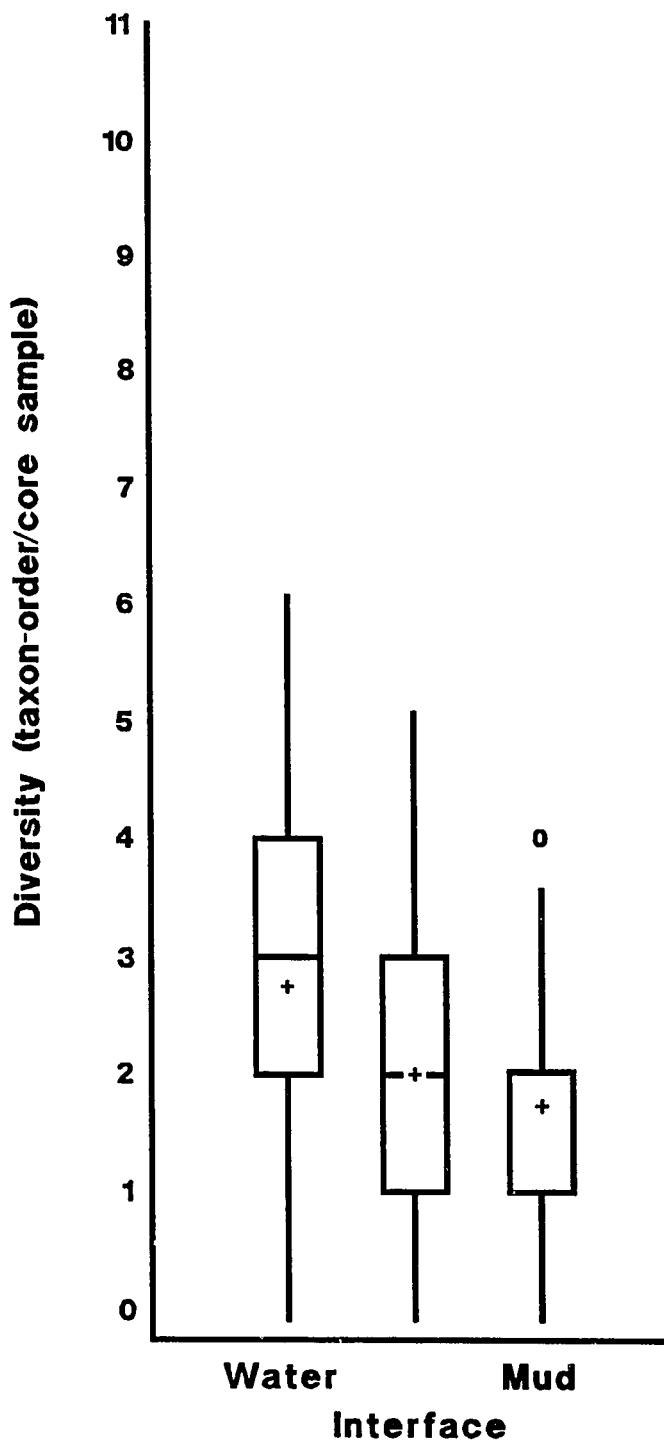


Fig. 46 Total freshwater oligochaetes
(individuals/ m^3 \times 1,000) at king rail brood
foraging sites. Foraging locations include:
water, water/mud interface, and mud
substrates.

