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GREAT BLUE HERON NESTING BIOLOGY AND HABITAT
USE ON THE JAMES RIVER IN SOUTH DAKOTA

BY

EILEEN M. DOWD

A thesis submitted
in partial fulfillment of the requirements for the
degree Master of Science, Major in
Wildlife and Fisheries Sciences
(Wildlife Option)
South Dakota State University
1982

GREAT BLUE HERON NESTING BIOLOGY AND HABITAT
USE ON THE JAMES RIVER IN SOUTH DAKOTA

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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GREAT BLUE HERON NESTING BIOLOGY AND HABITAT

USE ON THE JAMES RIVER IN SOUTH DAKOTA

Abstract

EILEEN M. DOWD

Breeding biology, nest site activities, and habitat use of great blue herons (Ardea herodias) nesting in the Glendale heronry, South Dakota, were investigated in 1980 and 1981. Mean brood size was 3.35 nestlings. The predicted number of feeding trips of adult birds peaked when nestlings were 29 days old. A significant amount of variance in adult feeding trips per hour was accounted for by southerly winds and the time period from 1800-2100 hours. The variables that were not significantly related to the number of feeding trips were temperature, wind speed, wind directions other than south, cloud cover, and the 4 time periods occurring from 0600-1800 hours. Nest attentiveness of adult birds declined with increasing nestling age, with feeding the predominant nest activity of adults once nestlings reached 5-6 weeks of age. Standing at the nest, standing on branches, and gular fluttering increased as nestlings matured, while the inactive behavior and not visible categories decreased. Gular fluttering by nestlings and ambient temperature were significantly correlated. Important feeding habitats of adult herons included the James River and its inlets, streams, intermittent streams, and pastures. Forty-eight of 65 radiolocations occurred on the James River and its inlets. Unmarked herons travelled average and maximum distances of 3.15 and 24.40 km, respectively.

Foraging herons occurred at a rate of 2.33 birds/km of Timber Creek and 3.56 birds/km of the James River. Departure directions of herons from the colony differed significantly during the 2 years of study. A significant amount of departure clumping in the same flight directions occurred, although data collected during the study did not allow the conclusion that the herons were following each other to feeding sites.

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INTRODUCTION

The great blue heron (Ardea herodias) is the largest and most widely distributed North American heron. Despite a large volume of literature on this bird, there has not been a detailed study of the ecology of the great blue heron in a prairie river ecosystem.

The James River represents the only forested north-south corridor for birds migrating through South Dakota. Debate over the completion of the Garrison Diversion Project continues to threaten wildlife populations dependent upon the James River. The great blue heron has been discussed as an indicator species of environmental quality (Custer and Osborn 1977). Herons live at a high trophic level, making them subject to biomagnification of toxic materials (Hoffman 1974). For these reasons, it is important to obtain detailed information on such a species as the great blue heron in order to assess possible impacts of future water projects and environmental contamination.

This thesis is presented in 2 independent sections to facilitate publication of the results. In Chapter 1 I deal with several reproductive and behavioral aspects of the heron colony based on observations from a tree blind. In Chapter 2 I discuss important foraging habitats of the herons as determined by radio telemetry equipment, habitat censusing, and random following of unmarked herons to foraging sites.

The objectives of this study were;

- (1) To determine nesting success and formulate activity budgets for nestling and adult herons.
- (2) To examine the relationship between feeding trips of adult herons and environmental factors, growth of nestlings, and feeding trips of other herons.
- (3) To determine preferred foraging habitats of great blue herons during the breeding seasons in a prairie river ecosystem.

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CHAPTER 1

ACTIVITY BUDGETS AND REPRODUCTIVE SUCCESS AND PHENOLOGY OF A SOUTH DAKOTA GREAT BLUE HERON COLONY

INTRODUCTION

Much of the literature on great blue herons has dealt with documentation of clutch and brood size, nesting success, and breeding phenology. Reproductive studies include Brandman (1976) in California, Cottrille and Cottrille (1958) in Michigan, Edford (1976) in Ohio, Henny and Bethers (1971) in Oregon, and Pratt (1970) in central California. Reproductive data are not well-documented for a prairie river heronry.

Heron behavior in the heronry has been discussed by Cottrille and Cottrille (1958), Meyerriecks (1960), Stephens (1980), and Mock (1976) for the great blue heron, and by Milstein et al. (1970) for the grey heron (Ardea cinerea). One aspect of heron behavior that has received little attention in the literature is activity budget information on nestling and adult herons. Brandman (1976) studied the annual behavioral cycle and time budget of adult great blue herons at Morro Bay, California. Clark (1980) determined a time budget for a pair of nesting wood storks (Mycteria americana) in Florida. Neither of these authors determined activity budgets for the nestling birds.

The relationship between feeding trips of adult herons and external factors such as time of day and weather conditions has been investigated in several studies. These include Bovino and Burt (1979) in Tennessee, Krebs (1974) in British Columbia, Parris (1979) in Ohio, Quinney and Smith (1980) in Nova Scotia, and Warren (1979) in Idaho.

The objectives of this study were:

- (1) To determine nesting success and phenology of great blue herons in a prairie river heronry.
- (2) To formulate activity budgets for nestling and adult herons in the heronry.
- (3) To investigate feeding trips of adult herons as influenced by environmental factors, time of day, and growth of nestlings.

STUDY AREA

The Glendale heronry is located on the James River in Spink County, approximately 7.2 km south of Frankfort, South Dakota (Fig. 1). Hereafter, the heronry may also be referred to as the Glendale colony. The James River is meandering in this region, with a river gradient of 8.1 cm/km (Tol 1976:3). Low flow periods usually occur in late summer autumn, and winter (Young 1973:8).

The study area has a continental climate and a flat to undulating topography. The average annual precipitation is 48.7 cm, with 75% of the precipitation falling from April to September. The mean annual temperature is 6.0 °C. Relative humidity ranges from 65-75% during winter months and from 50-70% during summer months. Wind speeds average 17.7 km/hour from the south during the summer and 19.3 km/hour from the northwest in the winter (Spuhler et al. 1971:32).

The study area lies in the James River Lowland physiographic region. Dominant soil types include loess and Late Wisconsin glacial drift (Westin et al. 1967:16). Predominant vegetation types are small grains, grassland, and, in a narrow corridor along the James River, riparian forests (Schneider 1978).

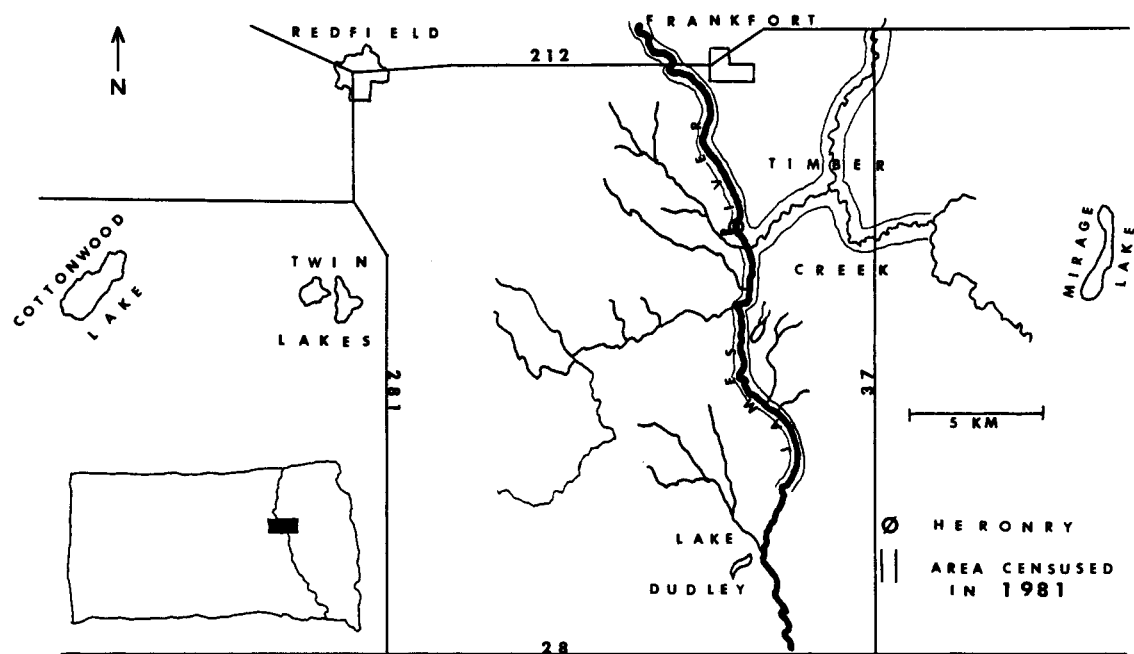


Fig. 1. Location of the Glendale great blue heron colony in Spink County, South Dakota.

MATERIALS AND METHODS

Observation Techniques

In the spring of 1980 a camouflaged observation blind was constructed in a tree across the river from the heronry, a distance of 45-55 m. The blind was approximately 6 m aboveground and measured about 2 m square. A large window allowed viewing of the heronry and smaller openings allowed additional viewing of birds approaching or departing from the heronry. Observations from the blind were begun in the middle of May, 1980. At this time, the nestlings in approximately 50% of the nests had hatched. Observations were concluded at the beginning of August, 1980, when nestlings in all but 1 nest had fledged.

