Foraging Behaviour of American White Pelicans
(*Pelecanus erythrorhynchos*)

by

Blair F. McMahon

A thesis
presented to the University of Manitoba
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TABLE OF CONTENTS

ABSTRACT

Foraging behaviour of American White Pelicans (P. erythrorhynchos) was studied at Dauphin River, Manitoba, Canada in 1985 and 1986. Pelicans concentrated foraging activity around dusk and dawn and were more active at night than during the day. Time-dependent changes in activity appeared related to predicted fish abundance. Proximate factors such as temperature and wind speed also modified the timing of foraging activity. Most pelicans at Dauphin River foraged near the base of rapids, especially at night. Foragers preferred slow-moving water less than one meter in depth.

Pelicans most frequently joined small foraging flocks. The total number recruited to flocks increased with flock size. Only during daylight hours did pelicans selectively join flocks that were capturing prey. During the day, pelicans departed a flock when capture rates were declining.

Pelicans used six distinct foraging strategies which differed in flock size, structure, relative degree of coordination among participating flock members and foraging success. Only uncoordinated foraging strategies were frequently formed by the restructuring of existing flocks. The most coordinated strategies were also the most effective and, except for Semicircles, were employed by the most foragers.

Semicircles were the most highly coordinated foraging strategy of all. Pelicans using this strategy captured the largest number and size of fish, but could evidently use this strategy only in special circumstances of prey clumping and location. The greater feeding success of pelicans using coordinated strategies indicates a degree of cooperation. Socially facilitated feeding behaviour was also demonstrated by a positive relationship between rates of bill dipping and flock size independent of prey capture. Other foraging adaptations included flock movement in the direction of greatest foraging success which was higher in the front than the middle or back of flocks, "leap-frogging" from the rear to the front of flocks, and enhanced search effort in the form of increased rate and duration of bill dipping combined with decreased turning immediately after prey capture. Pelicans also preferentially foraged in habitats where rates of prey capture were highest.

ACKNOWLEDGEMENTS

Dr. Roger Evans gave me the chance to work on the topic of my choice. I am grateful for his guidance, ideas and skill at editing. I also want to extend a special word of thanks to my parents.

The people at Anama Bay were very friendly and helpful throughout the course of this study. The friendship of Helgy and Dale Einarsson will long be cherished. Chris Einarsson was always there to cheer me up if I was feeling down. Huey Hunter and Ken Campbell provided valuable information pertinent to this study. The compassion and warmth of Peter and Anne Davidson, from Oakview, will long be remembered. Ken and John Sigurdson provided a welcomed distraction from what otherwise would have been a lonely existence. Stuart MacMillan has been a close friend during my years as a graduate student.

Dr. Robert Barclay provided the infrared scope used during this study. I want to thank William Koonz and Ken De Smet for their comments on this thesis. Dr. Rick Baydack and Dr. William Pruitt reviewed this thesis and served as committee members. This work was supported by a grant from the Wildlife Branch of the Manitoba Department of Natural Resources and a grant from the Natural Science and Engineering Council of Canada presented to Dr. Roger Evans.

This thesis is dedicated to both God and my wife, May McMahon. May has been my best friend, my counsellor and my dearest love. She supported me and gave me the perseverance to finish the task.

LIST OF FIGURES

LIST OF TABLES

Table Page

GENERAL INTRODUCTION

American White Pelicans (Pelecanus erythrorhynchos) breed from southern interior British Columbia to western Ontario in Canada, south to California, northern Utah, southern Montana and South Dakota in the United States (Godfrey 1986). In Manitoba, pelicans breed on the islands and reefs of several shallow lakes in the southern half of the province. Pelicans travel up to 100 km from their breeding colonies to lakes, rivers and marshes where they feed (Palmer 1976, Lingle and Sloan 1980). Pelicans prefer to feed in shallow waterbodies (Knopf and Kennedy 1980, Lingle and Sloan 1980). They are surface feeders which capture prey by plunging their heads under water and scooping up fish in their gular pouches. Pelicans forage throughout the day, but have peaks of feeding activity in the early morning and late evening (Palmer 1976). Some studies suggest that pelicans also forage at night (Schaller 1964, O'Malley and Evans 1984). As my first objective in this study, surveys of Dauphin River, Manitoba, were performed in 1985 and 1986, to determine where pelicans foraged and loafed during the day and night, and to identify factors which potentially influenced abundance, size and location of foraging and loafing flocks. This material is treated in Chapter 1.

As indicated above, most American White Pelicans foraged in groups. For group foragers, the ability to find food can be significantly increased when birds use the presence or absence of conspecifics as a measure of food availability and location (Waite 1981), or actively join successful foragers (local enhancement, Thorpe 1956). For seabirds, flocks often form around a single forager that locates food (Hoffman *et al*. 1981). Flocks subsequently build up rapidly until the food source dissipates or is depleted, then disband as feeding rates drop off (Bartholomew 1942, Porter and Sealy 1982). A second objective of this study (Chapter 2) was to determine how foraging flocks form and breakup. The importance of food availability on the decision to join or leave a flock was also examined.

Pelican foraging flocks can exhibit a range of sizes, shapes and may differ markedly in the extent to which activities within the group are coordinated as they search for food. Recognizably different patterns of foraging will be referred to as different foraging strategies. Many species use a variety of such strategies. American Kestrels (*Falco sparverius*), for example, not only search for prey while actively flying and hovering, but also use a sit-and-wait strategy and will occasionally hawk for insects (Rudolph 1982). A similar classification of strategies was used for Northern Shrikes (*Lanius excubitor*)(McNicholl 1972). Identification, description and analysis of pelican foraging strategies constituted a primary part of this study (Chapter 3). Most studies of pelican foraging describe cooperative feeding flocks in which foragers either trap or herd a school of fish (Cottam _et_ _al_. 1942, Anderson 1987). In these studies, the existence of cooperation has been inferred by the behaviour of foraging pelicans; there has been no investigation of whether or not the participating members of these flocks benefit from such formations, as is more usually implied by the term cooperation (Brown 1975). Assessing the extent of cooperation within foraging strategies was one of my main objectives. I also looked for manifestations of social facilitation, where the presence of conspecifics stimulates birds to eat more food and at faster rates (Tolman and Wilson 1965, Turner 1965). In addition, variables such as flock size, activity patterns and forager location may also influence rates of searching and feeding, and were examined as part of my analysis of foraging strategies in Chapter 3.

CHAPTER 1. DIURNAL AND NOCTURNAL PATTERNS OF ABUNDANCE AND DISTRIBUTION OF FORAGING AMERICAN WHITE PELICANS

INTRODUCTION

American White Pelicans (*Pelecanus erythrorhynchos*) traditionally have been assumed to be diurnal, although a few researchers have observed them feeding at night (Goss 1888, Hall 1925, Low *et al*. 1950, Schaller 1964). O'Malley and Evans (1984) provided qualitative evidence suggesting that foraging activity along a riverine site was highest at night. However, no systematic examination of the distributional patterns or of the foraging behaviour of these nocturnally active pelicans yet exists.

American White Pelicans range widely in search of food, often travelling from 50 to over 100 km from their breeding colonies (Cottam and Williams 1939, Low *et al*. 1950, Behle 1958, Lingle and Sloan 1980, Trottier *et al*. 1980). During the breeding season, white pelicans prefer to forage on freshwater lakes, rivers and marshes, but have also been seen on small ponds having fresh or brackish water (Palmer 1976, Lingle and Sloan 1980). Factors influencing the selection of feeding sites are at present not documented, but appear to be related primarily to the relative abundance and accessibility of fish. Knopf and Kennedy (1980) suggested that pelicans used Pyramid Lake, in Nevada, when spawning Tui Chubs (Gila bicolor) moved into the shallows in large numbers during June. Abundance of foraging pelicans at a lake not normally used increased dramatically after declines in water levels stranded Carp (Cyprinus carpio) and other fish species in shallow water. Similar preferences for shallow water have been documented in the Great White Pelican (P. onocrotalus) of Africa (Guillet and Crowe 1981, 1983).

This study uses surveys of Dauphin River and Lake Winnipeg to determine the distributional patterns of foraging and loafing pelicans during both day and night. Factors potentially influencing pelican distribution, especially those attributes of preferred foraging locations, were examined. Environmental factors such as temperature, wind speed, water depth and speed, which could potentially influence abundance, size, and location of foraging and loafing flocks, were also examined.

MATERIALS AND METHODS

Study area

American White Pelicans were studied on and adjacent to Dauphin River, a river 54 km long and located in south-central Manitoba, Canada (51°58'N, 98°07'W) that carries water from Lake St. Martin northeast to Lake Winnipeg (Fig 1). The areas examined included a 6 km^2 section of Lake Winnipeg shoreline and adjacent water extending directly northeast from the river mouth, and a 17 km stretch of river extending upstream (southwest) from its mouth (Fig 2). The closest known pelican breeding colony contained 3800 nests and was located at St. Martin Isles, 50 km northeast from the mouth of Dauphin River (Koonz 1987).

The width of Dauphin River in the study area ranged from 50 to 210 m, averaging 115 m. Vegetated banks, rising from 5 to 30 m above the water level, extended for 12 km upstream from the river mouth. River bank vegetation was predominately willows (*Salix spp.*), white birch (*Betula papyrifera*), jack pine (*Pinus banksiana*) and spruce (*Picea spp.*) intermixed with some trembling aspen (*Populus tremuloides*). Low lying shoreline areas extending 12 to 17 km from the river mouth were dominated by sedges (*Carex spp.*) and meadow grasses, while sparse stands of bullrush (*Scirpus spp.*)

Figure 1. Map of southern Manitoba showing the location of: A) Lake Winnipeg, B) St. Martin Isle, C) Dauphin River, D) Lake St. Martin, and E) Lake Manitoba.