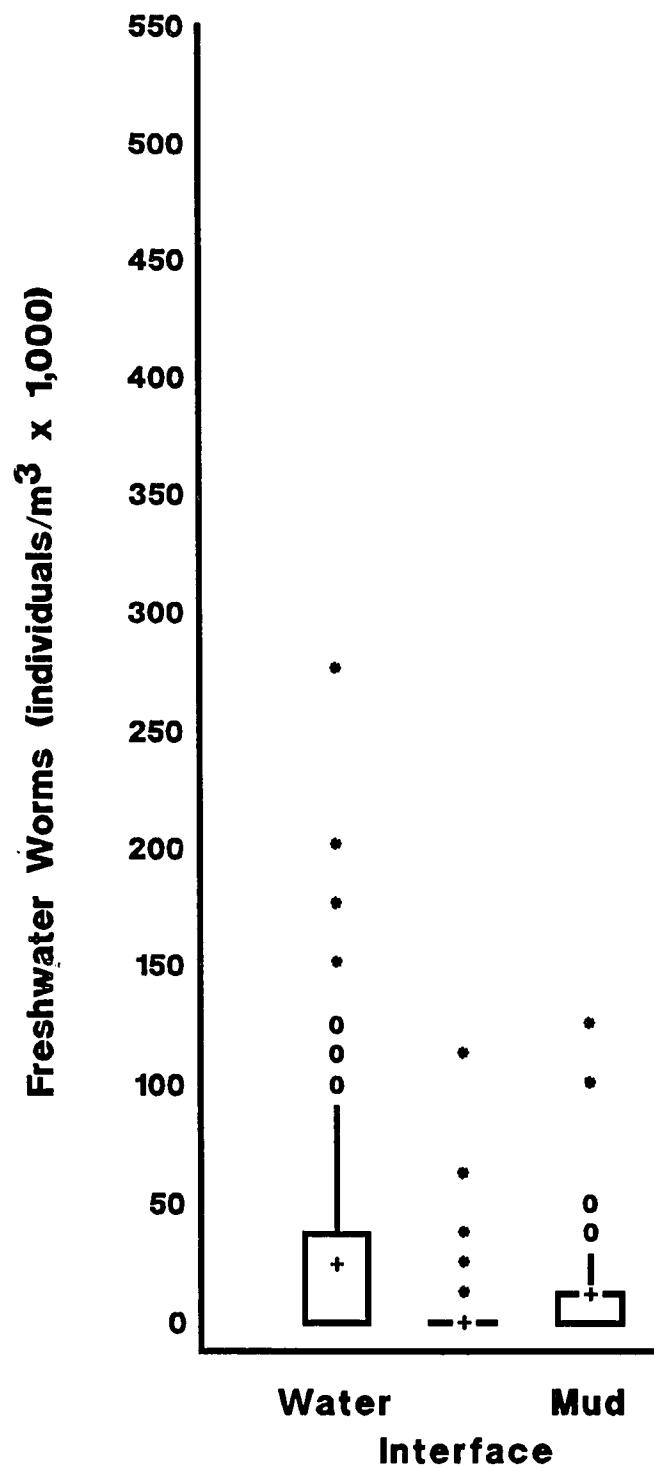


Fig. 47 Total leeches (individuals/m³ x 1,000) at
king rail brood foraging sites. Foraging
locations include: water, water/mud interface,
and mud substrates.