The heronry consisted of 83 nests visible from the blind and a smaller group of 15-20 nests located approximately 18 m south of the main colony. The latter group was not visible from the blind. Twenty of the visible nests were randomly selected for intensive observation. Observations were made with 7 X .35 mm binoculars and a Balscope Zoom 60 spotting scope.

Data collected from the blind included information on the arrivals and departures of adult herons to and from all nests in the main colony. The nest number, time, and general direction of arrivals or departures were recorded.

Activity categories were devised for adult and nestling herons at the 20 nests. The 20 selected nests were observed for 2 8-hour periods each week from the middle of May until the beginning of August.

One observation period commenced at sunrise and continued for 8 hours. A second observation period began at midday of a second day and continued until sunset. By combining these time periods, the nests were observed from sunrise to sunset once each week. The activity category of any heron present at the nest was noted, as well as the number of nestlings involved in each recorded activity.

The 20 nests under intensive observation were divided into 4 nest groups based on fledging dates. The oldest and youngest groups were discarded, since each contained only 1 nest. The 18 remaining nests comprised 2 nest groups. Nestlings in 1 nest group fledged from 16 July to 19 July and will be referred to as the older nestling group. Nestlings in a second nest group fledged from 22 July to 25 July, and will be called the younger nestling group. The adults in the forthcoming discussion will likewise be described as corresponding to the older or younger nestling group. Because of the distance and position of the blind from the heronry, clutch sizes could not be determined. Nestlings were counted while being fed by adult birds.

Each of the 20 nests was observed once during each 15-minute interval, with the activity of each nestling or adult noted. The number of nestlings or adults exhibiting each particular activity was divided by the total number of nestlings or adults observed during the appropriate time period and converted to a percentage. Activity budget information is expressed as the percentage of nestlings or adults involved in the various activities for a particular time period.

Following the breeding season, data were collected in the heronry on tree species, diameter at breast height (dbh), and the number of nests/tree. A Ranging Opti-Meter was used to determine nest and tree heights. Thirty-three nests located in 19 trees were visible from the ground directly below the colony. Only 33 nests were examined because foliage blocked the view of some nests.

Data Analysis

Step-wise multiple regression was used to determine possible relationships of time of day, temperature, wind speed, wind direction, and cloud cover with the number of arrivals to all nests in the colony (SAS Institute, Inc., Raleigh, NC). All other analyses utilized data collected only on the 20 nests under intensive observation.

Polynomial curve-fitting analysis was used to describe the relationship between the arrivals of adult birds to the nests/hour and the days since clutch initiation. Linear regression analysis was used to test for a relationship between ambient temperature and gular fluttering of nestlings or the wing spread posture of nestlings. Chi-square analysis was used to test 3 pairs of factors. These factors were clutch initiation dates and clutch sizes, clutch initiation dates and fledging success, and clutch sizes and fledging success.

RESULTS AND DISCUSSION

Nest Site Characteristics

All 33 nests examined in the heronry were found in green ash (Fraxinus pennsylvanica), although all nest trees were not examined. The predominant understory plant was stinging nettle (Urtica dioica). The number of nests/tree ranged from 1-4, with a mean of 1.74 nests/tree. Nest heights ranged from 8.60-14.60 m, with a mean of 11.72 m. Tree heights averaged 13.15 m, with a range of 9.60-15.60 m. Diameter at breast height (dbh) of nest trees ranged from 36.50-49.00 cm, averaging 42.90 cm.

Nesting Success

Nesting success for 1980 was estimated from data on the 20 nests under intensive observation. Mean brood size was 3.35 nestlings (2-5). In Edford's (1976) study in Ohio, the mean number of fledglings/nest was 2.75 and 2.90 for successful nests. The mean number of fledglings/nest was 3.00 (2-4) in the Glendale colony. Other published results for comparison with my study include: 2.27 fledglings/nest in Ohio (Edford 1976), 2.04 in Oregon (Henny and Bethers 1971), 2.5-2.9 in British Columbia (Kelsall and Simpson 1979), 2.84 in Nova Scotia (McAloney 1973), 1.30 in California (Pratt 1970), and 2.5 in Idaho (Warren 1979). Henny (1972) defined a stable great blue heron population as one in which 1.91 young/breeding pair were fledged. Based on the 20-nest sample for the Glendale colony, this population, at least in 1980, was maintaining itself.

Chi-square analysis was used to determine whether nests with larger broods produced significantly more fledglings than smaller broods. Edford (1976) studied 2 heron colonies on Lake Erie in Ohio and found that clutches of 3-4 eggs produced the most fledglings and had the highest fledging success. Brandman (1976) found that larger broods in a California colony produced more fledglings. Brood size and fledging success for the Glendale colony nests exhibited no statistically significant relationship in 1980 ($\chi^2 = 15.88$, $df = 19$, $P > 0.05$).

Several authors have noted that the earliest herons to begin nesting in a colony may have higher nesting success than birds that begin nesting at a later time. Brandman (1976) found that early nesters had larger broods and greater nesting success than later nesters in a California colony. Edford (1976) compared fledging rates for high and low nests, which corresponded to early and late nests, respectively. Early nests fledged 60% of the nestlings, while later nests fledged only 36%. Chi-square analysis on data collected in the Glendale colony indicated no relationship between nest initiation dates and fledging success ($\chi^2 = 4.02$, $df = 6$, $P > 0.05$).

Another facet of nest site selection is the choice of central vs. peripheral nests in a colony. Various authors have tested the hypothesis that birds nesting in the central area of a breeding colony have greater nesting success than peripheral nesters due to differing predation pressures, the effects of crowding, or the advantage of

better access to feeding site information by central nesters (Coulson 1968, Dexmeier and Southern 1974, Tenaza 1971). The 20 nests under intensive observation in this study were classified subjectively as either central or peripheral in location. Nests were situated in 3 nest groups; 1 central and 2 peripheral groups. Peripheral nests were separated from the central group by areas of shorter trees containing no nests. Chi-square analysis indicated no significant relationship between nest location and fledging success ($\chi^2 = 1.54$, $df = 1$, $P > 0.05$).

Central nests in Edford's (1976) study produced more nestlings but not more fledglings than peripheral nests. She speculated that nestling rivalries in the more crowded central nest area may have caused a higher fledgling loss. Warren (1979) found no difference in brood size or nest success for central vs. peripheral nests in an Idaho colony.

Feeding Trips

Curve-fitting of polynomial equations was used to determine the possible relationship between arrivals at the nest/hour and days since clutch initiation for each of the 20 nests (Fig. 2). For this analysis, the assumption was made that the number of arrivals to the nests corresponded to the number of feeding trips of adults. The linear and quadratic equations were significant ($R^2 = 0.0979$, $p < 0.01$, $df = 419$). The predicted number of arrivals/hour peaked 57 days after clutch initiation, then decreased as the fledging period approached. Assuming



Fig. 2. Predicted nest site arrivals per hour of adult great blue herons in relation to days since clutch initiation for the Glendale heronry, 1980.

a 28-day incubation period (Bent 1926), nestlings were 29 days old when the feeding trips of adult birds peaked as indicated by arrivals. The observed trend of a decline in feeding of nestlings by adult birds as nestlings mature has been reported by several authors. Brandman (1976) found that feeding trips by adult birds rose a week after hatching and peaked 3 weeks later, then declined as nestlings matured. He reported that as nestlings aged from 5 to 15 days, feeding trips of adult birds increased from 1.5 to 3.0/day, peaking at 3.7/day when nestlings were 25 days old. In a study of an Idaho colony, nestlings of 7-10 weeks of age were fed 2-3 times/day, with feeding dropping to once/day when nestlings were 11-14 weeks old (Collazo 1979). Pratt (1970) found that herons were fed most frequently during the first week of age, from 6-10 times/day. Feeding then averaged 4 times/day until the fledging period, when feeding fell to twice/day. Parris (1979) observed that prey intake by adult herons in Ohio increased from April through June, then declined during July and August, as young birds were becoming less dependent on parent birds for food.

Step-wise multiple regression indicated that southerly winds and the time period from 1800-2100 hours accounted for a significant amount of the variance in the number of arrivals/hour to the colony ($R^2 = 0.2612$ $P < 0.05$). The assumption was again made that the number of arrivals to the colony was a function of the number of feeding trips of adult birds. The significant positive relationship between southerly winds and feeding trips appears to be peculiar to my study and without obvious

explanation. Krebs (1974) observed that herons in British Columbia were significantly more successful when foraging under cloudy or rainy skies. Quinney and Smith (1980) found that windy conditions decreased foraging success for great blue herons in Nova Scotia. Bovino and Burt (1979) noted that herons in Tennessee were more successful when foraging on calm days and on days with overcast skies. I found no significant relationship between feeding trips and wind or cloud cover. Parris (1979) also found that light and wind conditions had no significant relationship with heron foraging success in Ohio.

The time periods 1500-1800 hours and 1800-2100 hours were both negatively correlated with the number of feeding trips of adult birds, although neither time period was significantly correlated with feeding trips (1500-1800 hours, $r = -0.0280$, $P = 0.8291$; 1800-2100 hours, $r = -0.2178$, $P = 0.1102$). Brandman (1976) in California and Warren (1979) in Idaho both noted increased activity by herons during the hours near dusk, although neither author discussed the statistical significance of the observations.

