

for 19-day-old *Momotus momota* (11/h). One parent (#2) visited with significantly greater frequency than the other ($\chi^2 = 16.86$; $df = 1$, $P < 0.005$; excluding visits affected by human disturbance), but this division of effort may not be representative of that over an entire day. Mean time spent per visit (room entry to exit) was 79.5 sec ($N = 123$; $SE = \pm 4.7$ sec). Few food items carried could be identified, but adult lepidopterans (≥ 3 species) represented at least 13% of provisions. At 17:30, 24 June, the (unmarked) nestlings appeared healthy and weighed 45, 43, 41, and 33 g; they had collectively gained 24 g during the preceding 3 days. Observations of this brood were terminated well before its projected potential fledging date.

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Arrival and departure patterns of Great Blue Herons at a South Dakota colony.—Two of the potential benefits of colonial nesting or roosting are predator protection (Lack, *Ecological Adaptations for Breeding in Birds*, Methuen and Co., London, England, 1968) and the use of the colony or roost as an “information centre” (Ward and Zahavi, *Ibis* 115:517–534, 1973). Weatherhead (*Am. Nat.* 121:237–243, 1983) recently suggested that the principal advantages of communal roosting may differ among birds in the same roost. Central roosters may benefit more from predator protection provided by roosting, rather than from information exchange, whereas less-dominant birds roosting on the edge may derive the most benefit from information exchange on favorable feeding sites. Evans (*Auk* 99:24–30, 1982) hypothesized that colonies in group-foraging birds may play an important role in preventing dispersal of foraging individuals by serving as central assembly points.

The Great Blue Heron (*Ardea herodias*) has been discussed as a colonial nester that may use the colony as a source of information on feeding areas (for differing opinions see Krebs, *Behaviour* 51:99–134, 1974; Pratt, *Wilson Bull.* 92:489–496, 1980; Bayer, *Auk* 98:589–595, 1981). Weatherhead’s (1983) “two-principle strategies” hypothesis may provide an explanation for these differences.

Here, we report on departure directions, arrival and departure frequencies, the degree of colony synchrony, and the extent of clumping at arrival and departure from a colony of Great Blue Herons.

Study area and methods.—We observed arrivals and departures of Great Blue Herons at the Glendale heronry on the James River in Spink County, South Dakota. The heronry consisted of 66 active nests, all of which were visible from a blind constructed in a tree 50 m across the river from the heronry. A large opening allowed a view of the heronry, and smaller openings permitted the viewing of all birds approaching or departing from the colony. Observations were made from the blind from sunrise to sunset once each week from May through August 1980 for 156 h; the number of active nests did not change substantially

during this time. Time and flight direction (N, NE, E, SE, S, SW, W, NW) were recorded for all nest departures and arrivals.

To determine the extent of clumping during arrivals and departures, each arrival or departure was placed in one of four categories: (1) an arrival from the same direction as the most recent arrival; (2) an arrival from a different direction than the previous arrival; (3) a departure in the same direction as the previous departure; or (4) a departure in a different direction than the most recent departure. Times between successive arrivals or departures were measured in 1-min intervals. The arrival and departure patterns within the four categories were tested statistically using a Chi-square analysis described by O'Malley and Evans (Can. J. Zool. 60:1024–1031, 1982) in work on White Pelicans (*Pelecanus erythrorhynchos*) in Manitoba. This method tests for clumping by testing arrival and departure distributions for randomness and is applicable to our study because, as in their study, our data were derived from observations of an inland colony, not influenced by tides.

In an effort to determine more precise departure directions, observations were also made from a hill located approximately 110 m northwest of the heronry. All departures except those due east and due south were observable from this vantage point. Another observer was stationed so that he or she could see herons departing east and south. Information recorded at these sites included the time of departure and a compass reading of the point at which a bird disappeared. These data were collected once each week from sunrise until 2 h after sunrise for 2 consecutive breeding seasons in 1980 and 1981 and were used only in calculation of predominant flight lines.