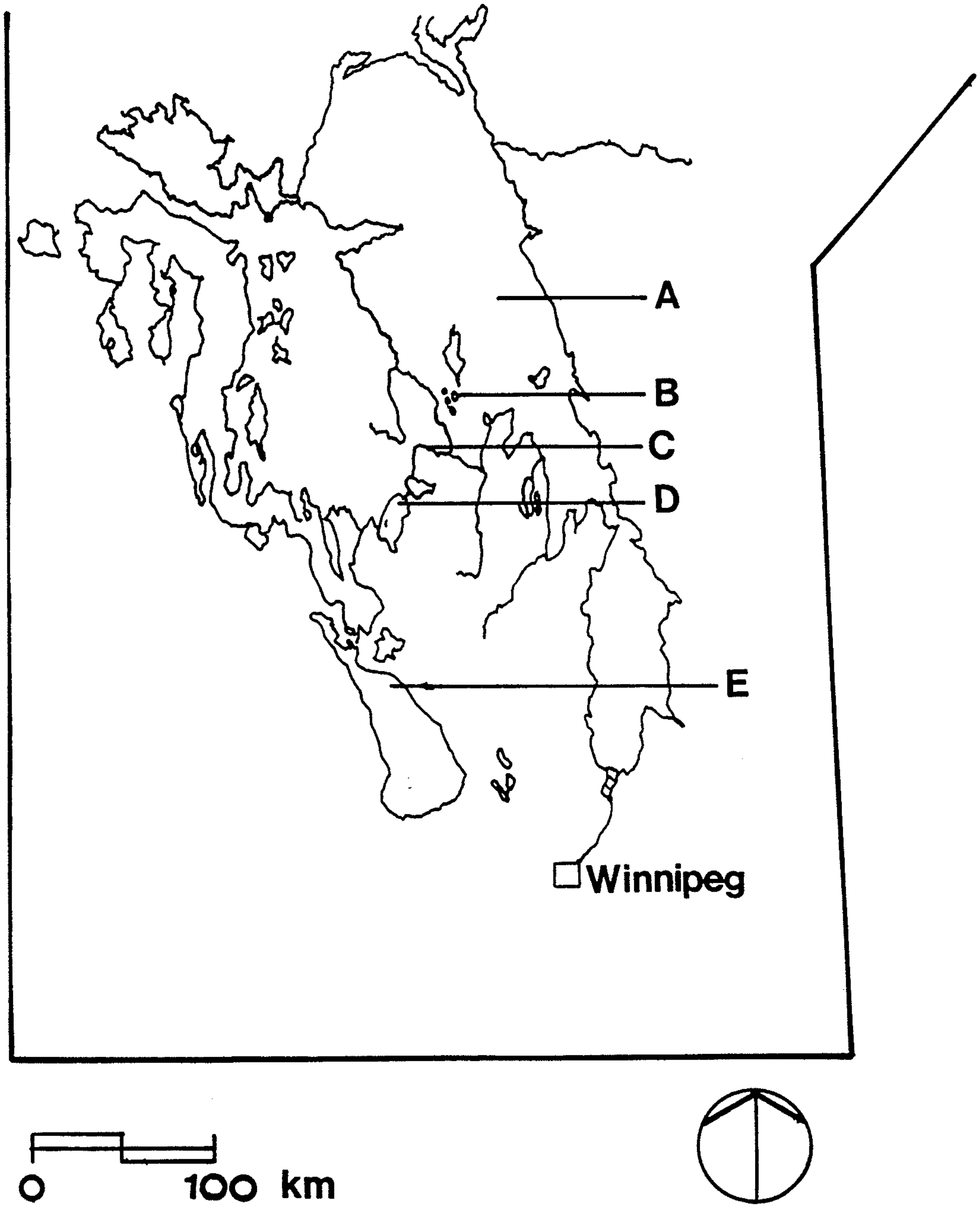
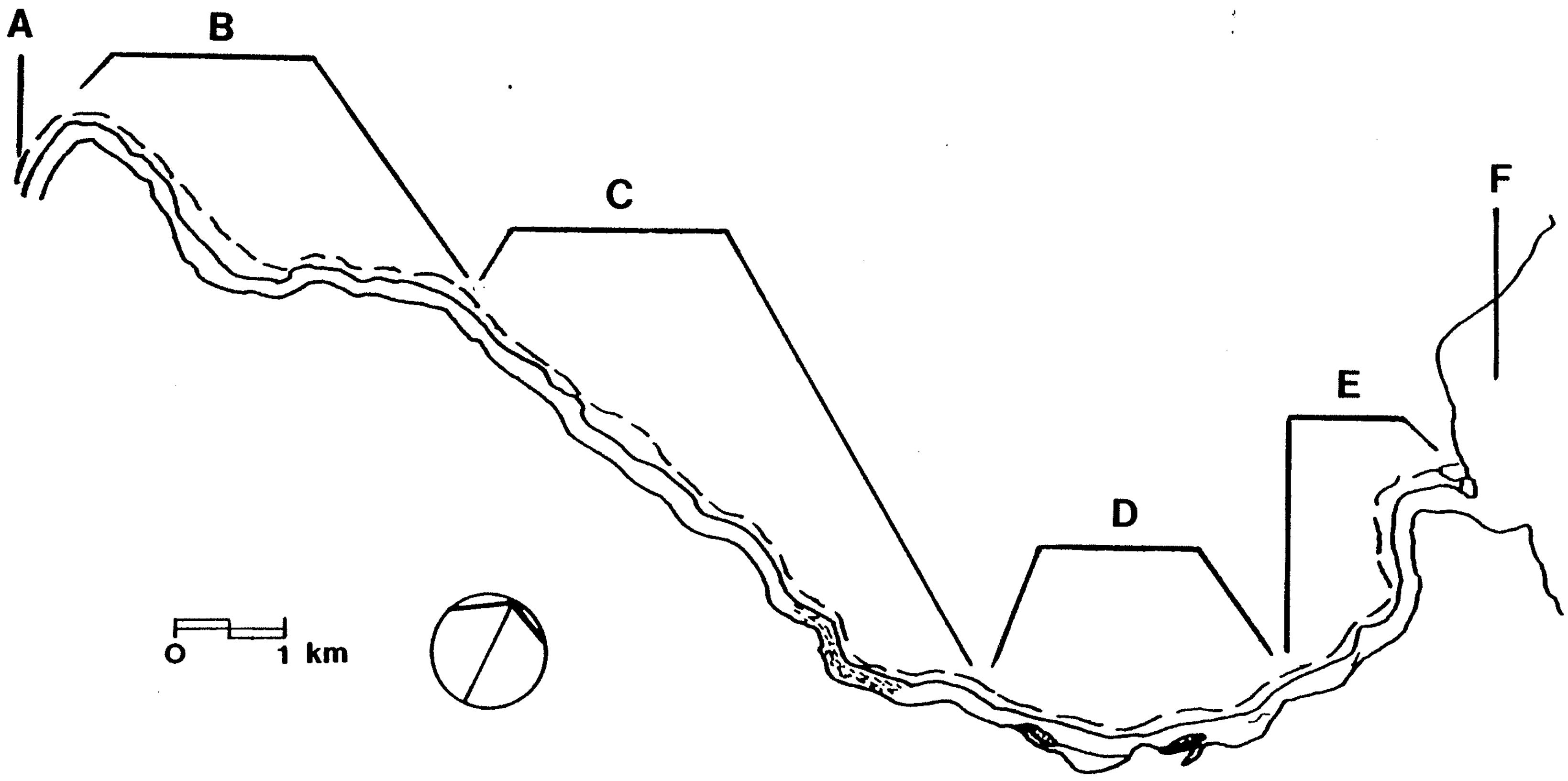

A
B
C
D
E
Winnipeg
0
100 km

Figure 2. Map of Dauphin River and Lake Winnipeg study sites showing: A) road, B) upriver habitat, C) white water region of rapids, D) intermediate habitat, with associated islands and mudflat, E) downriver, and F) Lake Winnipeg.


A
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0
1 km

and reedgrass (Phragmites communis) occurred intermittently near the shoreline. The river substrate was rocky and fairly homogeneous; relative water turbidity was low and aquatic vegetation virtually nonexistent. A road adjacent to the northern river bank provided easy access to the entire study area.

Various locations along Dauphin River were visited by canoe in August (1985) and water depths were measured. Forty deep-water samples were taken using an enumerated nylon rope that was attached to the base of a 200 x 300 mm, 2000 g metal weight. A wooden meter stick was used for sampling water depth in shallow water. Thirty estimates of surface water speed were made by tossing a piece of wood in the river, approximately 10 m from the northern shore and recording the time required for it to travel 10 m downstream. Additional water depth and water speed measurements were taken in 1986.

For data collection and analysis, Dauphin River was segregated into four distinct habitats (Fig 2) based on a combination of location, water depth and speed: A)Upriver - The area extending farther than 12 km upstream from the river mouth, where banks were low, and the water was deep (2-4 m, at midstream), with slow current (<0.5 m/s), B)Rapids - This included the region extending from 6 to 12 km upstream from the river mouth, where the water was shallow (<0.5 m deep) and moving fast (>2 m/s); C) Intermediate - This habitat extended for 3 km downriver from the base of the rapids. The river was shallow (<1.5 m) near midstream and had a water speed of 1-2 m/s; D) Downriver - An area of deep (2-5 m) and slow-moving (<1 m/s) water extending 3 km upstream from the river mouth.

Water depth increased more rapidly from the southern than the northern shore. A channel approximately 2 m deep was located 15 to 25 m from the south shore and extended upriver for 12 km. Sandbars were present in the region extending from 2.5 to 5.5 km upstream from the river mouth (Fig 2). Two vegetated islands, 50x100 m in area, were situated near these sandbars, equidistant from the two shores. Sandbars became prominent during late summer of 1985, but most were absent during the following spring when water levels in Lake St. Martin were 1 m higher (Huey Hunter, pers. comm.).

Fish distribution and activity patterns

The most common species of fish found within or near Dauphin River include: Cisco (*Coregonus artedii*), lake whitefish (*C. clupeaformis*), northern pike (*Esox lucius*), white sucker (*Catostomus commersoni*), longnose sucker (*C. catastomus*), burbot (*Lota lota*), yellow perch (*Perca flavescens*), walleye (*Stizostedion vitreum*), sauger (*S. canadense*), emerald shiner (*Notropis atherinoides*), spottail shiner (*N. hudsonius), fathead minnow (Pimephales promelas), brook stickleback (Culaea inconstans), johnny darter (Etheostoma exile), trout-perch (Percopsis omiscomaycus) (Keleher 1952, Scott and Crossman 1973, Lysack 1980, 1981)

All except burbot, cisco and whitefish spawn in the shallows of rivers and lakes from May to mid-June (Scott and Crossman 1973). Most species of fish are active within 30 min of dusk and dawn, when they move into shore to feed (Emery 1973). Yellow perch, minnows and darters form relatively small schools in rivers in early May. They are frequently found in water less than 1 m in depth during daylight hours (Keast and Welch 1968, Emery 1973, Hall and Werner 1977). Yellow Perch are most active from 0600-0800 hrs and 1800-2200 hrs (Hasler and Bardach 1949).