Nest Attentiveness and Activity Budgets

Nest attentiveness of adult birds with nestlings in the older and younger nestling groups was determined (Fig. 3). Adult birds with younger nestlings were attentive to the nests for 99% of the observed time when nestlings were 1 week old and 83% of the time during the second week of age. A rapid decline in nest attentiveness is evident as nestlings aged from 3 to 11 weeks. Adults with older nestlings were

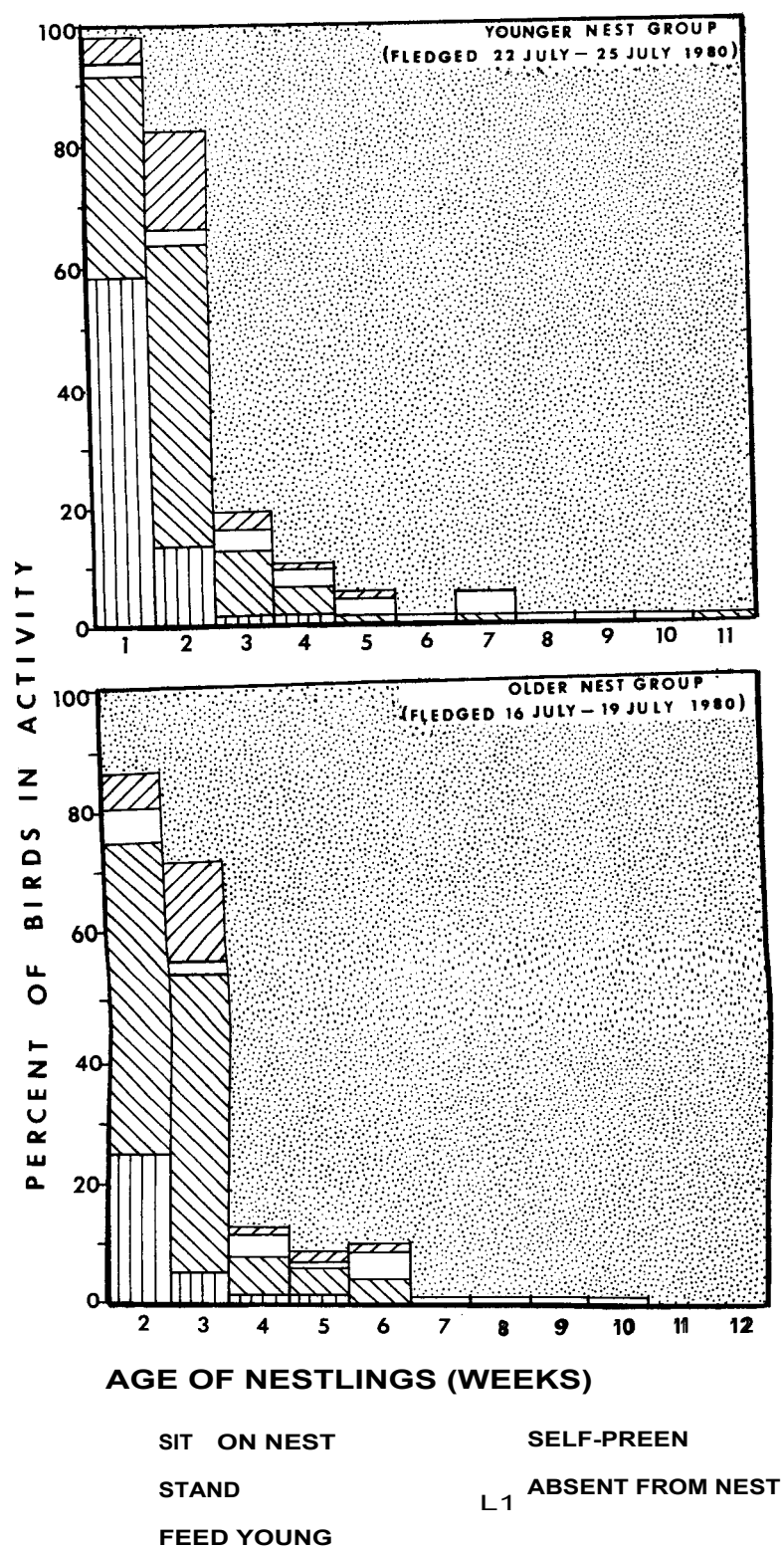


Fig. 3. Activities of adult great blue herons at the nest site, including absence of birds from the colony, for 2 nest groups in the Glendale heronry, 1980, (Younger nestling group = 32 birds; Older nestling group = 29 birds).

present for 86% and 74% of the observed time when nestlings were 2 and 3 weeks old, respectively. As these nestlings aged from 4 to 10 weeks, nest attentiveness declined, since adults presumably returned to nests only to feed young.

Several studies have indicated that adult herons will be in almost constant attendance at the nest for the first 2-3 weeks after nestlings hatch. At 3-4 weeks of age, nestlings may be left unattended for at least a portion of the day. When nestlings reach 4 weeks of age and thereafter, adults normally return to the nest only to feed young (Brandman 1976, Collazo 1979, Edford 1976, Pratt 1970). Brandman (1976) observed that adults spent 100% of their non-foraging time at the nest when nestlings were brooded from 1-8 days of age. When nestlings were 9-30 days old, adult male herons spent 51% and females 31% of their non-foraging time at the nest. Other than feeding the young, Brandman found that adults spent almost no time at the nest after nestlings reached 40 days of age. Pratt (1970) observed that heron nests in a central California colony were never left unattended for the first 3 weeks after nestlings hatched. After 28 days, adults returned to the nests only to feed nestlings.

Behavior of adult birds that were attentive to the nest was examined to determine any apparent activity patterns. Major adult activities at the nest were sitting, standing, feeding young, and self-preening (Fig. 3). These activities are expressed as the percentage of the total number of adult birds observed in each nest group that exhibited the particular behavior discussed. Absence of adult birds from the 20

nests was also noted.

Most adults sitting on the nest were brooding in my study. The age difference of 1 week between nest groups is obvious when comparing the percentages of adult herons sitting on the nest during the first week of observation; 58% for the younger nestling group vs. 25% for the older nestlings. Another indication of the difference in the amount of brooding of nestlings was the observation that 27% more of the adults with older nestlings were standing at the nest during the first observation week than were adults with younger nestlings. The percentages of adults sitting (brooding) and standing at all nests rapidly declined as adults became less attentive to the nests. Brandman (1976) found that adult male herons spent 20-45% of their time brooding when nestlings were 1-8 days old. By the time nestlings were 30 days old, he found that males spent 13% and females 6% of their time brooding nestlings. McAloney (1973) observed that young birds were brooded constantly for the first 2 weeks of age. Pratt (1970) noted that 8-day old chicks were brooded for approximately 44 minutes/hour, a drop from 55 minutes/hour for 2-day old chicks.

Of the total number of observations of adult birds with younger nestlings, 1-4% were feeding nestlings (Fig. 3). Feeding peaked when nestlings were 3 weeks old, then gradually declined. Feeding of the older nestlings ranged from 0-5% of the adult observations, with peak feeding activity during the second, fourth, and sixth week of nestling life. The number of arrivals of adult birds to the nest peaked when nestlings were 29 days old (Fig. 2).

Brandman (1976) found that the percentage of time spent by male great blue herons feeding young peaked at 5.5% when young were 1-8 days old. Peak time for female adults was when nestlings were 3 weeks old, when 2.6% of the adult female time was spent feeding young. Milstein et al. (1970), in a study of the grey heron in England, also observed a declining parental interest in feeding nestlings as they matured. The authors theorized that Holstein's (1927) "starvation" hypothesis may apply to this observation; that is, adults feed older nestlings less often to encourage their independence. This feeding pattern was also observed in the Glendale colony. Feeding of nestlings gradually increased to peak when nestlings were approximately 4 weeks old, then declined as young birds became more independent of adult birds.

Adult preening peaked at 16% for both nest groups, when younger nestlings were 2 weeks old and older nestlings were 3 weeks of age. The subsequent decline in preening reflects the decreasing nest attentiveness of adults as nestlings mature. Brandman (1976) found that self-preening by adults at the nest peaked near the fledging period of nestlings.

If adult birds that were absent from the nests are excluded from the analysis of adult bird activities, the changes in the nest time budgets become more apparent (Fig. 4). Feeding was the predominant activity of adults at the nest site after younger nestlings reached 6 weeks of age and older nestlings were 7 weeks old. No adults with older nestlings were seen at the nest after older nestlings reached 10 weeks of age.