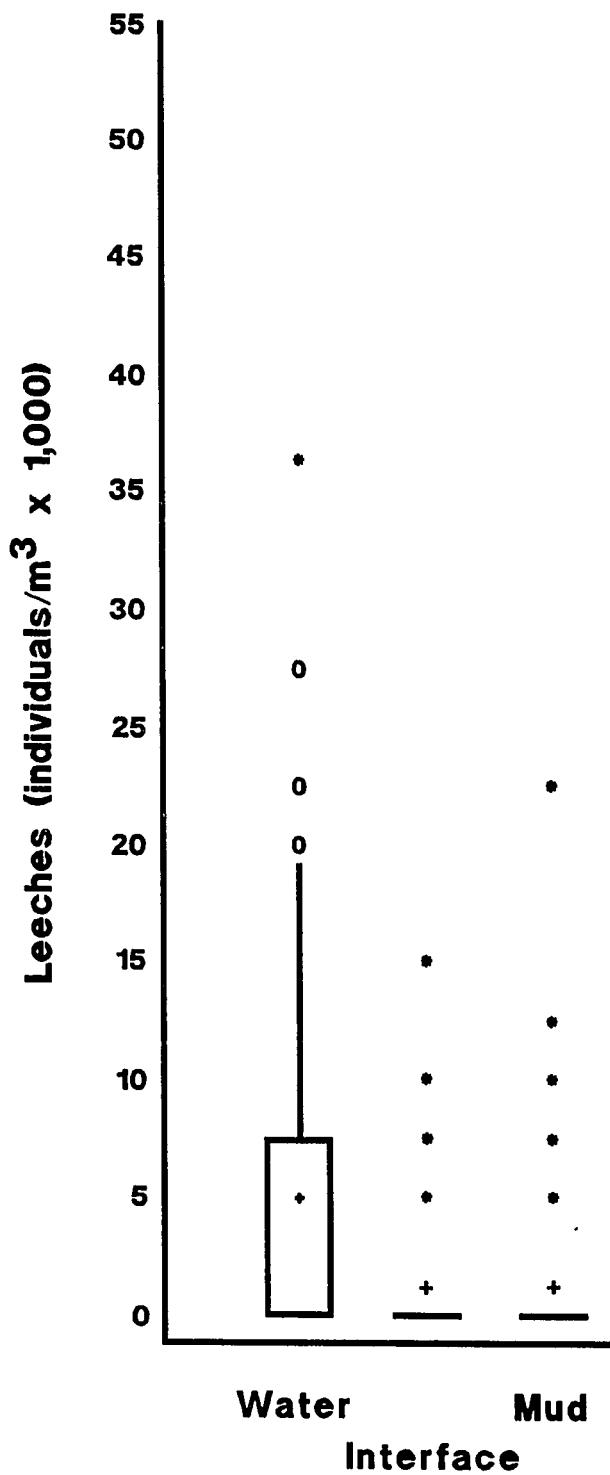


Fig. 48 Total snails (individuals/m³ x 1,000) at king rail brood foraging sites. Foraging locations include: water, water/mud interface, and mud substrates.