Walleye, sucker, trout-perch, burbot, whitefish and cisco are nocturnal species that move into shore at dusk and remain active in shallow water until dawn (Carlander and Cleary 1949, Lawler 1969, Emery 1973, Engel and Magnusson 1976, Rudstam and Magnusson 1985). The periods of greatest activity, in order from highest to lowest, are: 1) Walleye and sauger: 2000-0700 hrs, 1900-2000 hrs and 1500-1900 hrs, 2) Sucker: 2200-0600 hrs and 1000-1200 hrs, 3) Lake whitefish and cisco: 2000-0700 hrs (see references above).

Lake whitefish made spawning runs up Dauphin River to Lake St. Martin from early August to mid-September. Small schools of minnows were observed periodically during daylight hours, but whitefish greatly exceeded all other species of fish during the summer study period (Huey Hunter, Chris and Helgy Einarsson, pers. comm.). These sources, and results from fish-tagging experiments (Ken Campbell, pers. comm.), suggested that extended spawning runs occurred primarily around dusk (1900-2300 hrs), with smaller ones immediately after dawn (0600-0800 hrs), around noon (1000-1300 hrs) and the afternoon (1600-1900 hrs). Many whitefish made spawning runs at night, but at unpredictable times.

Pelican abundance and distribution

A flock was defined as any group containing pelicans that were within approximately 5 m of each other (O'Malley and Evans 1982a). Foraging flocks consisted of birds that were on water and were actively striking (dipping) their bills into water; this is characteristic of foraging behaviour in this species (Palmer 1976). Loafing flocks consisted of birds that were standing on a solid substrate, such as exposed sandbars or in shallow water adjacent to shore, and were not dipping for food. The size and location of all foraging and loafing flocks observed on the river and adjacent lake were recorded onto data sheets during vehicle-based surveys performed from 31 May to 10 June and 23 August to 5 September in 1985, and from 11 to 28 May in 1986. These seasons will be referred to as spring (May, June) and summer (August, September), respectively. Locational information included the distance of flocks from the river mouth (to the nearest 100 m) and from the nearest shore (to the nearest 10 m). Type of substrate (shoreline, sandbars, islands or rocks) used by each loafing flock was recorded. Foraging flock density was determined from estimates of the average distance between neighbouring pelicans. The values recorded for group density were based on the following inter-pelican distance: 1)Very high density - one bill length, 2)Dense - between one bill length and one body length, 3)Moderate density - between one and two body lengths, 4)Low density - two to three body lengths, and 5)Very low density - greater than three body lengths.

The starting location for surveys was alternated between the lake shore and the farthest point upriver. In 1985, surveys were performed in the morning (0430-0830 hrs, CDT), near midday (1030-1430 hrs), in the evening (1700-2000 hrs) and at night (2300-0300 hrs). In 1986, nocturnal surveys were replaced by afternoon (1430-1830 hrs) surveys and the timing of transects performed during both the midday and evening were changed to 1130-1300 hrs and 2000-2200 hrs, respectively. Transects required approximately 90 min to complete during daylight hours and 120 min at night. All observations were made with either 10x50 Bushnell binoculars or an infrared night scope (Javelin, model #325), depending on lighting conditions. Due to the limited visual range of the infrared scope (300 m) and obstructions created by riverbank vegetation, nocturnal transects only extended from 0 to 4 km and 13 to 17 km from the river mouth. A total of 52 surveys were performed in 1985 and 28 in the following spring. Many morning surveys were aborted in 1985 due to the presence of dense fog which obscured much of the river.

A compass and hand-held anemometer (MET-5500, Le Naturaliste, Rimouski, Quebec) were used prior to each survey to discern wind direction and speed. The relative amount of cloud cover was estimated. Daily temperature and rainfall data were obtained from the local meterological station at the Dauphin River Hatchery.

Variations in the abundance and distributional patterns of foragers and loafers were assessed primarily with Kruskal-Wallis (K) rank tests (Neter and Wasserman 1974). To determine if any combination of environmental parameters could explain the variation in forager and loafer abundance observed during the daytime surveys, stepwise regression was used in conjunction with tests for determining maximal-r-squared and Mallows Cp coefficient (Berenson _et al_. 1983). The suitability of temperature, windspeed, relative cloud cover, date and time of day as predictors of pelican abundance was tested for each model. Linear regression was used to test the above models and to determine if the total abundance of foragers or loafers along the river was related to flock size. Correlation analysis was used to establish whether or not the number of loafers increased with forager abundance.

RESULTS

Pelican abundance

Daytime abundance (N pelicans x survey^{-1}) of all pelicans, whether foraging or loafing, varied significantly over seasons (Table 1). Significantly more pelicans were along Dauphin River during the summer than either spring. Pelicans were more numerous in spring of 1986 than the preceeding spring. Day-night comparisons, in the river regions extending from 0 to 4 km and 13 to 17 km from Lake Winnipeg, revealed no significant difference in number of pelicans during the spring (mean ± s.d.: day=199.6±70.35 pelicans x survey^{-1}, N=18 vs. night=201.7±72.55, N=9; t=0.07, p>0.90) or summer of 1985 (day=1353.1±571.52, N=16 vs night=1608.0±710.03, N=9; t=0.98, p>0.30). In contrast to the river, significantly more pelicans used Lake Winnipeg in the spring of 1985 than in either the summer or the following spring (Table 1). The area covered by the lake study site was three times larger than the river site, but the latter contained from 5- to 200-fold more pelicans during the day.

Foragers. Diurnal river foragers were significantly more abundant in summer than in either spring season (Table 2). Flocks were also more numerous, but significantly smaller, in summer. Of the spring study periods, foragers were slightly (but not significantly) more abundant along the river in 1986 than 1985, while flock size was similar in the

Table 1. Mean ± s.d. number of pelicans per survey during the day in both river and lake habitats (N surveys in parenthesis).

	Season[1]				
Habitat	Spring '85 (18)	Summer '85 (16)	Spring '86 (28)	K	p
River	263.0±106.56^{a}	1827.9±452.35^{b}	355.7±158.44^{c}	37.40	<0.001
Lake	47.1±49.75^{a}	9.1±13.66^{b}	10.6±15.33^{b}	9.97	<0.01
Total	310.1±95.82	1837.1±451.05	366.3±164.12		

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[1] Values in same row having different superscripts are significantly different at p=0.05 (Mann-Whitney U test).

Table 2. Mean ± s.d. number of foragers per survey and foraging flock size during the day.

		Season[1]				
Variable	Habitat	Spring '85	Summer '85	Spring '86	K	p
N surveys		18	16	28		
N foragers x survey^{-1}	River	53.6±57.64^{a}	299.5±251.54^{b}	107.4±97.20^{a}	16.67	<0.001
	Lake	12.2±26.63	9.1±13.66	1.7±2.45	1.34	>0.50
K(p)	River vs. lake	16.28(<0.001)	23.25(<0.001)	38.63(<0.001)		
Flock size N flocks	River	9.2±24.37^{a} 105	3.7±34.90^{b} 1294	7.8±16.25^{a} 387	677.02	<0.001
	Lake	3.6±13.18^{a} 61	1.1±0.96^{b} 130	1.5±1.39^{a} 31	19.93	<0.001
K(p)	River vs. lake	22.72(<0.001)	2.14(>0.10)	20.72(<0.001)		

[1] See Table 1, footnote

two years. On the lake, the number of foragers did not differ significantly among seasons (Table 2). Flocks were significantly smaller on the lake during the summer than in either spring. Diurnal foragers were more numerous and flock sizes larger along the river than the lake during both spring study periods (Table 2). During the summer, foragers were more numerous on the river, but flocks were similar in size in the two areas.

Nocturnal foragers on the river were significantly more numerous in summer than spring of 1985, but flocks were larger in the spring (Table 3). Comparing nocturnal transects with the same portion of river surveyed during the day revealed that larger numbers of foragers and larger flock sizes were present at night in both spring and summer (Table 3). Wide ranges in foraging flock size, from 1 to 200 pelicans in spring and 1 to 900 pelicans in summer, account for the high variance observed during periods of greatest activity.

In spring, forager abundance (Fig 3A,C) and flock size (Fig 4A,C) were high within an hour of twilight in evening and, to a lesser extent, in morning. Numbers of foragers remained high throughout the night, with minor peaks in abundance and flock size ocurring in early afternoon. In summer (Fig 3B, 4B), peaks in flock size and number of foragers occurred from 2200 to 0200 hrs, with smaller peaks around 1100 hrs. Summer flock size peaked at 1730 hrs (Fig 4B).

Table 3. Mean ± s.d. number of diurnal and nocturnal foragers per survey and foraging flock size in 1985.

		Period			
Variable[1]	Season	Day	Night	K	p
N foragers x survey^{-1} (N surveys)	Spring	51.7±56.72 (18)	160.7±78.21 (9)	11.01	<0.001
	Summer	292.5±252.67 (16)	622.1±394.20 (9)	5.39	<0.05
K (p)	Spring vs. summer	12.88(<0.001)	10.96(<0.001)		
Flock size (N flocks)	Spring	9.8±25.54 (95)	28.9±40.24 (50)	19.81	<0.001
	Summer	3.8±35.93 (1220)	9.7±40.84 (578)	45.45	<0.001
K (p)	Spring vs. summer	252.09(<0.001)	121.55(<0.001)		

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[1] Areas sampled extended from 0-4 km and 13-17 km from the river mouth

Figure 3. Temporal changes in abundance of foraging and loafing pelicans, plotted on a semi-log scale, on Dauphin River and Lake Winnipeg study sites combined during (A) spring '85, (B) summer '85, and (C) spring '86. Nocturnal transects were performed in 1985 and covered 47% of the river study area. Horizontal bars show morning and evening twilight.