The relationship between arrivals/h and hour of the day was analyzed by analysis of variance. Potential relationships between arrivals/h and hour of the day were analyzed using regression analyses testing the linear, quadratic, cubic, and quartic models. Analyses of arrivals and departures were divided into early (15 May–12 June) and late (20 June–29 July) portions of the 1980 breeding season.

Arrival and departure rates, synchrony, and direction.—Hérons arrived at the colony at an average rate of 12.4 herons/h. The average departure rate was 10.1 birds/h. Maximum hourly arrival and departure rates were 51 herons/h and 45 herons/h, respectively. Theoretically, arrival and departure rates should be similar, as each arrival will presumably be followed by a departure and vice versa. The difference in the arrival and departure rates can be partially explained by human sampling error. An arriving bird emits a "landing call" when returning to the nest to alert its mate (Mock, Wilson Bull. 88:185–230, 1976), making arrivals easy to detect. On the other hand, birds depart quietly and occasionally may have been missed by observers during periods of great activity in the heronry.

Colony synchrony can be measured by dividing hourly arrival or departure rates by the total number of breeding herons (Bayer 1981). The average degree of colony synchrony for arrivals was 9.4% of breeding birds/h and 7.6% for departures. The maximum arrival and departure synchrony rates were 38.6% and 34.1% of breeding birds/h, respectively.

Bayer (1981) defined the average time between an individual bird's arrival or departure as the inverse of the mean of the average hourly arrival and departure rates. The mean of the average hourly arrival rate was 0.09 arrivals/heron/h of observation. The corresponding departure rate was 0.08 departures/heron/h of observation. An average of 11.1 h elapsed between an individual's arrivals and 12.5 h between an individual's departures.

Relationships between arrival and departure and time of day.—The relationship (ANOVA) between total arrivals/h and the different hours of the day (06:00–21:00) did not differ significantly in either the early or late portions of the breeding season. Departures for the early period were significantly related to hour of the day (ANOVA; $F = 1.97$, $P = 0.04$) but departures for the late period were not significantly related to time of day. When departures/h for the early period were regressed against hour of the day, the quadratic model, which

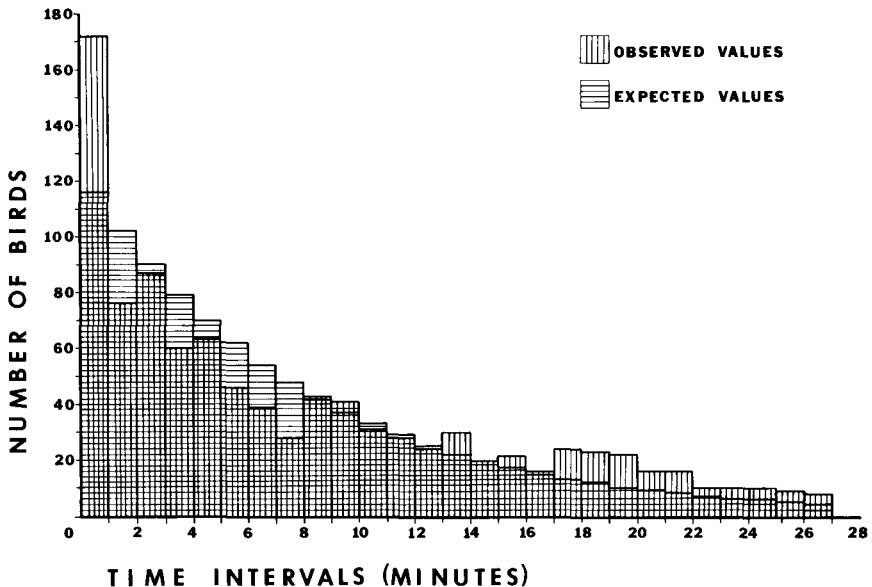


FIG. 1. Observed and expected (based on O'Malley and Evans, *Can. J. Zool.* 60:1024–1031, 1982) departure frequencies of Great Blue Herons flying in the same directions from the Glendale heronry in 1980.

explained 24.9% ($N = 62$) of the variance, was significantly better than the linear model; the cubic and quartic models provided no significant improvement over the quadratic model.