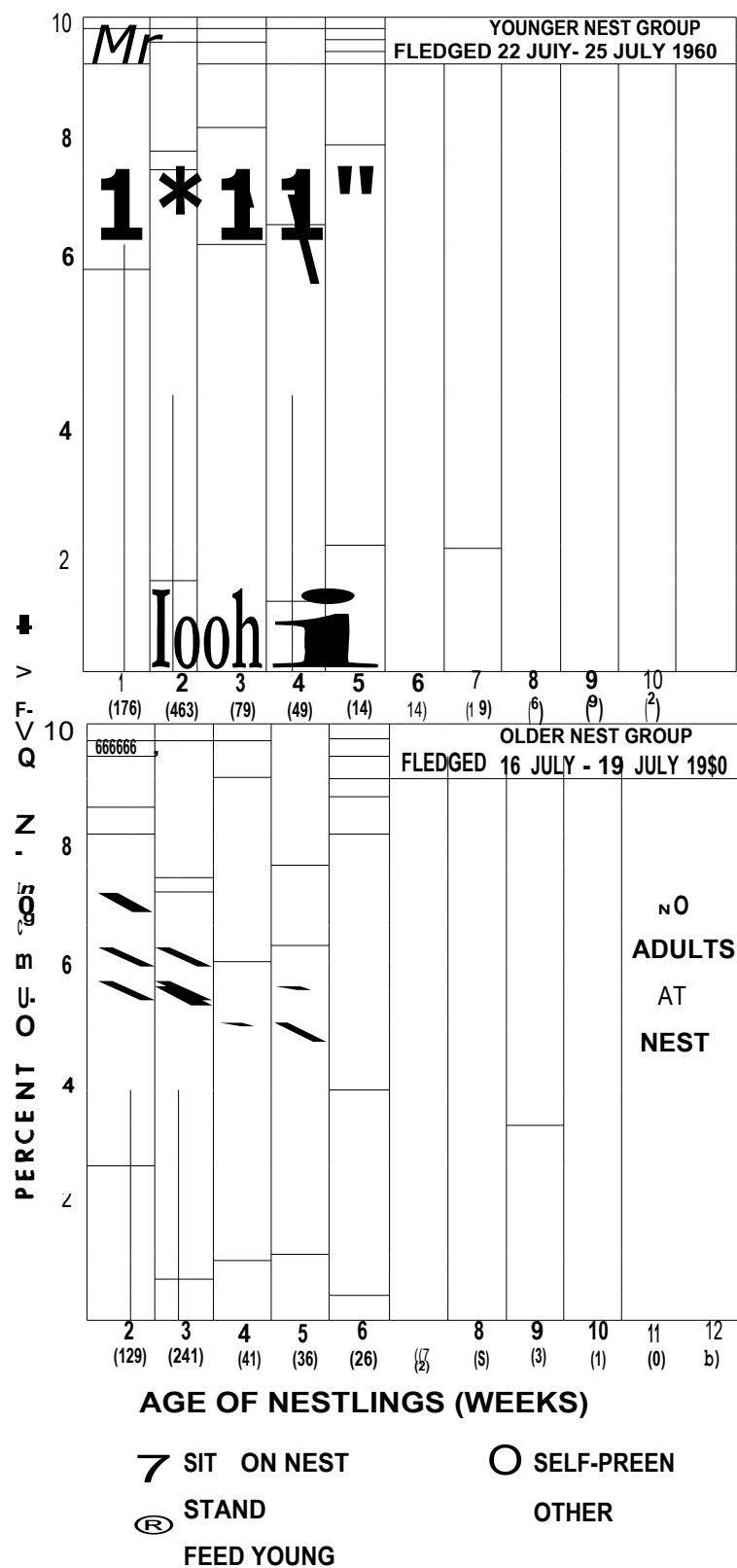


Fig. 4. Activities of adult great blue herons at the nest site, excluding absence of birds from the colony, for 2 nest groups in the Glendale heronry, 1980 (Sample sizes are in parentheses).

Age-related changes in the percentages of the younger nestlings engaged in various activities were apparent in all categories except feeding and preening (Fig. 5). The "not visible" category refers to birds too small to be seen from the blind or not visible because they were sleeping or being brooded. This was a prominent category during the first 3-week observation period. Thereafter, the percentage of nestlings not visible to observers decreased to almost 0 since young birds grew large enough to be seen from the blind. The no visible activity (inactive behavior) category decreased as herons matured and were able to display other activities. The percentage of birds observed standing increased with the increasing strength and maturity of nestlings. Gular fluttering increased to reach fairly constant levels during the second and third 3-week periods. Pratt (1970) observed that 18-day old nestlings in a California colony were able to use gular fluttering as a cooling mechanism. The percentage of birds observed on surrounding branches exhibited an obvious increase as nestlings began exercising their wings on nearby limbs in preparation for flight. McAloney (1973) observed young birds on branches at 35 days of age and short jump flights at 40 days. Pratt (1970) reported short jump flights to and from branches when nestlings reached 7 weeks of age.

Older nestlings showed very similar age-related changes in activity patterns. Because these nestlings were approximately 1 week older than the younger nest group, slight differences in the "not visible" and on branch categories were observed. By the second 3-week period, all older nestlings were visible. Also during this period, more

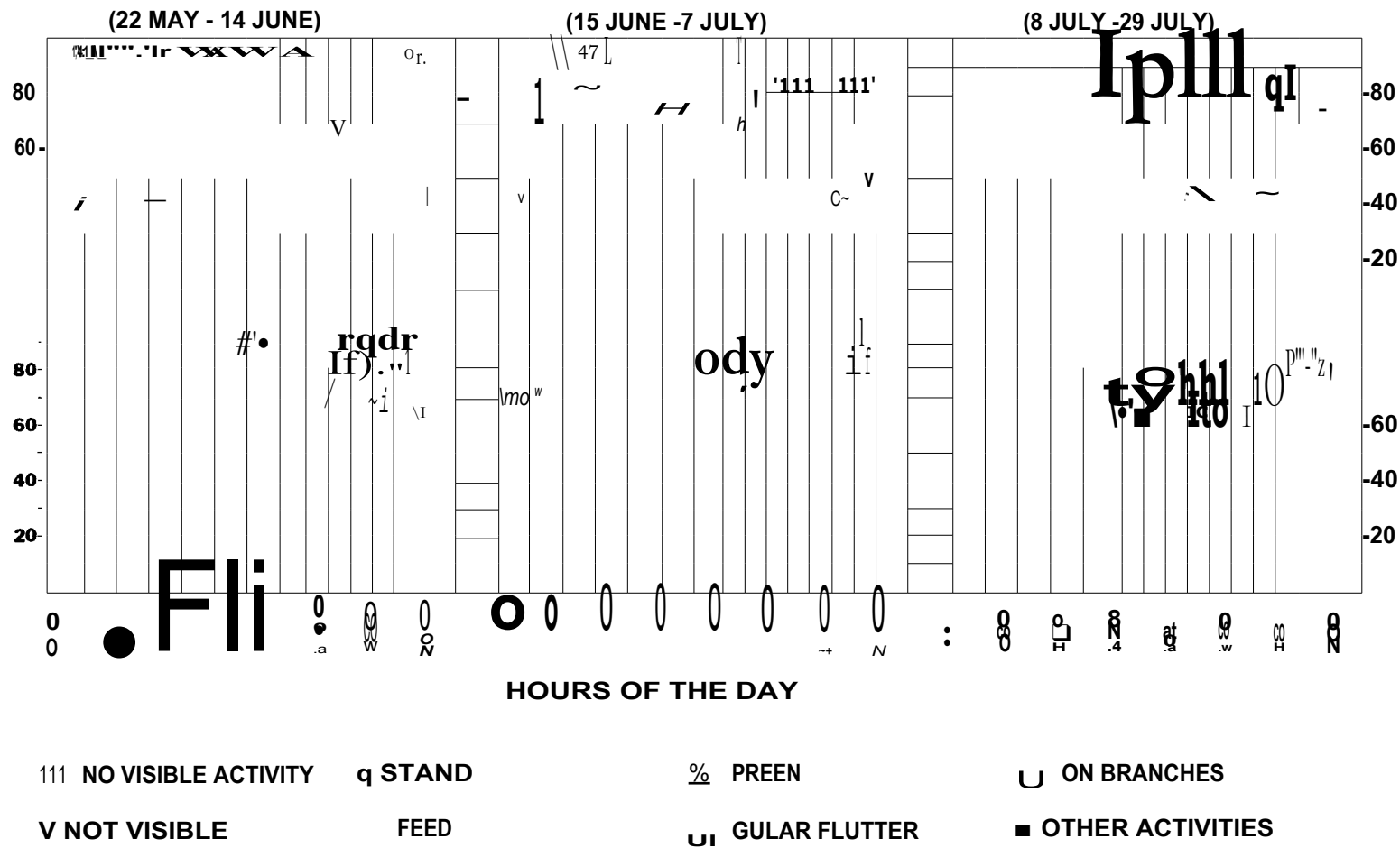


Fig. 5. Hourly activity patterns of nestlings at the Glendale great blue heron colony for 2 nest groups during 3 time periods in 1980 (22 May through 14 June, 15 June through 7 July, and 8 July through 29 July). Upper tier represents nestlings fledged from 22 July through 25 July; lower tier represents nestlings fledged from 16 July through 19 July.

older nestlings were observed on branches than younger nestlings. During the third time period, 26% of the younger nestlings were observed on branches. The corresponding figure for older nestlings was 16%. The fact that older nestlings fledged 1 week earlier than the younger birds may explain the difference in the percentages, since the older birds were absent from the nests in greater numbers by this time. This is apparent from the difference in sample sizes; 4086 bird observations of younger nestlings vs. 2144 bird observations of older birds during the last time period.

Both nest groups displayed similar hourly activity patterns. Gular fluttering peaked during the late afternoon hours. A highly significant correlation was found between gular fluttering and ambient temperature for both nest groups (Younger birds, $R^2 = 0.3425$, $P < 0.01$, $n = 48$; Older birds, $R^2 = 0.3600$, $P < 0.01$, $n = 54$). None of the other activity categories displayed such an obvious hourly pattern, but several categories exhibited a tendency to peak before or after 1200 hours. The no visible activity category peaked before 1200 hours for all birds in all time periods. Feeding peaks always occurred after 1200 hours.