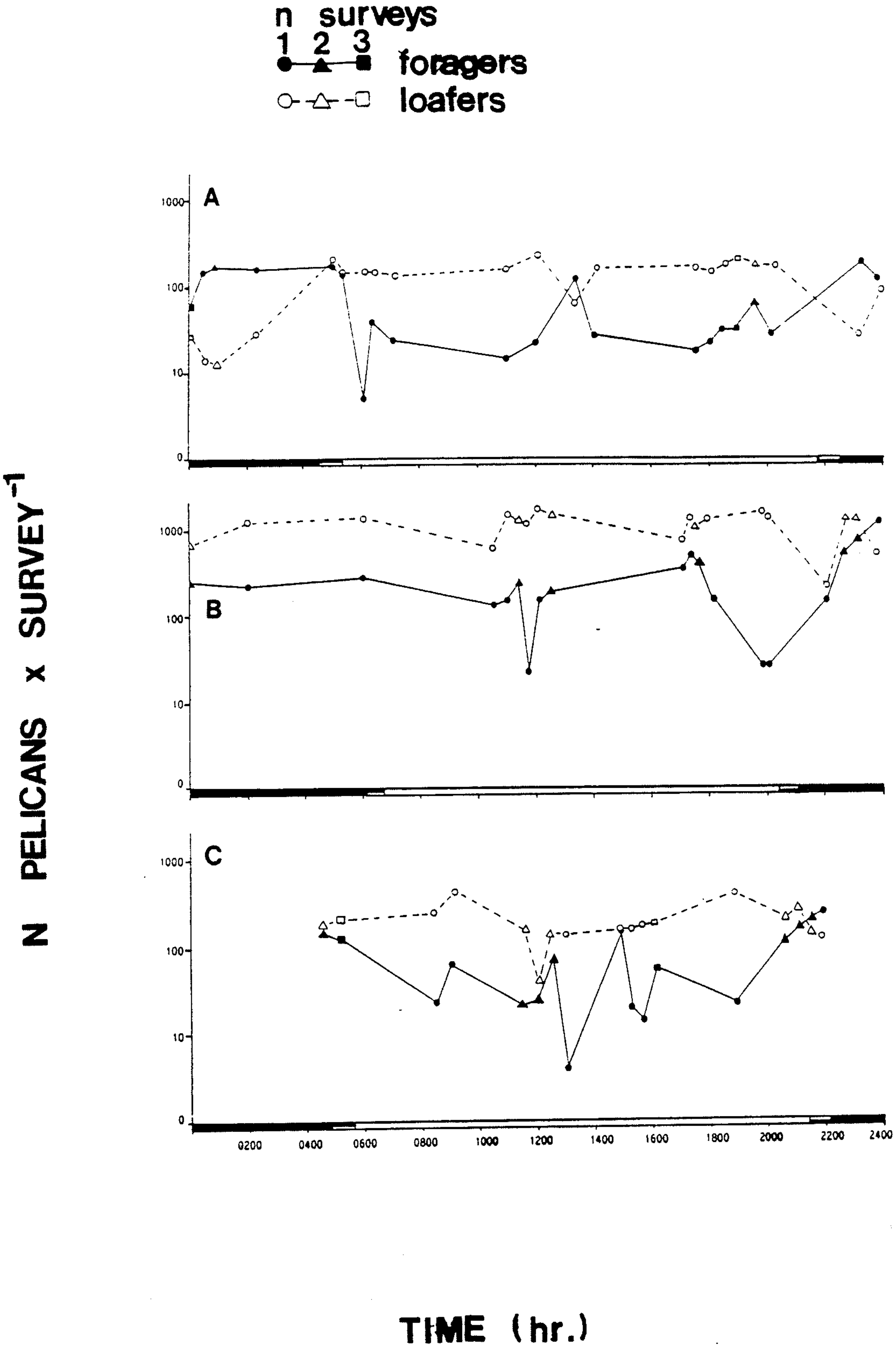
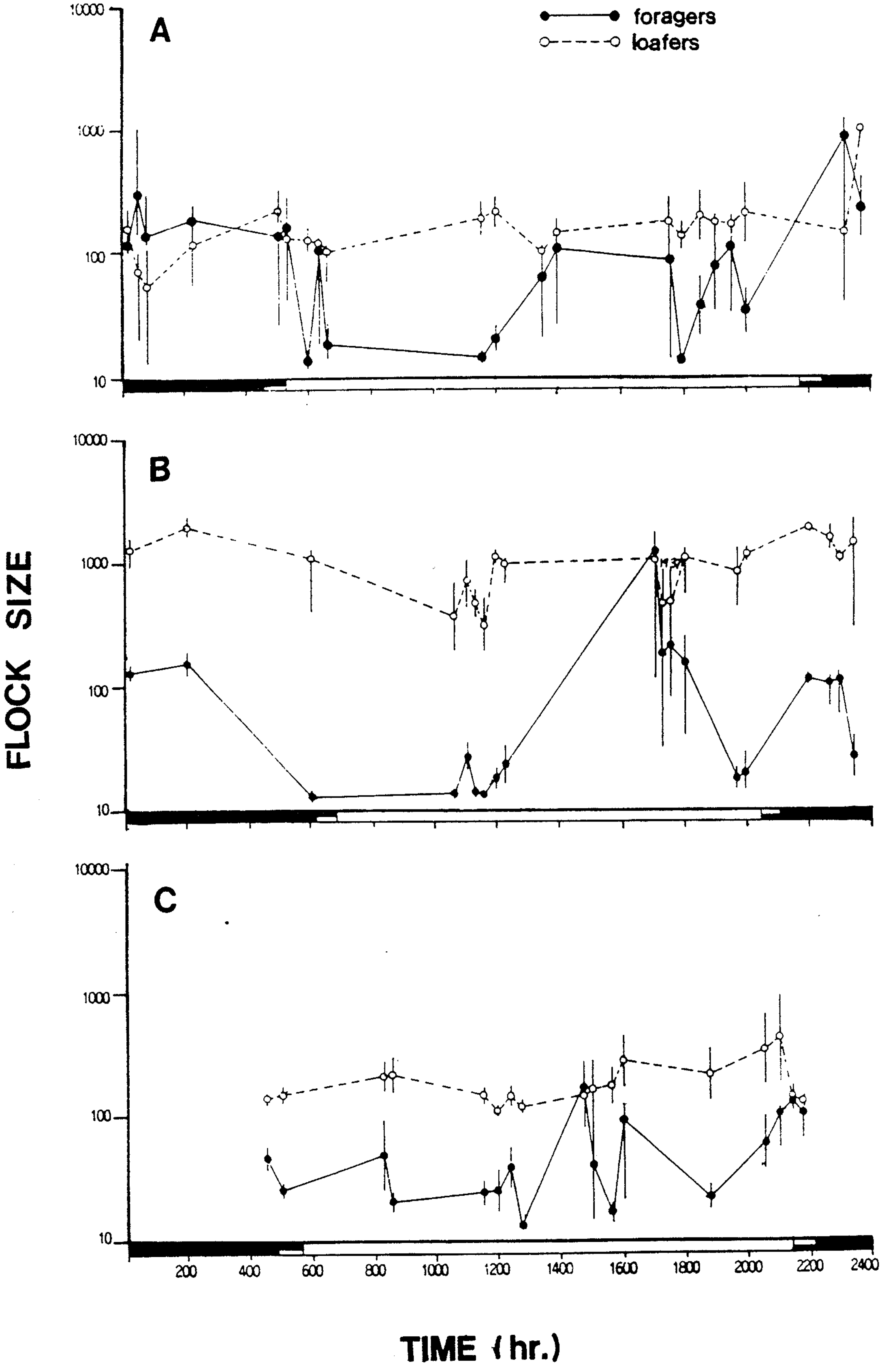

n surveys
1 2 3
foragers
loafers
N PELICANS x SURVEY^{-1}
A
B
C
1000
100
10
0
0200
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
2400
TIME (hr.)

Figure 4. Temporal changes in flock size of foraging and loafing pelicans, plotted on a semi-log scale, on Dauphin River and Lake Winnipeg study sites combined during (A) spring '85, (B) summer '85, and (C) spring '86. Nocturnal transects were performed in 1985 and covered 47% of the river study area. Horizontal bars show morning and evening twilight.


A
foragers
loafers
10000
1000
100
10
B
10000
1000
100
10
C
10000
1000
100
10
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
2400
FLOCK SIZE
TIME (hr.)

Loafers. Diurnal loafers along the river were significantly more abundant, and formed larger flocks, in summer than either spring (Table 4). No significant difference in number of loafers or size of flocks occurred between either spring. On the lake, loafers were significantly more abundant in spring 1985 than any other time. Loafing flock size on the lake was similar between springs. Pelicans were never seen loafing on or near shores of the lake during summer. Significantly more pelicans loafed along the river, than the lake, during all seasons (Table 4). Loafing flocks did not vary significantly in size between these two habitats.

During night, loafers were significantly more numerous and formed larger flocks in the summer than spring (Table 5). Loafers were more abundant during the day than night in spring, but not summer (Table 5). Loafing flocks were significantly larger during summer nights, but not in spring.

Pelicans normally loafed during periods of low foraging activity; increase in number of loafers during the day usually followed declines in number of foragers (Fig 3A-C). Sudden increases in loafer abundance between 1100 and 1230 hrs (Fig 3A-B) were associated with both the influx of pelicans into Dauphin River from the breeding colony, located 50 km northeast, or other areas and the cessation of foraging by local flocks. Peaks in loafing also occurred around morning twilight and late evening. No consistent pattern of variation in loafing flock size was seen throughout the solar day (Fig 4A-C).

Table 4. Mean ± s.d. number of loafers per survey and loafing flock size during the day.

		Season[1]				
Variable	Habitat	Spring '85	Summer '85	Spring '86	K	p
N surveys		18	16	28		
N loafers x survey^{-1}	River	209.4±86.32^{a}	1528.4±461.02^{b}	248.3±148.81^{a}	35.22	<0.001
	Lake	34.9±40.81^{a}	0.0±0.00^{b}	8.9±15.26^{c}	20.77	<0.001
K(p)	River vs. lake	24.56(<0.001)	26.59(<0.001)	41.70(<0.001)		
Flock size N flocks	River	25.5±33.43^{a} 148	90.9±115.31^{b} 269	31.7±48.81^{a} 219	59.31	<0.001
	Lake	30.0±31.81 21	— 0	22.7±16.84 11	0.00	>0.90
K(p)	River vs. lake	1.37(>0.20)	—	0.41(>0.50)		

[1] See Table 1, footnote

Table 5. Mean ± s.d. number of diurnal and nocturnal loafers per survey and loafing flock size in 1985.