Arrival and departure clumping.—Departures in the same directions were nonrandomly distributed in time ($\chi^2 = 112.62$, $df = 25$, $P < 0.005$) (Fig. 1); however, departures in different directions also exhibited a clumped distribution ($\chi^2 = 201.29$, $df = 25$, $P < 0.005$). A similar clumped pattern resulted from the analysis of arrivals from the same directions ($\chi^2 = 200.97$, $df = 25$, $P < 0.005$) and arrivals from different directions ($\chi^2 = 201.29$, $df = 25$, $P < 0.005$). Using Bayer's (1981) definition of a flock as a group of birds departing one min or less apart, roughly one-third of Glendale colony herons arrived and departed in flocks. Thirty-five percent of arrivals and 28% of departures occurred in flocks.

Discussion.—Data presented here on colony synchrony and average times between an individual bird's arrivals or departures suggest that Glendale colony herons arrived and departed infrequently and solitarily. This conclusion is misleading, however, as these figures represent averages. The fact that arrivals and departures were clumped in both the same and different directions indicates that a significant number of birds tended to arrive and depart in flocks but did not necessarily follow each other to and from feeding areas. Although some researchers have discussed relationships between Great Blue Herons' departures and time of day (Brandman, Ph.D. diss., Univ. California, Los Angeles, California, 1976; Warren, M.S. thesis, Univ. Idaho, Moscow, Idaho, 1979), our analysis indicated that arrivals or departures could not be predicted well on the basis of time of day.

Heron demonstrating clumping during departures from heronries with a few predominant flight lines will likely show significant departure clumping in the same direction. The Glendale

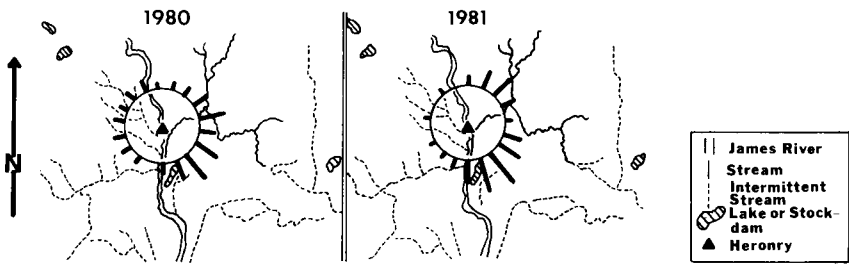


FIG. 2. Relative distribution of departure directions to nearest 20° interval based on points of disappearance of herons from the Glendale heronry in 1980 and 1981.

colony had from 6–8 predominant flight lines and numerous lesser routes (Fig. 2). Part of the directional clumping of arrivals and departures in our study may have been related to use of these dominant flight lines. One possible explanation of the significant arrival and departure clumping by Glendale colony herons may be provided by findings (Pratt 1980) based on observations of a California heronry. Pratt (1980) reported that the timing of nest departures was dependent on the times at which nest relief occurred. Assuming that herons spend a similar amount of time in the process of nest relief and that they tend to arrive in flocks, birds would also tend to depart in flocks.

Krebs (1974) reported that herons leaving a colony in British Columbia tended to depart in groups and shift from one area to another in unison. DesGranges (Proc. Colonial Waterbird Group 2:192–201, 1978) found that successive departures from a Quebec colony were usually in the same direction, leading him to conclude that the birds were using the colony as an information source on local feeding conditions. Bayer (1981) and Pratt (1980) found that herons in their respective studies did not follow each other to feeding areas.

Although some herons in the Glendale colony may have been following others to foraging sites, clumping of departures in the same and different directions indicates that other factors are involved. Clumped arrivals from the same and different directions cause similar interpretation difficulties. We suggest that the information hypothesis provides at best a partial explanation for arrival clumping in the Glendale colony.