SUMMARY

Nest heights averaged 11.72 m in nest trees that averaged 13.15 m in height. Mean brood size in 1980 was 3.35 nestlings. The predicted number of feeding trips of adult birds peaked when nestlings were 29 days old. No relationship was found between nesting success and nest initiation dates or brood sizes. No relationship was found between nest locations and clutch initiation dates, brood sizes, or fledging success. Regression analysis indicated that southerly winds and the time period from 1800-2100 hours accounted for a significant amount of variance in adult feeding trips/hour. The variables that were not significantly related to the number of adult feeding trips/hour were temperature, wind speed, wind directions other than south, cloud cover, and the 4 time periods occurring from 0600-1800 hours.

Nest attentiveness of adult birds decreased with increasing age of nestlings. Feeding was the predominant nest activity of adults after nestlings reached 5-6 weeks of age. Standing, standing on branches, and gular fluttering by nestlings increased with increasing nestling age, while the inactive behavior and "not visible" categories decreased in importance as time progressed. Feeding and preening showed no apparent relationship to increasing age of nestlings. Gular fluttering by nestlings and ambient temperature were significantly correlated.

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CHAPTER 2

FORAGING HABITATS OF GREAT BLUE HERONS

ON THE JAMES RIVER, SOUTH DAKOTA

INTRODUCTION

Relatively few studies have been conducted to determine specific foraging habitat preferences of great blue herons. Parris (1979) in Ohio and Peifer (1979) in central Minnesota followed the movements of radio-tagged great blue herons to determine foraging habitats. Warren (1979) in Idaho and Thompson (1978) in Wisconsin examined feeding areas of great blue herons nesting in riparian habitats.

A specific issue in habitat preference studies has been the use of foraging territories by great blue herons. This question has been examined by Bayer (1978) in Oregon, Dennis (1971) in Wisconsin, Hedeon (1967) in Minnesota, Kushlan (1976) in Florida, Parris (1979) in Ohio, and Peifer (1979) in Minnesota. Cook (1978) discussed the use of foraging territories in the grey heron and Recher (1972) in the reef heron (Egretta sacra).

Recently, a much-debated facet of the colonial habits of the great blue heron has been the possible use of the colony as an "information centre". Ward and Zahavi (1973) have proposed the theory that breeding and resting colonies of birds may serve as information centers whereby birds that are unsuccessful in foraging may benefit from knowledge obtained from successful neighbors in the colony. Several studies have been conducted in attempts to test whether this hypothesis applies to breeding colonies of great blue herons. Krebs (1974) observed departures from a heronry in British Columbia. Bayer (1981) recorded heron arrivals and departures from 2 Oregon estuarine

MATERIALS AND METHODS

Departure Directions, Habitat Use, and Radio Telemetry

The study was conducted on the same heronry and area indicated in Fig. 1 (Chapter 1).

Data on departure directions of adult herons from the heronry were obtained from observations from a hill located approximately 110 m northwest of the colony. All departures except those due east and due south were observable from this vantage point. A second observer was stationed either south or east of the heronry. The presence of observers did not appear to cause herons to veer from their desired flight directions. Information recorded at these sites included the time of departure, a compass reading of the point at which a departing heron disappeared, and general weather conditions. These data were collected once/week from sunrise until 2 hours after sunrise for 2 consecutive breeding seasons.

To gain information on important feeding areas, departing herons were followed by automobile to a landing point or until the observers could no longer keep the birds in sight. The tracking was generally assumed to be random, since the first heron to leave the colony was followed, regardless of flight direction. Sources of bias in tracking were caused by difficulty in following herons travelling in directions with poor road access and difficulty in following herons feeding at distances in excess of 12 km from the study area. Birds feeding closer to the colony flew at lower altitudes and were easiest to track. The outcome of each tracking effort was categorized as a landing, a probable

landing, or a disappearance. A siting represented a non-random observation of a heron already at a feeding site. If a heron was followed to a feeding area, but tracking did not originate at the heronry, it was recorded as a landing site. Thus, the 5 observation categories were landing, probable landing, disappearance, siting, and landing site. In addition to the observation category, each site was described as to habitat and degree direction and distance from the colony. Time of day and general weather conditions were also recorded for each observation. Herons were followed in this manner for 2 consecutive breeding seasons.

During the 1981 breeding season, heron censuses were conducted on 24.5 km of the James River and approximately 14 km of a tributary of the river, Timber Creek, to determine the importance of these areas to foraging herons (Fig. 1). These censuses were conducted weekly for 3 weeks from the end of June until the middle of July of 1981. The river was surveyed by canoe and the location of each heron sighting recorded. Herons sighted on the river immediately adjacent to the heronry were not recorded, as these birds were presumed fledglings. This presumption was based on observations made during the preceeding breeding season. Adult herons were rarely observed feeding on the river in the immediate vicinity of the heronry, normally using this area only for drinking and gathering nest materials. However, fledglings were often observed feeding on the river in this vicinity. Timber Creek was searched by 3 people walking different sections of the stream.

O'Malley (1980) and presented in Appendix A.

Chi-square analysis was also used in all other statistical tests. Differences between 1980 and 1981 were tested for the following categories: (1) distances flown by birds observed landing, (2) distances flown by birds in all 5 observation categories (landing, probable landing, disappearance, siting, and landing site), (3) habitats used by birds observed landing, (4) habitats used by birds in all categories except disappearances, (5) directions flown by birds in the landing, probable landing, and disappearance categories, and (6) departure directions of herons from the colony. Chi-square analysis was also used to make the following comparisons: (1) habitats used by birds observed landing vs. habitats used by birds in all categories except disappearances for both 1980 and 1981, (2) departure directions flown by birds in the landing, probable landing, and disappearance categories in 1980 vs. the directions flown in 1981, and (3) distances from the colony of birds sighted during heron censusing on Timber Creek vs. distances of birds sighted on the James River in 1981.

RESULTS AND DISCUSSION

Feeding Habitats

Foraging habitats used by birds followed until they landed showed no significant differences between 1980 and 1981, so results were combined ($\chi^2 = 1.97$, $df = 4$, $P > 0.05$). The most important habitats were the James River and inlets, streams, and intermittent, or partially dry streams (Fig. 6). When habitats used by birds observed landing were combined with probable landings, sitings, and landing sites, there was a significant difference between habitats used in 1980 and 1981 ($\chi^2 = 35.35$, $df = 8$, $P < 0.005$). Listed in order of importance, foraging habitats for herons in these 4 observation categories combined in 1980 were streams, the James River and inlets, pastures, and intermittent streams. In 1981, the order became intermittent streams, the James River and inlets, streams, and pastures. Several times in 1981 I observed groups of up to 7 herons feeding together on fish stranded in isolated pools of intermittent streams. These birds flew before ages could be determined.

Other studies of great blue herons nesting in riparian systems have also indicated heavy utilization of rivers and tributary streams for feeding. Thompson (1978) reported that 86% of observed herons foraged in the Mississippi River floodplain. Warren (1979) found that herons nesting along a river in Idaho foraged primarily on tributaries of the river. Parris (1979) followed the movements of herons nesting on Lake Erie. Important foraging areas in these colonies were shallow water areas of marshes and rivers.