Variable[1]	Season	Period		K	p
		Day	Night		
N loafers x survey^{-1} (N surveys)	Spring	136.1±57.63 (18)	41.2±39.95 (9)	11.88	<0.001
	Summer	1092.5±561.07 (16)	986.7±574.75 (9)	0.16	>0.60
K (p)	Spring vs. summer	20.12(<0.001)	7.99(<0.005)		
Flock size (N flocks)	Spring	22.9±32.75 (107)	23.2±28.19 (16)	0.28	>0.50
	Summer	89.6±119.52 (195)	206.5±215.81 (43)	12.41	<0.001
K (p)	Spring vs. summer	37.07(<0.001)	13.98(<0.001)		

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[1] See Table 3, footnote

Influence of environmental parameters on abundance. Diurnal forager abundance increased marginally with time of day during all seasons (Table 6). In spring 1985, date was the best estimator of forager abundance. In summer 1985 and spring 1986, wind speed contributed inversely to the models explaining forager abundance (Table 6). In summer, temperature and forager abundance were inversely related. Changes in loafer abundance in both spring seasons were not related to any of the variables tested (Table 6). An increase in both amount of cloud cover and time of day were associated with increasing loafer abundance in summer.

Relationship between abundance and flock size. Regression of forager and loafer flock size on abundance (Table 7, data from Figs 4, 5) indicated the presence of a strong positive relationship between these variables during both day and night in both spring seasons, but not in summer.

Table 6. Stepwise and multiple linear regression, assessing effects of time and weather on number of pelicans foraging and loafing during diurnal surveys.

Activity	Season	Variables accepted[1]		N surveys	F	r^2	p
N foragers x survey^{-1}	Spring '85	Date	(+)	17	6.81	0.312	<0.025
		Time	(-)	17	4.42	0.165	=0.05
		Date x time		17	0.02	—	>0.80
	Summer '85	Time	(+)	10	14.57	0.089	<0.01
		Temp	(-)	10	5.38	0.473	<0.001
		Wind speed	(-)	10	26.48	0.402	<0.001
		Time x temp		10	1.33	—	>0.20
		Time x wind speed		10	0.51	—	>0.40
		Temp x wind speed		10	1.02	—	>0.30
	Spring '86	Time	(+)	25	3.92	0.131	=0.05
		Windspeed	(-)	25	3.53	0.133	<0.05
		Time x wind speed		25	0.51	—	>0.40
N loafers x survey^{-1}	Spring '85	None		17	0.75	0.148[2]	>0.05
	Summer '85	Time	(+)	10	5.55	0.099	=0.05
		Cloud cover	(+)	10	27.75	0.776	<0.001
		Time x cloud cover		10	0.82	—	>0.30
	Spring '86	None		25	0.64	0.137[2]	>0.05

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[1] Direction of slope, positive or negative, provided in parenthesis

[2] r^2 provided for all environmental parameters: Date, time of day (time), temperature, wind speed and cloud cover

Table 7. Results of regression analyses between mean flock size and number of pelicans foraging or loafing. Data for river and lake combined.

Season	Period	Activity	N Surveys	Equation of line	F	r^2	p
Spring '85	Day	Foraging	17	$y=3.52+0.110x$	24.74	0.623	<0.001
		Loafing	15	$y=6.22+0.093x$	21.77	0.626	<0.001
	Night	Foraging	9	$y=-8.02+0.260x$	8.64	0.552	<0.025
		Loafing	5	$y=3.06+0.310x$	38.73	0.928	<0.001
Summer '85	Day	Foraging	16	$y=-2.34+0.081x$	3.86	0.216	>0.05
		Loafing	16	$y=46.59+0.033x$	3.78	0.212	>0.05
	Night	Foraging	9	$y=32.25-0.019x$	2.09	0.230	>0.05
		Loafing	7	$y=192.75+0.026x$	0.09	0.018	>0.05
Spring '86	Day	Foraging	28	$y=3.20+0.044x$	18.62	0.417	<0.001
		Loafing	28	$y=14.82+0.076x$	11.87	0.313	<0.005

Pelican distribution within habitats

Foragers. The few diurnal foragers observed on the lake were normally located within 500 m of shore. The limited range of the infrared scope (<300 m) did not allow an extended examination of the lake at night. Near-shore observations provided no evidence that pelicans foraged on the lake at night.

Differences in daytime forager abundance and flock size were present among river habitats during every season in day and night (Table 8). Foragers were normally more numerous in the downriver and intermediate river habitats, while few used the rapids and upriver habitats. Significantly more foragers were in the intermediate than downriver habitat during spring nights in 1985, and daytime in 1986. Foraging flocks were significantly larger in the intermediate than downriver habitat during all periods, except summer nights. Day-night differences in forager abundance were significant in the intermediate habitat during the spring and summer (Table 8); at these times, more pelicans foraged at night. With the exception of the intermediate habitat in summer, flocks were significantly larger at night than day.

Forager abundance increased closer to shore (Table 9). To determine if forager distribution might result from a preference for decreasing water depth, Spearman's correla-

Table 8. Differences in mean ± s.d. forager density (N foragers x survey^{-1} x km^{-1}) and flock size among river habitats and between day and night.

Variable	Season	Period	N surveys	River habitats[1] Downriver	Intermediate	Rapids	Upriver	K	p
N foragers x survey^{-1} x km^{-1}	Spring '85	Day	18	7.9 ± 18.36^{a}	9.3 ± 11.39^{a}	0.2 ± 0.51^{b}	0.1 ± 0.39^{b}	39.13	<0.001
		Night[2]	9	7.9 ± 11.29^{a}	45.6 ± 26.78^{b}	—	0.0 ± 0.13^{c}	21.17	<0.001
K(p)		Day vs. night		0.24(>0.60)	13.36(<0.001)	—	0.17(>0.60)		
	Summer '85	Day	16	53.7 ± 75.46^{a}	45.9 ± 61.24^{a}	0.1 ± 0.38^{b}	0.0 ± 0.00^{b}	30.96	<0.001
		Night	9	103.4 ± 118.15^{a}	103.9 ± 105.48^{a}	—	0.0 ± 0.00^{b}	16.31	<0.001
		Day vs. night		4.15(<0.05)	3.08(>0.05)	—	0.00(>0.90)		
	Spring '86	Day	28	9.5 ± 14.87^{a}	19.4 ± 21.51^{b}	3.1 ± 4.40^{c}	0.5 ± 1.98^{d}	56.83	<0.001
Flock size (N flocks)	Spring '85	Day	18	6.5 ± 24.99^{a} (66)	17.3 ± 25.63^{b} (29)	$3.8\pm2.48^{a,b}$ (6)	3.0 ± 2.83 (4)	15.82	<0.005
		Night	9	10.7 ± 15.36^{a} (20)	42.4 ± 47.14^{b} (29)	— —	2.0 ± 0.00 (1)	8.90	<0.005
K(p)		Day vs. night		8.02(<0.005)	4.14(<0.05)	—	—		
	Summer '85	Day	16	2.5 ± 28.61^{a} (1033)	8.5 ± 52.82^{b} (260)	9.0 ± 0.00 (1)	—[3] (0)	32.07	<0.001
		Night	9	12.6 ± 51.49^{a} (221)	7.9 ± 32.50^{b} (357)	—	— (0)	10.70	<0.005
		Day vs. night		78.29(<0.001)	0.03(>0.80)	—	—		
	Spring '86	Day	28	4.4 ± 6.90^{a} (181)	12.5 ± 24.12^{b} (130)	7.7 ± 13.87^{b} (67)	$7.2\pm8.30^{a,b}$ (9)	17.47	<0.001

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[1] See Table 1, footnote

[2] See Table 3, footnote (Daytime values based on complete surveys of entire river study site)

[3] Area sampled, but no flocks present

Table 9. Mean ± s.d. number of foragers per survey at varying distances from shore.

Season	Period	N Surveys	Distance (m)					r	p
			0-9	10-19	20-29	30-39	40-49		
Spring'85	Day	18	30.5±31.44	4.7±8.19	1.8±2.82	3.6±5.58	0.4±1.25	-0.478	<0.001
	Night	9	119.2±95.96	9.6±17.27	6.6±8.25	19.0±52.56	0.6±1.67	-0.499	<0.001
Summer'85	Day	16	134.8±265.20	32.4±63.99	13.0±15.59	10.6±19.95	20.9±36.56	-0.275	<0.025
	Night	9	184.0±197.43	153.6±232.23	81.7±141.57	50.3±58.59	37.7±42.56	-0.359	<0.025
Spring'86	Day	28	65.7±60.50	8.4±13.71	12.6±23.39	9.3±17.62	11.4±14.37	-0.402	<0.001

tion coefficient (rs) was used after dividing water depth into discrete 50 cm units. During both day and night, most foragers were located over very shallow (<1 m) water (Fig 5). Abundance of foragers increased significantly with decreasing water depth, this relationship being slightly stronger at night.

Similar tests were performed for water speed, separated into 0.5 m/s units. During both years, water speeds up to 2 m/s were preferred over faster speeds (Fig 6). These values coincided with the most heavily used intermediate habitat.

Loafers. Significant differences in loafer densities among river habitats occurred during all periods (Table 10). Loafer density was always higher in the intermediate than in any other habitat. Significant day-night differences in loafer density occurred in the intermediate and downriver habitats in spring and downriver in summer; there were more loafers during day than night. Loafing flock sizes differed significantly among river habitats during daytime in spring 1985 and during both day and night in summer (Table 10). Loafing flocks were normally most numerous and largest in the intermediate habitat, and moderately large downriver and in the rapids. Only within the intermediate habitat during summer were loafing flocks significantly larger at night than day (Table 10). These findings demonstrate that differences in overall loafer abundance noted above were primarily due to large fluctuations within the intermediate habitat and, to a lesser extent, downriver.

Figure 5. Relationship between water depth and abundance of foragers on the river, plotted on a semi-log scale, during the (A) spring '85, (B) summer '85, and (C) spring '86.