Weatherhead's (1983) "two-principle strategies" hypothesis would explain directional departure clumping in some, perhaps subordinate, birds, while not suggesting that all birds follow others for foraging reasons. We feel the departure and arrival patterns in the Glendale colony may indeed reflect social relationships and may differ considerably among individual herons. Some clumping of arrivals and departures in the same direction could be explained by the predominance of several flight paths over others (Bayer, *Auk* 99:31–40, 1982). Because of the lack of group foraging in Glendale colony herons, we did not feel Evans' (1982) hypothesis was applicable. We suggest that much clumping of departures or arrivals may occur simply through social facilitation of "flight-primed" birds that take flight after observing other colony or feeding area departures (Bayer 1982); this could explain the clumping observed in both arrivals and departures. As suggested by Bayer (1982), flights involving information exchange are socially facilitated, but all socially facilitated flights need not involve information exchange.

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Notes on the relationships of island area and distance from mainland to the presence of Herring Gull colonies in Lake Nipigon, Ontario.—Breeding colonies of most gulls and terns are more common on islands than on mainland (Bent, U.S. Natl. Mus. Bull. 113, 1921; Tinbergen, *The Herring Gull's World*, Basic Books, New York, New York, 1961). This observation is most often explained in terms of avoidance of predation (Strong, *Auk* 31: 22–49, 178–200, 1914; Burger and Lesser, *Ibis* 120:433–449, 1978). Avoidance of predation by birds (e.g., American Crows, *Corvus brachyrhynchos*; Common Ravens, *Corvus corax*; Great Blue Herons, *Ardea herodias*) and by mammals (e.g., humans; dogs, *Canis familiaris*; red fox, *Vulpes vulpes*; mink, *Mustela vison*; otter, *Lutra canadensis*) may be important in explaining the island preference of Herring Gulls (*Larus argentatus*) (cf. Harris, *Ibis* 106: 432–456).

Other factors are involved in colony selection by gulls and terns, such as proximity to feeding areas, vegetation type and plant density (Burger and Lesser, 1978), height above water level (McNicholl, *Auk* 92:98–104, 1975; Southern, *Auk* 94:469–478, 1977), exposure to open water (Burger and Lesser, 1978), and suitability of nesting substrates (Ludwig, *Auk* 91:575–594, 1974).

The reconnaissance nature of this study precludes discussion of the relative influences upon colony selection of factors other than island area and distance from mainland. This paper reports on the relationships of island area and distance from mainland to the presence of Herring Gull breeding colonies in Lake Nipigon, Ontario.

Methods.—Research was conducted along with a study of the island biogeography of seed plants in Lake Nipigon. The area is described by Timoney (*Can. Field-Nat.* 97:16–25, 1983).

From mid-June to mid-August 1979, the presence or absence of Herring Gull breeding colonies was noted for 48 islands. A colony or pair was recorded present if at least one nest with incubated eggs or young was observed. If no nests, or only abandoned nests were observed, no colony was recorded. Island areas were determined by planimeter from Canada NTS maps (scale = 1:50,000). Distance from mainland was measured as the shortest distance between an island's shore and the mainland shore.

Results.—Islands ranged in size from <0.1 ha to 19.4 ha and in distance from mainland from 50 m to 10.5 km. Distance from mainland and island area were not correlated significantly ($r = 0.22$, $0.2 > P > 0.1$). No mainland colonies were found.

Island area bore no linear correlation with presence-absence of Herring Gull colonies (Kendall's Tau, two-tailed P , Mann-Whitney U -test: $\rho = 0.05$, $P = 0.76$). The six smallest islands (all <0.1 ha) also were the lowest and flattest and were subject to inundation. None of these low-lying islands supported a Herring Gull colony. Timoney observed waves or spray saturating four of these islands. The meager heights above water and the near barrenness of the other two small islands (with only mosses and *Potentilla norvegica* in rock cracks, and saxicolous lichens) suggest that they too were inundated regularly.