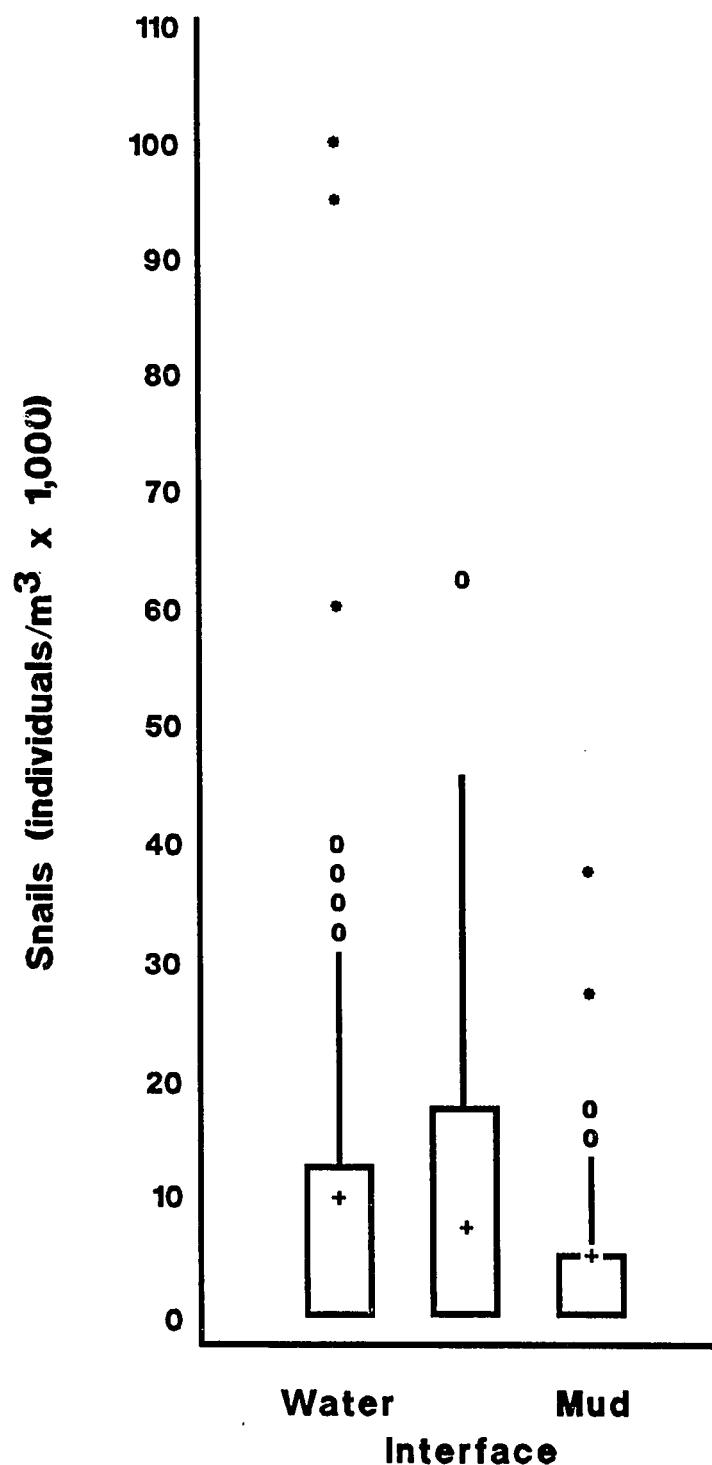


Fig. 49 Total aquatic beetles (individuals/ m^3 x 1,000) at king rail brood foraging sites.
Foraging locations include: water, water/mud interface, and mud substrates.