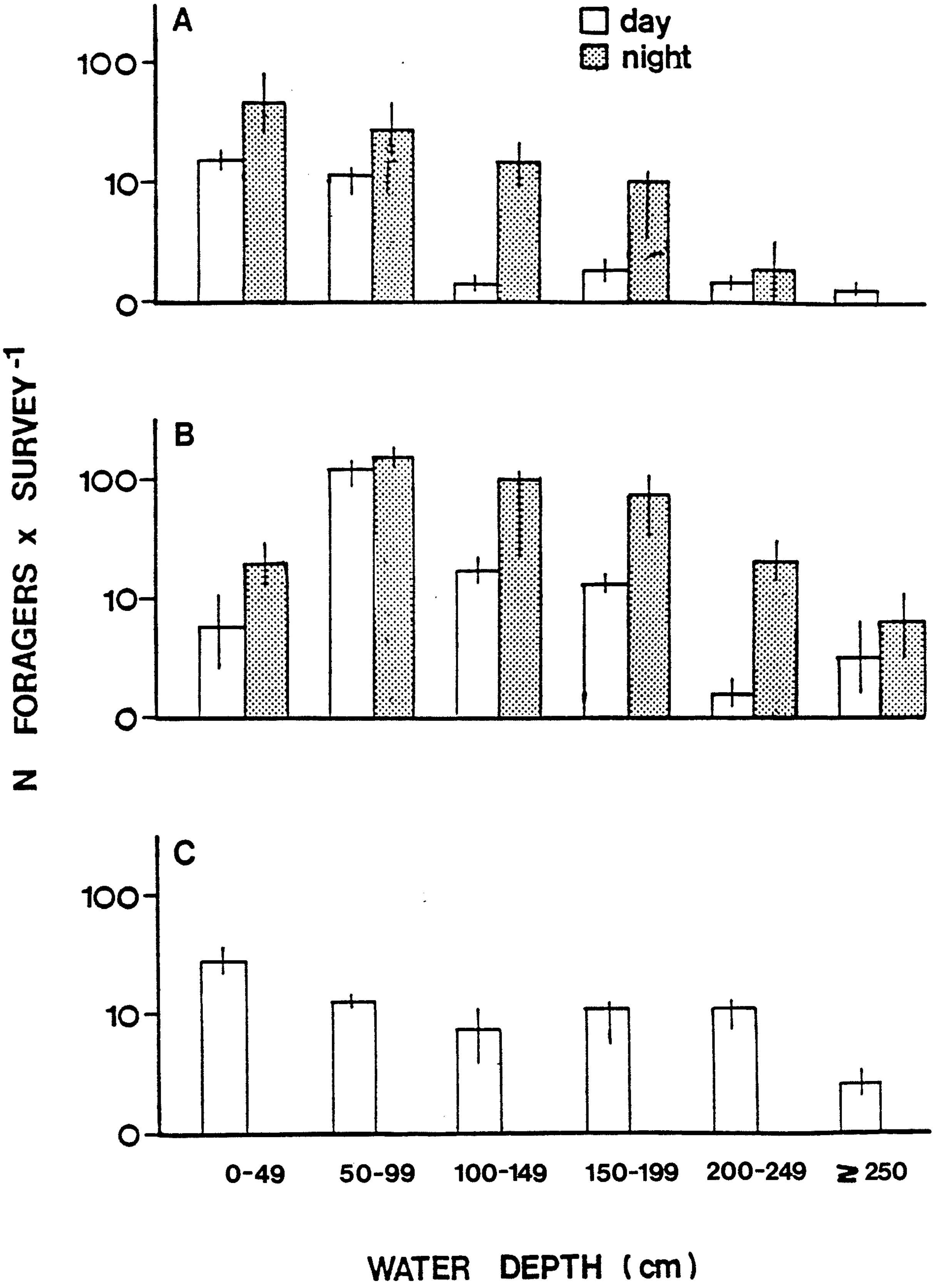
A
□ day
▨ night
100
10
0
B
100
10
0
C
100
10
0
N FORAGERS x SURVEY-1
0-49
50-99
100-149
150-199
200-249
≥ 250
WATER DEPTH (cm)

Figure 6. Relationship between water velocity and abundance of foragers on the river during the day.

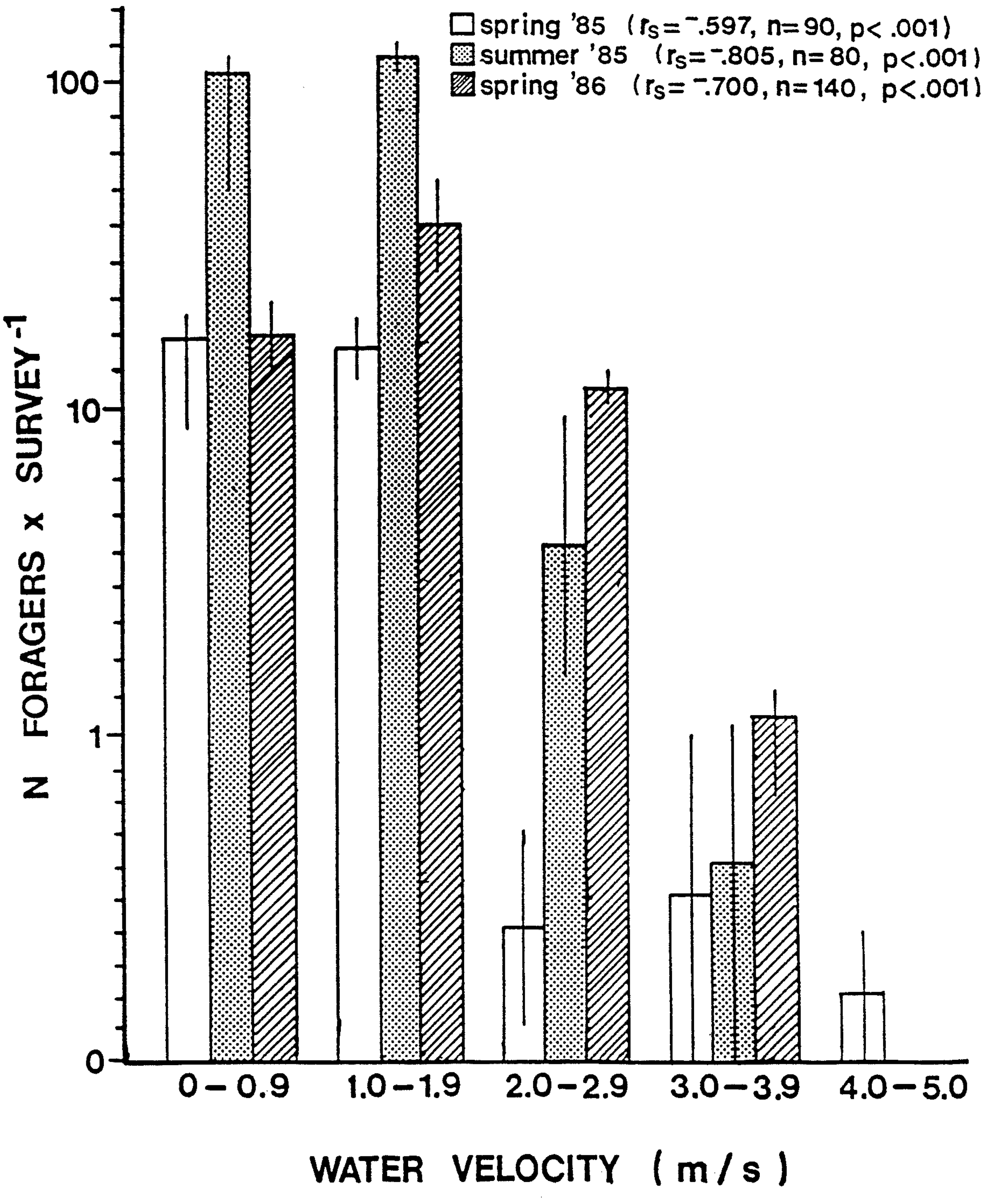
☐ spring '85 ($r_s = ^{-}.597$, n=90, p< .001)
▩ summer '85 ($r_s = ^{-}.805$, n=80, p<.001)
▨ spring '86 ($r_s = ^{-}.700$, n=140, p<.001)
100
10
1
0
N FORAGERS x SURVEY^{-1}
0 – 0.9
1.0 – 1.9
2.0 – 2.9
3.0 – 3.9
4.0 – 5.0
WATER VELOCITY (m / s)

Table 10. Differences in mean ± s.d. loafer density (N loafers x survey^{-1}x km^{-1}) and flock size among river habitats and between day and night.

Variable	Season		N surveys	River habitats[1]				K	p
				Downriver	Intermediate	Rapids	Upriver		
N loafers x survey^{-1} x km^{-1}	Spring '85	Day	18	15.9±15.23^{a}	48.8±27.54^{b}	2.5±9.30^{c}	0.1±0.28^{c}	58.15	<0.001
		Night[2]	9	4.1±4.93^{a}	9.6±14.53	—[3]	0.0±0.00^{b}	9.32	<0.01
K(p)		Day vs. night		7.32(<0.01)	8.92(<0.005)	—	0.50(>0.40)		
	Summer '85	Day	16	17.3±31.40^{a}	491.1±137.99^{b}	0.5±2.08^{c}	0.0±0.00^{c}	54.79	<0.001
		Night	9	0.3±0.57^{a}	328.6±191.30^{b}	—	0.0±0.00^{a}	18.18	<0.001
		Day vs. night		9.82(<0.005)	0.08(>0.70)	—	0.00(>0.90)		
	Spring '86	Day	28	5.5±6.94^{a}	68.8±36.71^{b}	4.3±8.82^{a}	0.0±0.04^{c}	78.39	<0.001
Flock size (N flocks)	Spring '85	Day	18	16.2±27.10^{a} (53)	31.4±35.51^{b} (84)	27.0±38.68^{a,b} (10)	6.0±0.00 (1)	10.72	<0.025
		Night	9	12.3±10.86 (9)	37.1±37.75 (7)	— —	— (0)	1.49	>0.20
K(p)		Day vs. night		0.07(>0.70)	0.48(>0.40)	—	—		
	Summer '85	Day	16	31.9±53.51^{a} (26)	97.8±118.68^{b} (241)	26.0±33.94 (2)	— (0)	13.96	<0.001
		Night	9	3.5±2.12^{a} (2)	216.4±216.20^{b} (41)	— —	— (0)	5.22	<0.025
		Day vs. night		0.97(>0.30)	12.20(<0.001)	—	—		
	Spring '86	Day	28	21.8±19.71 (21)	33.6±52.59 (172)	28.6±38.05 (25)	1.0±0.00 (1)	2.83	>0.40

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[1] See Table 1, footnote

[2] See Table 3, footnote (Daytime values based on complete surveys of entire river study site)

[3] Area sampled, but no flocks present

The largest portion of total loafer population was present on sandbars, but relative use of different loafing substrates along the river varied with season and time of day (Table 11). Loafers prefered sandbars at night and during daylight hours in spring and summer 1985, but shore and islands maintained higher numbers of loafers in spring 1986. Seasonal changes in substrate use appeared to coincide with changing water levels. The number and surface area of sandbars and rocks were greater in 1985 than in 1986; in 1986, water levels approximately 0.9 m above normal covered most sandbars and sections of both islands. The presence of larger numbers of loafers (in 1985) on sandbars, which covered a negligible area in comparison to shore availability, illustrates the strong preference shown by pelicans for sandbars.