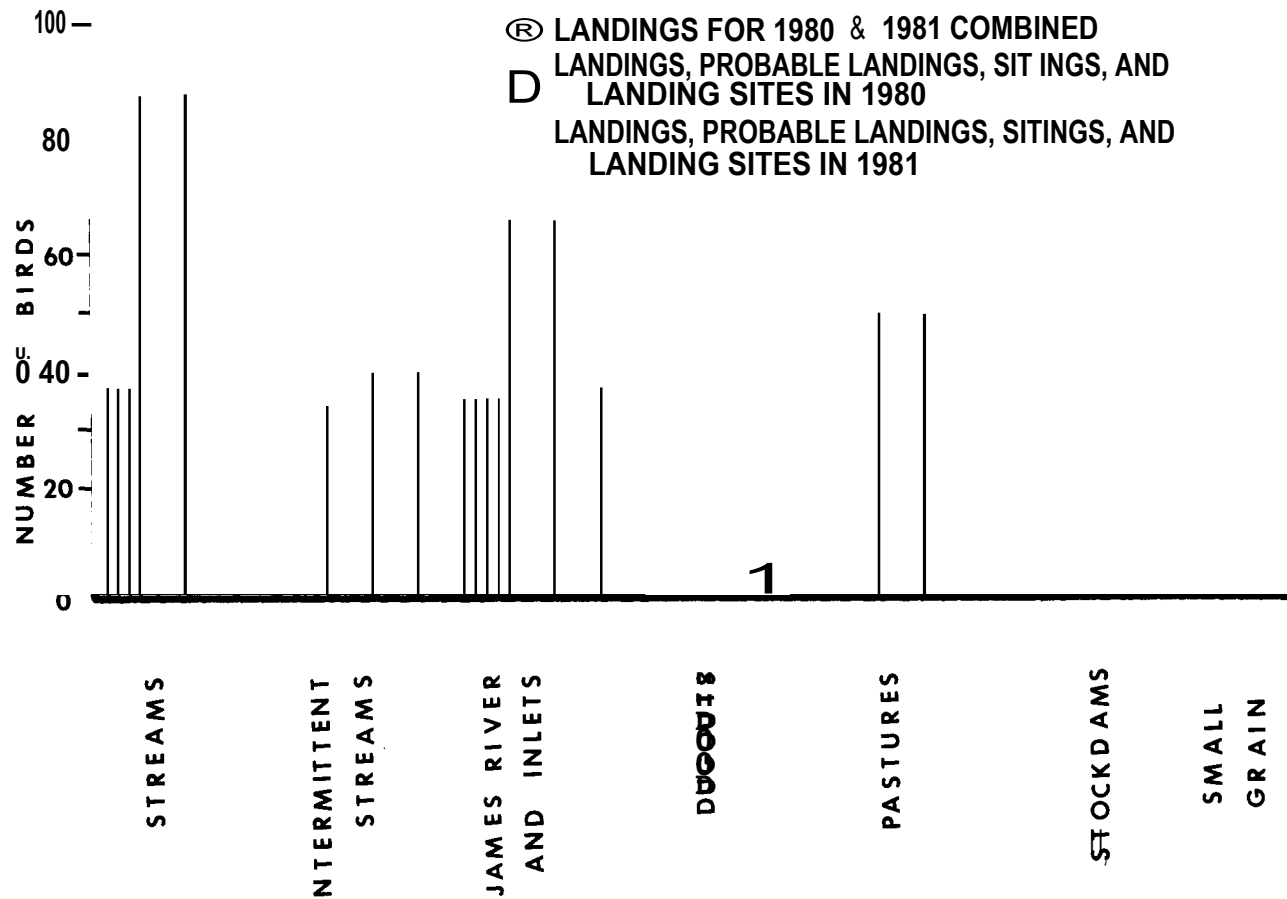


Fig. 6. Number of great blue herons from the Glendale heronry using various habitats in 1980 and 1981. Landings and probable landings resulted from following herons from the heronry by automobile to a landing or probable landing site. Sitings represent non-random observations of herons at feeding sites. Landing sites resulted from following herons to feeding sites where tracking did not originate at the heronry. Landings in 1980 and 1981 were combined due to similar results for the 2 years ($\chi^2 = 1.97$, $df = 4$).

The use of terrestrial habitats by great blue herons as foraging and resting areas has been reported by several authors (Bent 1926, Palmer 1962, Peifer 1979, Warren 1979). Considering the landing category only, 19% of the herons in my study were observed in the terrestrial habitats of pastures and small grain cropland. When the 4 categories were combined, 25% and 17% of the birds were observed in terrestrial habitats in 1980 and 1981, respectively. Since we did not routinely observe the feeding patterns of the herons that we followed, it is possible that some terrestrial areas were used for resting, rather than feeding, as Warren (1979) observed in Idaho. However, 5 or 6 herons were observed preying on 13-lined ground squirrels (Spermophilus tridecemlineatus) during the course of my study. Peifer (1979) reported that 2 radio-tagged great blue herons in Minnesota had a mixed diet of fish and terrestrial mammals. Parris (1979) in Ohio and Thompson (1979) in Wisconsin determined that herons in their studies did not use upland areas for feeding.

Locations of Radio-tagged Herons

Capture sites and subsequent locations of 5 radio-tagged herons as determined by radio telemetry equipment are presented in Figures 7 and 8. Birds numbered 8 and 17 were each located 3 times after capture. These radios may have malfunctioned or become dislodged from the birds.

Although bird #5 was captured on Timber Creek, it was not again located in this area. One possible explanation is the stress of capture. Another possibility is that the bird was feeding opportunistically in an area not normally occurring in its feeding range. Bird #5 restricted

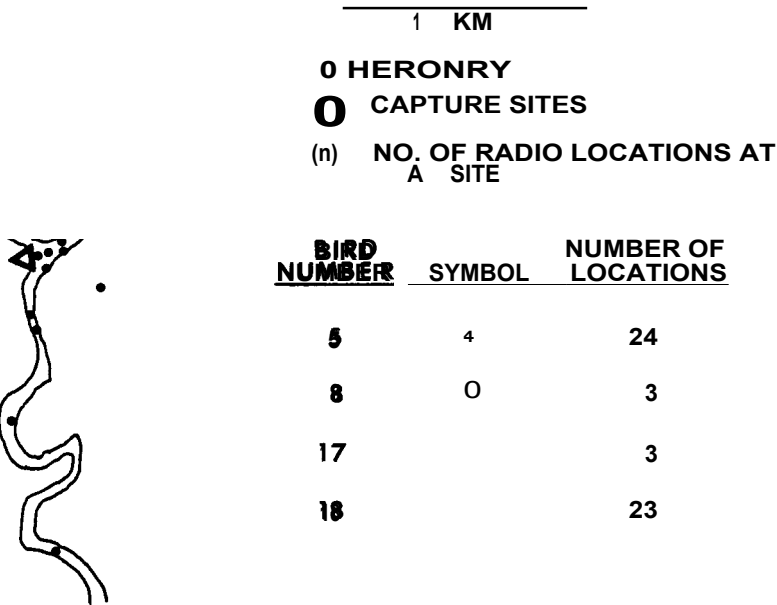
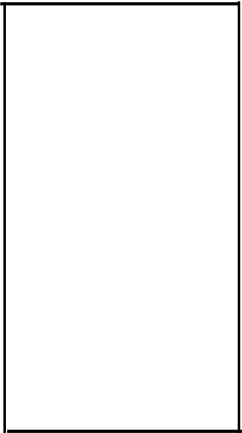


Fig. 7. Capture sites and radiolocations of radio-tagged great blue herons numbered 5, 8, 17, and 18'from the Glendale heronry, 1981.

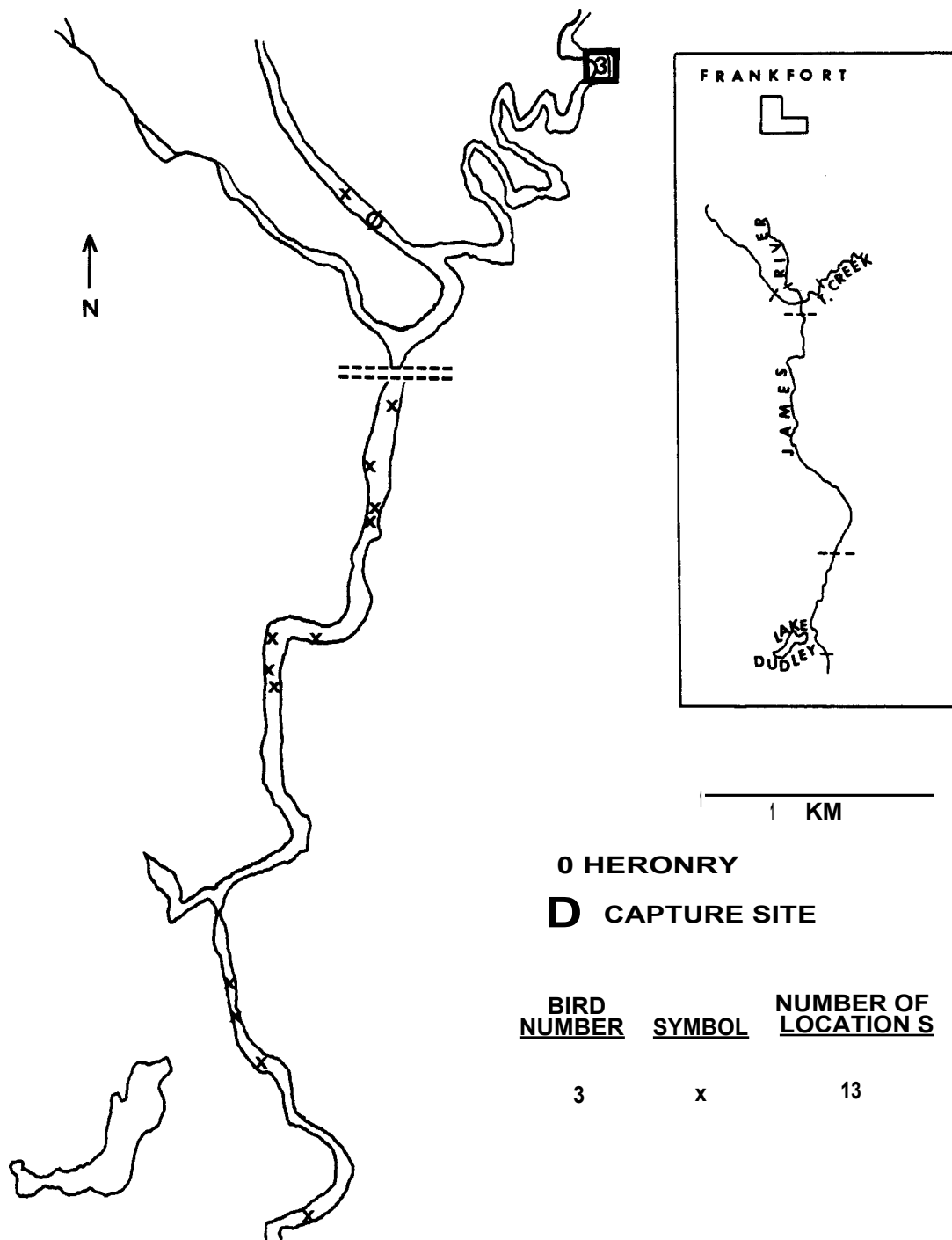


Fig. 8. Capture site and radiolocations of radio-tagged great blue heron numbered 3 from the Glendale heronry, 1981.

its movements to an area of the river approximately 3 km north of the colony. The maximum straight-line distance between feeding sites

Bird #18 was captured on an intermittent stream close to the colony. This bird continued to feed on the stream until it became dry in July of 1981. The bird also fed on the river north and south of the colony, within a 2.5 km range. Two of 23 radiolocations were in terrestrial habitats.