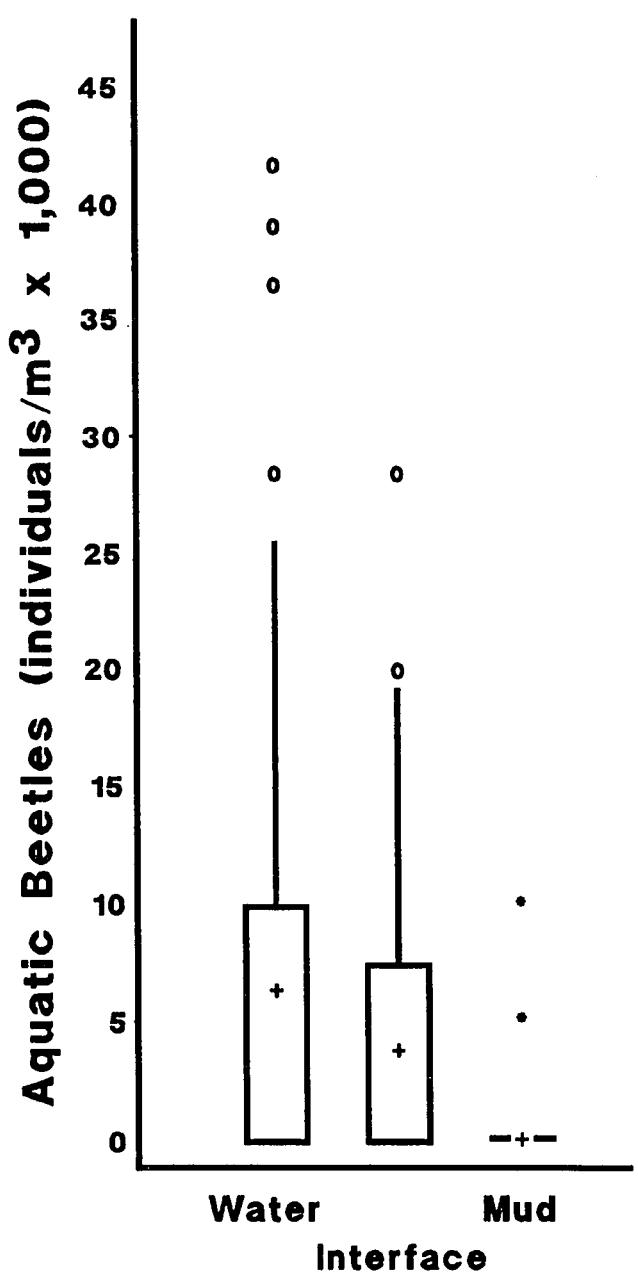


Fig. 50 Total semi-aquatic beetles (individuals/m³ x
1,000) at king rail brood foraging sites.
Foraging locations include: water, water/mud
interface, and mud substrates.