Relationship between forager and loafer distribution. It might be expected that loafers should position themselves to maximize their view of the most profitable foraging areas. To assess this possibility, tests of association between number of foragers and loafers during the day were performed by correlating numbers present in succesive 500, 1000 and 2000 m long sections of river (Table 12). Consistently strong and positive correlations were found during all seasons in both years when examined areas covered 1 or 2 km, but not for sections 500 m long. Loafing flocks thus appeared to position themselves 500 to 2000 m from foragers,

Table 11. Mean ± s.d. number of loafers per survey on each type of substrate during the day and night.

			Substsrate[1]					
		N surveys	Shore	Sandbars	Islands	Rocks	K	p
Spring '85	Day	18	83.0±66.04^{a}	142.7±82.53^{b}	14.4±25.65^{c}	4.1±5.57^{c}	45.28	<0.001
	Night[2]	9	2.9±4.11^{a}	26.7±31.88^{b}	11.7±35.00^{a}	0.0±0.00^{a}	14.28	<0.005
Summer '85	Day	18	301.6±240.22^{a}	1091.1±385.74^{b}	91.0±168.74^{c}	41.7±41.57^{c}	41.00	<0.001
	Night	9	50.8±83.31^{a}	929.4±542.49^{b}	0.6±1.67^{a}	5.9±16.57^{a}	19.84	<0.001
Spring '86	Day	18	127.8±105.85^{a}	20.4±22.38^{b}	95.7±88.25^{a}	4.1±3.99^{c}	57.47	<0.001

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[1] See Table 1, footnote

[2] Area sampled at night extended from 0-4 km and 12-17 km from river mouth

Table 12. Relationship between number of foragers and loafers in river sections of various sizes during daylight hours.

Season	Section length(m)	N^1	r	p
Spring '85	500	148	0.015	>0.80
	1000	107	0.354	<0.001
	2000	78	0.778	<0.001
Summer '85	500	150	0.144	>0.05
	1000	112	0.412	<0.001
	2000	82	0.675	<0.001
Spring '86	500	270	0.008	>0.80
	1000	204	0.268	<0.001
	2000	140	0.315	<0.001

[1] Number of river sections containing foragers or loafers

with increasing numbers of loafers present in areas of maximal foraging. The average distance that foraging pelicans were visible (in any given direction) to my unaided eye was 875 m. Evidently, loafing pelicans were usually within visual range of foraging flocks.

DISCUSSION

Activity patterns

American White Pelicans were thought to be a diurnal species. During my study at Dauphin River, most pelicans foraged at night and loafed during the day. In spring, forager abundance and flock size were highest within three hours of evening and morning twilight. These time-related changes closely reflect the findings of O'Malley and Evans (1984), whose one night of observation at Grand Rapids, Manitoba, in spring suggested pelican foraging activity was highest between midnight and 0300 hrs. Over 80% of the pelicans observed returned to the colony before 1030 and the daytime population at Grand Rapids was lowest at midday.

Timing of white pelican foraging activity at Dauphin River appears to reflect temporal changes in abundance of accessible prey species. Pelicans formed large numbers of widely dispersed flocks during the daytime. Numerous small schools of perch, minnows and darters predominate in shallow water at this time (Carlander and Cleary 1949, Emery 1973, Hall and Werner 1977). At night, a few very large pelican flocks were concentrated between 3 and 4 km from the river mouth. Large fish such as walleye, suckers and whitefish move into shallow water at dusk and apparently comprise the largest fish biomass at night. In summer, I noted large pelican flocks forming whenever whitefish made spawning runs up Dauphin River.

Abundance, accessibility and timing of activity in prey species are known to be important factors influencing foraging patterns in several species. According to current foraging theory (Stephens and Krebs 1986), animals are expected to forage at places and times that enhance the rate of food consumption. For example, levels of foraging activity in Brown Pelicans (*P. occidentalis*) varied markedly between localized food patches in accordance with fish density (Brandt 1984). Direct linear relationships have also been found between density of Redshanks (*Tringa totanus*) and crustaceans and worms on which they feed (Goss-Custard 1979). Timing of diurnal feeding in several species of wood warblers (Parulidae) are also influenced by insect availability (Hutto 1981).

Seasonal changes in energetic demands may also influence the selection of foraging time by pelicans. Alcock (1975) suggested that high food demands force many birds to feed throughout the day and night. The highest annual energy demands imposed on *P. erythrorhynchos* are during the breeding season; Hall (1925) estimated that 68 kg of fish are needed for young to reach the fledging stage and that adults require 1.8 kg per day. Anderson (1987) estimated adult food demand of this species at 1.1 kg per day. Increased energetic demands imposed by vernal migration and breeding may act as a selective force, similar to food scarcity, that partially explains why pelicans foraged throughout the night and most of the day during the breeding season. Segregating foraging between day and night has also been suggested to reduce competitive interference among sympatric, predatory birds having similar diets (Cody 1974, Partridge 1978). It could also reduce intraspecific competition among pelicans, thereby allowing large numbers to feed on a prey population that is numerically and spatially limited. In addition to providing access to prey, nocturnal foraging may also benefit American White Pelicans by allowing them to travel between feeding grounds and breeding colony during the heat of the day. Large travelling flocks and easily located thermals reduce energetic costs of flight at this time (O'Malley and Evans 1982a).

Other factors may also moderate the selection of foraging times by pelicans. For example, number of foragers was inversely related to temperature and wind speed in summer and to temperature in spring 1986. These may be proximate factors affecting pelicans directly or, more likely, influencing the timing of activity and/or abundance of their primary prey species. In contrast to this study, Croll et al. (1986) found no relationship between wind speed and number of foraging Brown Pelicans. Dunn (1973) discovered that increasing wind speed and wave action were positively correlated with number of foraging Sandwich Terns (Sterna sandvicensis) and Common Terns (S. hirundo)

A five-fold increase in total number of pelicans occurred at Dauphin River between spring and summer. The large daily fluctuation in total numbers observed in spring was absent in summer. These results suggest that summer birds were post-breeders that congregated at Dauphin River prior to migration. The summer study period, 23 August to 5 September, occurred about the time of pelican migration. At East Shoal Lake, Manitoba, fledglings began to leave breeding colonies during the last two weeks of August (O'Malley and Evans 1982a). Fall migration from Saskatchewan extends from 27 August to October (Anweiler 1970). Movement away from breeding colonies to favoured feeding locations prior to migration has been suggested for both American White (Palmer 1976) and Brown Pelicans (Briggs *et al*. 1981).

Forager and loafer distribution within the study area

More pelicans were present on Dauphin River than the Lake Winnipeg study site, especially in early May. Pelican abundance subsequently decreased on the river while increasing on the lake, suggesting a seasonal shift away from the river, possibly to Lake Winnipeg and/or surrounding lakes. During a visit in mid summer (16 July 1985), a diurnal maximum of only 60 pelicans was seen loafing along the Dauphin River study site. Other studies also suggest *P. erythrorhynchos* may shift foraging sites by mid summer (Hall 1925, Trottier *et al*. 1980, Knopf and Kennedy 1981). The absence of spawning runs and a tendency of fish to move into deeper, cooler waters of lakes in summer (Hall and Werner 1977, Rudstam and Magnuson 1985) may have induced pelicans to forage elsewhere.

Diurnal foragers and loafers were observed in all lake and river habitats, but were concentrated from 0 to 6 km upstream from the river mouth. At night, pelicans were never seen near the shore of Lake Winnipeg, but were concentrated near the base of rapids on Dauphin River. In the downriver habitat, 77% of all nocturnal foragers were located 2.5 to 3 km from the river mouth. Most of these pelicans were from the intermediate habitat and had ceased to forage prior to floating downstream. Periodic examination of rapids revealed the presence of loafers, but no nocturnal foragers, between 5 and 12 km from the river mouth at night. These results suggest that foragers were more widely dispersed during the day than at night.

Water depth and water speed appeared to be the most important proximate factors influencing forager distribution. Pelicans in all river segments preferentially foraged close to shore and in water less than 1 m in depth. Qualitative evidence from other studies has also suggested that white pelicans prefer shallow water (Knopf and Kennedy 1980, Lingle and Sloan 1980, O'Malley and Evans 1984). Their preference for shallow water corresponds with a maximum foraging depth capability of 1 to 1.25 m for pelicans (Hall

1925, Palmer 1976, Anderson 1987). Guillet and Crowe (1981) similarly found an inverse relationship between water depth and mean monthly abundance of Great White Pelicans in South Africa. At Dauphin River, foragers were also most abundant where water speed was high, at one to two meters per second. This was the area, at the base of the rapids, where reefs appeared and mean water depth suddenly rose from 1.1 to 1.9 m.

Predation risk, inter- and intra-specific competition and microclimate are other factors believed to modify habitat selection in many small avian species (Grubb 1977, Partridge 1978, Barnard 1980a, Emlen 1981, Grubb and Greenwald 1982). For Great White Pelicans, surface area of water bodies and length of shoreline were both important factors correlated with feeding site selection (Guillet and Furness 1985). Numbers of _P_. _onocrotalus_ at Rondevlei Sanctuary increased with water turbidity, temperature and day length (Guillet and Crowe 1983). These proximate factors apparently influenced pelican distribution by affecting accessibility and/or abundance of catchable prey. There was no evidence in the present study to suggest any of these factors directly influence foraging site selection.