Bird #3 was captured on Timber Creek and located once on the river near its capture site. Thereafter, this heron was found on the river approximately 15 km south of the heronry. While feeding in this area, the bird had a maximum linear range of 4.1 km. Peifer (1979) reported that 4 radio-tagged great blue herons in central Minnesota actively defended an average of 0.98 km of shoreline. The defended areas in his study ranged from 0.69-1.37 km. None of the 13 radiolocations of bird #3 was in terrestrial habitats or on Lake Dudley.

Many authors have discussed the use of foraging territories by great blue herons. Kushlan (1978) states that the degree of dispersion of the food resource may determine the territoriality of this bird. In the event of concentrated food patches, great blue herons tend to forage non-territorially in groups. If food is widely dispersed, they are more likely to defend a large territory.

Bayer (1978) found both territorial and non-territorial great blue herons in an Oregon colony. The same territory was sometimes defended for 3 consecutive years. Dennis (1971) reported that herons

nesting on an area of the Mississippi River in Wisconsin defended feeding territories throughout the summer and fall, possibly using tall trees as boundaries. Hedeon (1967) observed herons in Minnesota holding feeding territories during the breeding season. Peifer (1979) followed 4 radio-tagged herons in Minnesota and found that each defended 1 permanent feeding area away from the colony. Parris (1979) followed 18 radio-tagged great blue herons nesting on Lake Erie and concluded that the birds were non-territorial and defended only an individual distance from other herons.

The James River would be categorized as an area with a widely dispersed food supply. Based on personal observations during 2 breeding seasons, the adult herons nesting in this colony appear to defend foraging territories. Although direct observations were not made of territory defense by radio-tagged birds, unmarked herons were observed defending areas of Timber Creek. Adult herons were rarely seen feeding within sight of each other, although fledglings were often seen in foraging groups. From the locations of capture sites, it appears that the herons did not always forage within their territorial bounds, but may have demonstrated opportunistic feeding in temporarily undefended territories. Observations of groups of herons feeding together on stranded fish in pools may have also been birds feeding opportunistically if the birds were breeding adults. Another possibility is that the herons were groups of fledglings feeding together.

Table 1. Straight-line distances flown to feeding sites in 1980 and 1981 from the Glendale heronry, South Dakota (Percentages are in parentheses).

	N = .130	N = 486
DTSTANCE (KM)	LANDINGS ONLY	ALL OBSERVATION CATEGORIES
0.0-2.0	81 (62)	239 (49)
2.1-4.0	30 (23)	110 (22)
4.1-6.0	7 (5)	65 (13)
6.1-8.0	5 (4)	28 (6)
8.1-10.0	3 (2)	13 (3)
10.1-12.0	1 (1)	11 (2)
12.1-14.0	1 (1)	8 (2)
14.1-16.0	0 (0)	8 (2)
16.1-18.0	2 (2)	4 (1)

3 species of wading birds radio-tagged in Florida, cattle egrets (Bubulcus ibis), white ibises (Eudocimus albus), and little blue herons (Florida caerulea), travelled a maximum distance of 20 miles (32.2 km) to feeding areas. The average distance flown by Glendale colony herons in the 5 observation categories was 3.15 km, with a maximum distance flown of 24.40 km. Since 15.4% of these birds disappeared, these figures likely underestimate the actual average and maximum distances flown by birds in the 5 observation categories.

Heron Censusing on Timber Creek and the James River

The distances of heron sightings on Timber Creek differed significantly from sighting distances on the James River (Table 2) ($\chi^2 = 31.54$, $df = 4$, $P < 0.005$). This may be due to the distance interval of 6.1-8.0 km from the heronry, an area which was nearly dry on Timber Creek. Otherwise, herons occurred in fairly even densities in all distance intervals on both Timber Creek and the James River.

Birds sighted on Timber Creek occurred at a mean density of 2.33 birds/km of stream containing water. Dry areas of the stream were excluded in this calculation.

An equal number of river miles was surveyed north and south of the colony. Mean density of birds sighted on the James River was 3.56 birds/km. Of the birds sighted on the river, 41% occurred north and 59% south of the colony.

Table 2. Straight-line distances of censused herons from the Glendale
heronry, South Dakota, 1981 (Percentages are in parentheses).

	N = 96	N = 253
DISTANCE (KM)	TIMBER CREEK	JAMES RIVER
0.0-2.0	15 (16)	69 (27)
2.1-4.0	27 (28)	74 (29)
4.1-6.0	28 (29)	28 (11)
6.1-8.0 *	7 (7)	56 (22)
8.1-10.0	19 (20)	26 (11)

* This portion of Timber Creek was almost completely dry during the
censusing period.

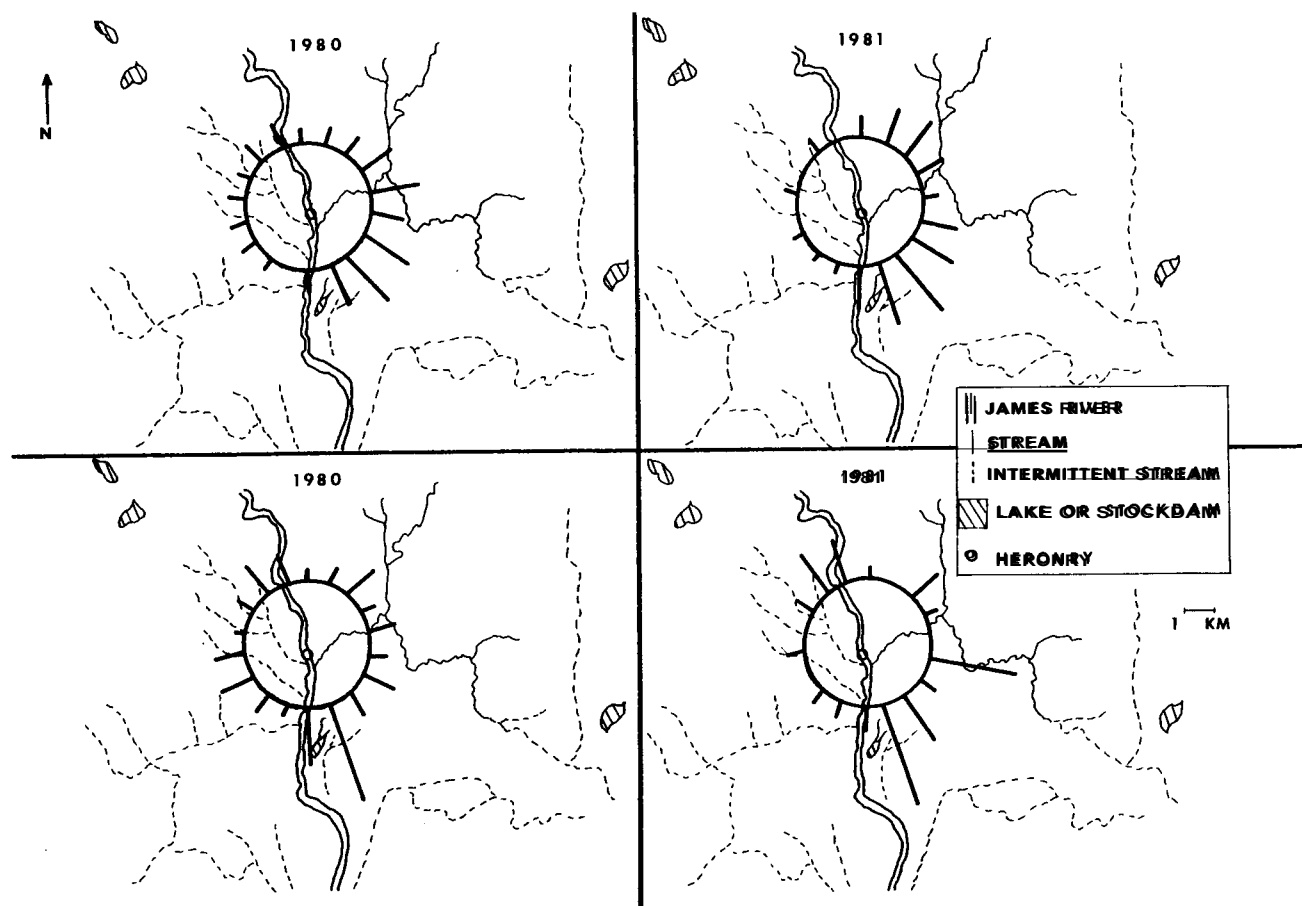


Fig. 9. Percentages of departure directions from the Glendale heronry in each 20° interval based on compass directions. Upper tier represents points of disappearance of birds departing from the heronry (D Herons); lower tier represents degree directions of landings, probable landings, and disappearances from the colony (L Herons) for 1980 and 1981. Birds in the upper tier were observed departing from the colony and points of disappearance noted by compass directions. Birds in the lower tier were followed by automobile until they landed, probably landed, or disappeared before a definite intention to land was shown.