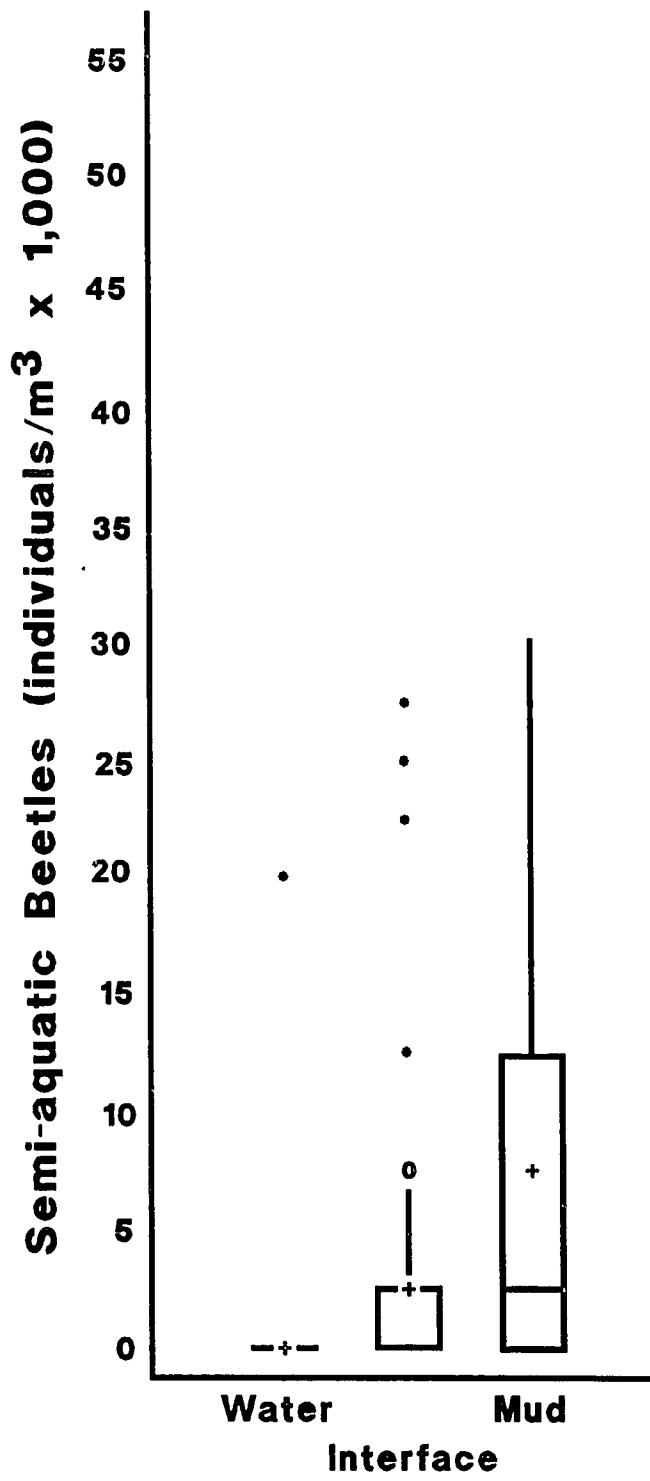
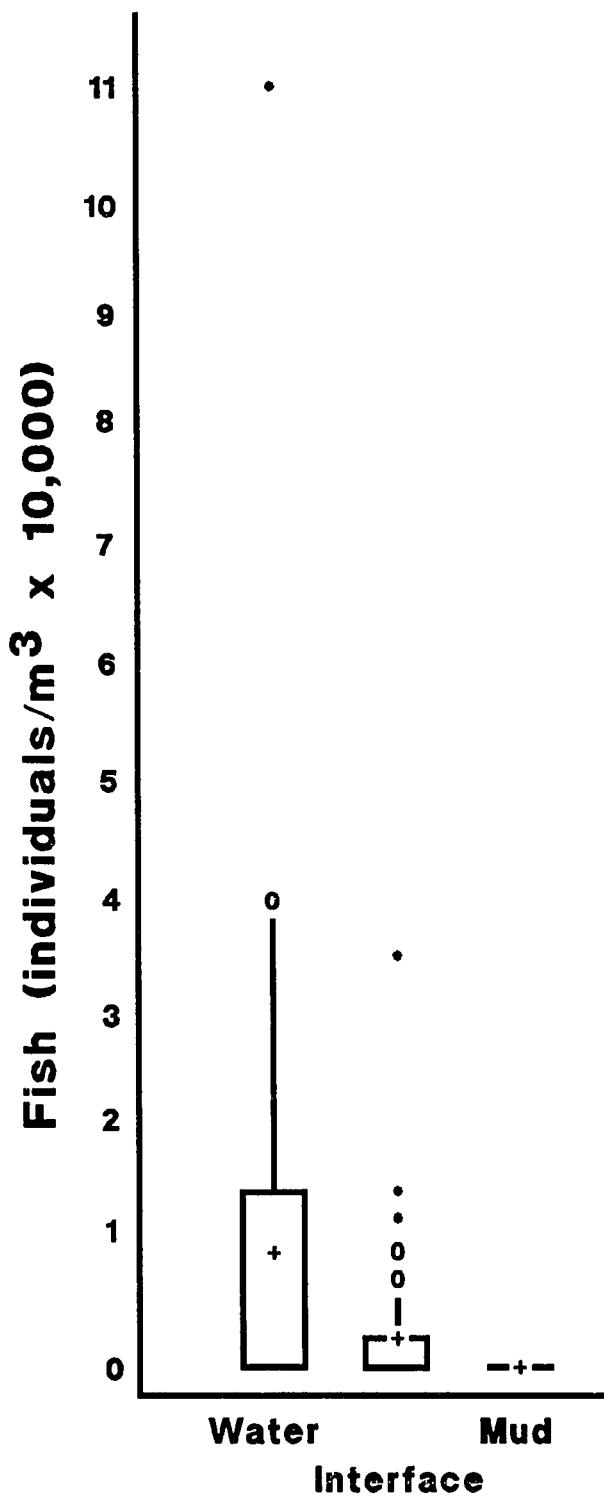


Fig. 51 Total fish (individuals/ m^3 \times 10,000) at king rail brood foraging sites. Foraging locations include: water, water/mud interface, and mud substrates.



Vita

Frederic Arthur Reid was born March 19, 1956 and attended public schools in Minnesota. He received an A.B. in Biology from Hamilton College at Clinton, New York (1978). After graduation he investigated target tissues of sexual steroids at the Laboratories for Sexual Reproduction, University of North Carolina at Chapel Hill under the direction of Dr. Walter E. Stumpf. He matriculated to the University of Missouri at Columbia for his graduate studies in wetland ecology under the direction of Dr. Leigh H. Fredrickson. There he received a M.S. (1983) and a Ph.D. (1989) in Fisheries and Wildlife.