(1980, $\chi^2 = 79.55$, $df = 17$, $P < 0.005$; 1981, $\chi^2 = 29.06$, $df = 14$, $P < 0.05$). This is not unexpected, since directions of D Herons represent flight line patterns, while directions of L Herons are based on feeding sites located after following herons. It is debatable whether the directions of D Herons or L Herons are the more accurate representation of flight directions to feeding sites. Personal observations during the study indicated that herons tended to fly in a relatively straight line toward their destinations. But, if birds were using the river as a landmark to fly toward a site not located on the river, departure directions would be misleading. The most accurate description of the actual directions flown by herons to feeding sites would likely fall somewhere between the directions indicated for D Herons and L Herons. The results of heron censusing of the James River indicated that 41% of the heron sightings occurred north and 59% south of the heronry. Comparison of the censusing results with departure direction data indicates that departure data may underestimate the percentage of herons feeding on the river north of the colony. Another possibility is that some birds sighted north of the heronry may have been using a second or third feeding site after first leaving the colony.

Departure Clumping

Ward and Zahavi (1973) have theorized that breeding colonies of birds may serve as "information centres", where unsuccessful birds may enjoy increased foraging success because of information provided by successfully-foraging birds. Krebs (1974) tested the applicability of this theory to great blue heron colonies. After observing departures

from a heronry in British Columbia, he concluded that the birds tended to leave the colony in groups and tended to shift from 1 area to another in unison. Bayer (1981) recorded arrivals and departures of great blue herons for 2 Oregon estuarine colonies. Since most herons departed alone, he postulated that clumping of departures may partly be due to coincidence. Pratt (1980) observed both departing herons from a California colony and heron landings at a feeding area nearby. The author concluded that the herons in this colony were not following each other, but rather departure times were determined by timing of nest relief. She theorized that the practice of following other herons to feeding areas would be more advantageous in seasonally-fluctuating wetlands than in estuarine locations. Des Granges (1978) reported that great blue herons nesting in a southern Quebec colony usually flew in the direction taken by the last bird to arrive at or depart from the colony. He concluded that the herons were influenced by the flight directions of other herons in the colony, but did not overlook the possibility that other factors may have been involved. Des Granges also found a positive correlation between colony size and the variability of an individual heron's catch rate. His interpretation of this correlation was that members of a larger colony are more likely to exploit unpredictable food supplies. Custer and Osborn (1978) found a correlation between ephemeral food sources and herons following each other. Werschkul et al. (1977) correlated fledging success and nest density of heron colonies. The authors theorized that increased fledging

success may result from increased foraging success due to feeding site information exchanged at the colony.

Chi-square analysis on herons departing from the Glendale colony indicated significant departure clumping of birds flying in the same direction as the previous departing heron ($\chi^2 = 130.30$, $df = 26$, $p < 0.005$). Departure clumping is especially evident during the first 1-minute interval when 172 birds departed, as compared with 116 birds expected to depart (Fig. 10). Because of the terrain and distances flown by departing herons, few observations were possible of actual landing sites of these birds. For this reason, this analysis does not allow me to conclude that herons were following each other to feeding sites, but only that a significant degree of departure clumping in the same flight directions occurred.

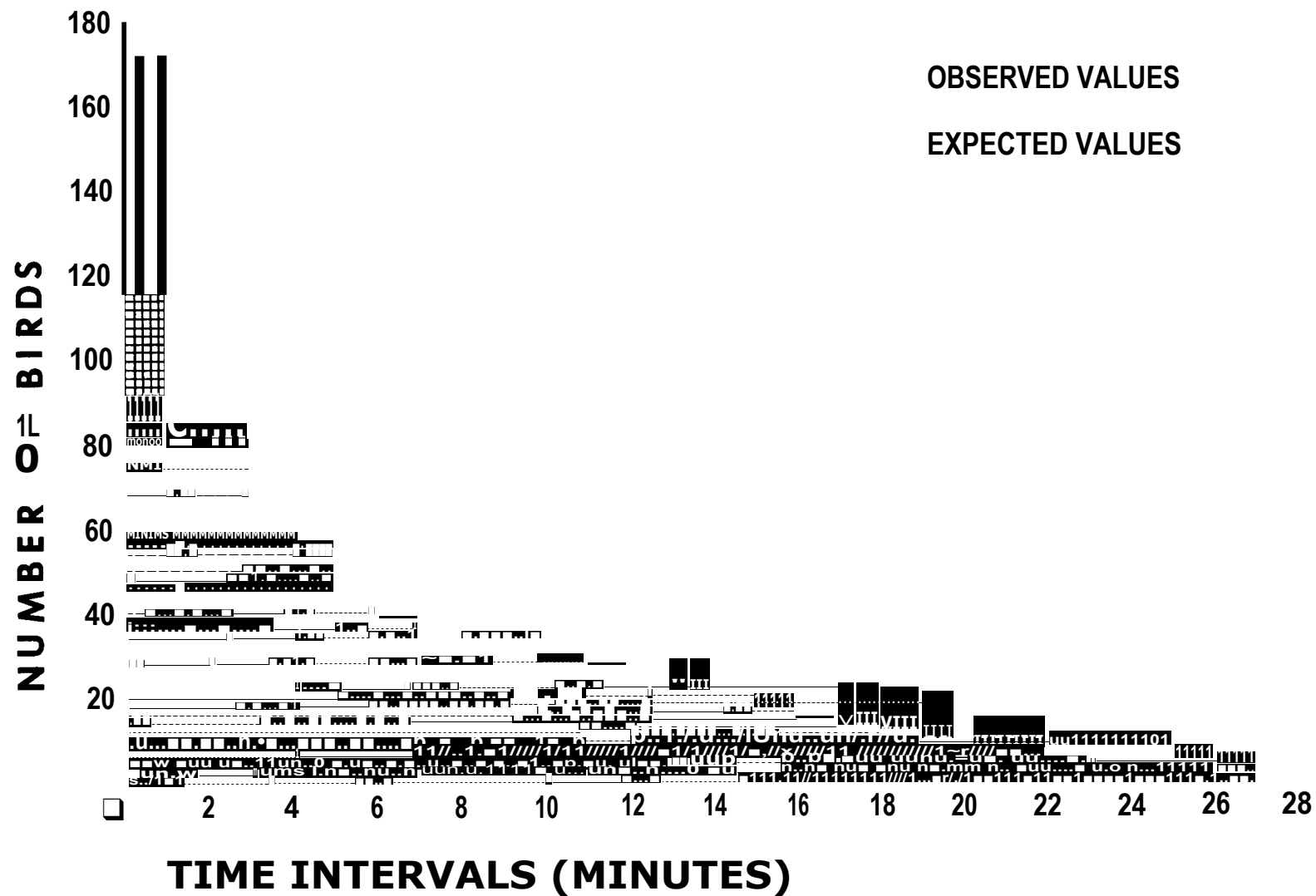


Fig. 10. Observed and expected departure frequencies of great blue herons flying in the same directions from the Glendale heronry in 1980. Expected values were calculated using a method described by O'Malley (1980).

SUMMARY

Important feeding habitats of adult great blue herons included the James River and its inlets, streams, intermittent streams, and pastures. Five radio-tagged birds foraged in areas from 2.0 to 4.1 km in linear range. Forty-eight of 65 radiolocations occurred on the James River and its inlets. Unmarked herons that were followed until they landed or disappeared travelled average and maximum distances of 3.15 and 24.40 km, respectively. During habitat searching in 1981, herons occurred at a mean density of 2.33 birds/km of Timber Creek containing water and 3.56 birds/km of the James River.

Observations of departure directions of herons indicated a significant difference in directions flown during 1980 and 1981, presumably due to the drought conditions in the latter year. A significant amount of departure clumping in the same flight directions occurred, although field work completed during the study did not allow the conclusion that herons were following each other to feeding areas.

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APPENDIX

APPENDIX A. Calculation of expected values for testing clumping of
departures from the Glendale heronry, South Dakota, 1981.

1-MINUTE INTERVAL (i)	OBSERVED FREQUENCY (O _i)	ESTIMATED FREQUENCY (P _i)	EXPECTED FREQUENCY
1	172.0	0.1190	115.8
2	76.0	0.1048	102.0
3	87.0	0.0924	89.9
4	60.0	0.0814	79.2
5	63.0	0.0717	69.8
6	46.0	0.0632	61.5
7	39.0	0.0556	54.1
8	28.0	0.0490	47.7
9	43.0	0.0432	42.0
10	41.0	0.0380	37.0
11	31.0	0.0335	32.6
12	28.0	0.0295	28.7
13	24.0	0.0260	25.3
14	30.0	0.0229	22.3
15	20.0	0.0202	19.7
16	21.0	0.0178	17.3
17	16.0	0.0159	15.3
18	24.0	0.0138	13.4
19	23.0	0.0122	11.9
20	22.0	0.0107	10.4
21	16.0	0.0094	9.1
22	16.0	0.0083	8.1
23	10.0	0.0073	7.1
24	10.0	0.0065	6.3
25	10.0	0.0057	5.5
26	9.0	0.0050	4.9
27	8.0	0.0044	4.3

The mean inter-departure interval: $\bar{x} = 1/N \sum_i (O_i) = 8194/972 = 8.42$

$$\bar{g} = 1 - 1/\bar{x} = .881$$

$$P_i = (\bar{g})^i - 1(\bar{g})^{i-1}$$

The expected frequency = $(P_i)(N)$ for each 1-minute interval.