Selection of loafing sites by pelicans at Dauphin River was strongly correlated with forager location. Most loafers were located within the intermediate microhabitat, where foraging activity was highest. The evidence suggests that loafers positioned themselves so as to maximize their view of the most profitable foraging areas. Similar positioning of loafers has been found for gulls that cue to other foragers to locate highly ephemeral but temporarily rich clumped prey (Evans 1982, Chilton 1985). American White Pelicans normally loaf in or beside water, on beaches, sandbars and driftwood (Palmer 1976, O'Malley and Evans 1984). Although the amount of suitable shoreline at Dauphin River was virtually unlimited, sandbars were preferred whenever available. Preference for sandbars may benefit pelicans through reducing risks of predation or disturbance from terrestrial predators. Being located near both midstream and bends in the river, sandbars apparently allowed an unobstructed view of foraging grounds in all directions.

CHAPTER 2. DEVELOPMENT AND BREAKUP OF DIURNAL AND NOCTURNAL FORAGING FLOCKS IN AMERICAN WHITE PELICANS

INTRODUCTION

Factors governing formation and breakup of groups varies widely between species. Increased reproductive potential, reduced predation risks and improved success at locating and/or capturing prey are some primary benefits associated with group living (Brown 1975, Bertram 1978, Grier 1984). Studies by Crook (1965) and Barnard (1980a, b) suggest that the density and distribution of food are major contributors to the formation of many avian social organizations. When food is scarce and ephemeral, rooks (*Corvus frugilegus*) increase their ability to find food by using the presence or absence of conspecifics as an indicator of food location (Waite 1981). Animals which have their attention directed to a particular part of the environment by the activities of others are said to be using local enhancement (Thorpe 1956). The preference of arriving pelicans, at Grand Rapids, to join large foraging flocks was considered to be indicative of local enhancement (O'Malley and Evans 1984). Local enhancement may be instrumental in the formation of many avian flocks and may be facilitated by certain colors; studies by Kushlan (1977) and Caldwell (1981) suggest that flocks are most likely to form around species having conspicous, white plumages.

The objective of this study was to determine if group size, foraging success or time of day had any influence on whether a flock would be joined by (recruit) other pelicans. It was predicted that pelicans should attempt to maximize their foraging success by selectively joining flocks that were capturing fish. From previous studies relating conspicousness to flock recruitment (cited above), it was also predicted that flock recruitment would correlate positively with group size, and that this relationship would be reduced in strength during the night, when lowered light levels would presumably reduce the visual acuity of pelicans.

MATERIALS AND METHODS

Study area

Dauphin River is a clear, fast moving river, draining into Lake Winnipeg, in south-central Manitoba, Canada (see Chapter 1, Figs 1-3). During the time of this study (May 1986), water ranged from 2.0 to 5.0 m in depth at midstream and increased from 0.1 to 1.0 m/s in speed within the first 3 km upstream from the river mouth. Reefs, where water became 0.8 to 1.5 m deep and speed increased to greater than 1.0 m/s, occurred at 3 km from the mouth. Data were collected from flocks located within 3 km upstream (downriver habitat) and between 3 and 4 km from the river mouth (intermediate habitat). Most foraging activity on the river occurred within this area (Chapter 1).

Flock development and breakup

Continuous focal group samples were obtained from diurnal and nocturnal foraging flocks between 11-28 May, 1986. During daylight (0450-2205 hrs, CDT) observations, samples were obtained from a position on top of an elevated river bank using 10x50 Bushnell binoculars or a 16-36x50 Bushnell spotting scope. At night, flocks were observed with a Javelin (model #325) infrared scope in conjunction with a 75-205 mm Vivitar lens, from a blind placed 3 km from the river mouth; this was consistently the area of greatest foraging activity. The size and behaviour of nocturnal flocks were only recorded when foragers were within 300 m, the maximum visual range of the infrared scope.

Pelicans are aquatic surface feeders that capture prey by striking, or dipping, their bill into the water and capturing fish in the distendable gular pouch (Low et al. 1950, Palmer 1976). The bill is then elevated above the water surface and, if prey has been captured, the head and bill are raised in a swallowing motion. The number of bill dips and prey captured by all pelicans within foraging flocks were recorded. The number of bill dips and prey captured were then converted to dip rates (N bill dips x $bird^{-1}$ x min^{-1}) and capture rates (N prey captured x $bird^{-1}$ x min^{-1}) for analysis. Flock size was assessed at the start and throughout each observation period. Flock density was assessed approximately every 15 sec and was based on the mean distance separating neighbouring foragers (see Chapter 1, Methods). Observations lasted 5 min unless the flock left the area prior to this. The length of time that each flock foraged in one localized area of the river (foray) was noted whenever a flock left the area within the five minute sample period. Data were recorded into a Sony cassette deck and later transcribed onto a 20 channel Esterline Angus event recorder.

RESULTS

Flock development

A repetitive pattern of foraging flock formation occurred throughout the night and during periods of the day when many fish were being captured. At these times, large flocks formed within the intermediate river habitat. Pelicans fed while floating 100 to 2000 m downstream, then disbanded and flew to nearby loafing sites or back upstream where they reformed into a foraging flock consisting mostly of the same individuals. Flock formation was observably different between dawn and 1100 hrs, when only a few widely dispersed foragers were present (see Chapter 1). During this period, one or more individuals would occasionally swim towards another pelican and form a loosely organized, highly transitory flock. Pelicans used flight to join flocks which formed farther than 3 km from the river mouth.

Flock size and recruitment. Foraging flocks containing less than 10 individuals were more likely to attract at least one pelican than were larger flocks (Fig 7, Table 13). The tendency for larger flocks to recruit pelicans less often was evident for flocks having 10 or more pelicans during the day and more than 5 pelicans at night (Fig 7). At night, a two-fold increase in the percentage of flocks recruiting at least one pelican was observed between single foragers and flocks containing two to five pelicans. For each group size, more foraging flocks recruited pelicans at

Figure 7. Percentage of foraging flocks, of varying sizes, recruiting at least one pelican.

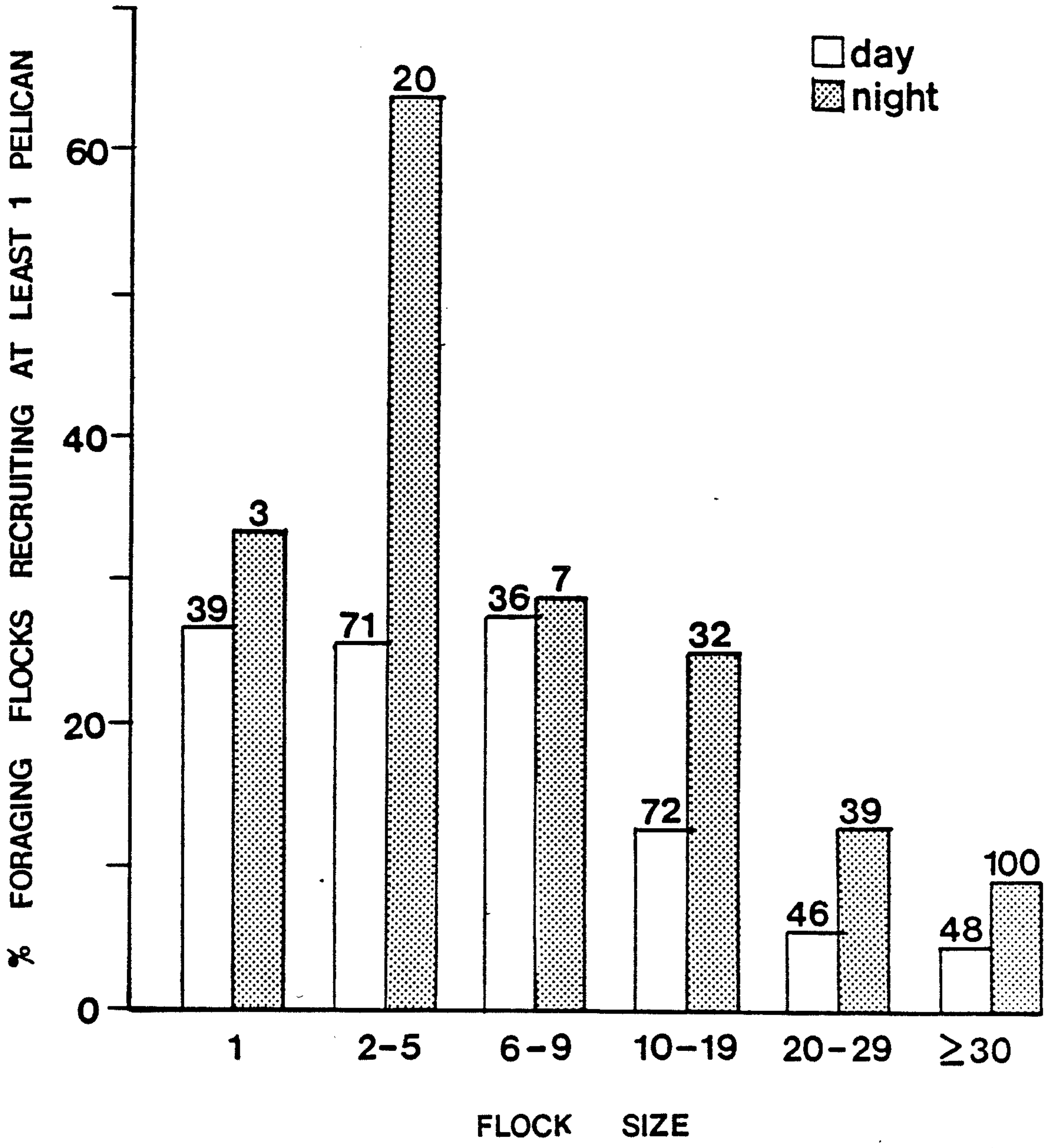

☐ day
▨ night
% FORAGING FLOCKS RECRUITING AT LEAST 1 PELICAN
0
20
40
60
39
3
71
20
36
7
72
32
46
39
48
100
1
2-5
6-9
10-19
20-29
≥30
FLOCK SIZE

Table 13. Percentage of small (<10 pelicans) and large flocks joined by at least one pelican (N flocks in parenthesis).

	Flock size[1]			
Period	1-9	$\geq$10	X^2	p
Day	25.0(132)	8.4(166)	13.97	<0.001
Night	51.4(35)	12.9(171)	25.20	<0.001
X^2;p	7.91;<0.005	1.30;>0.20		

---

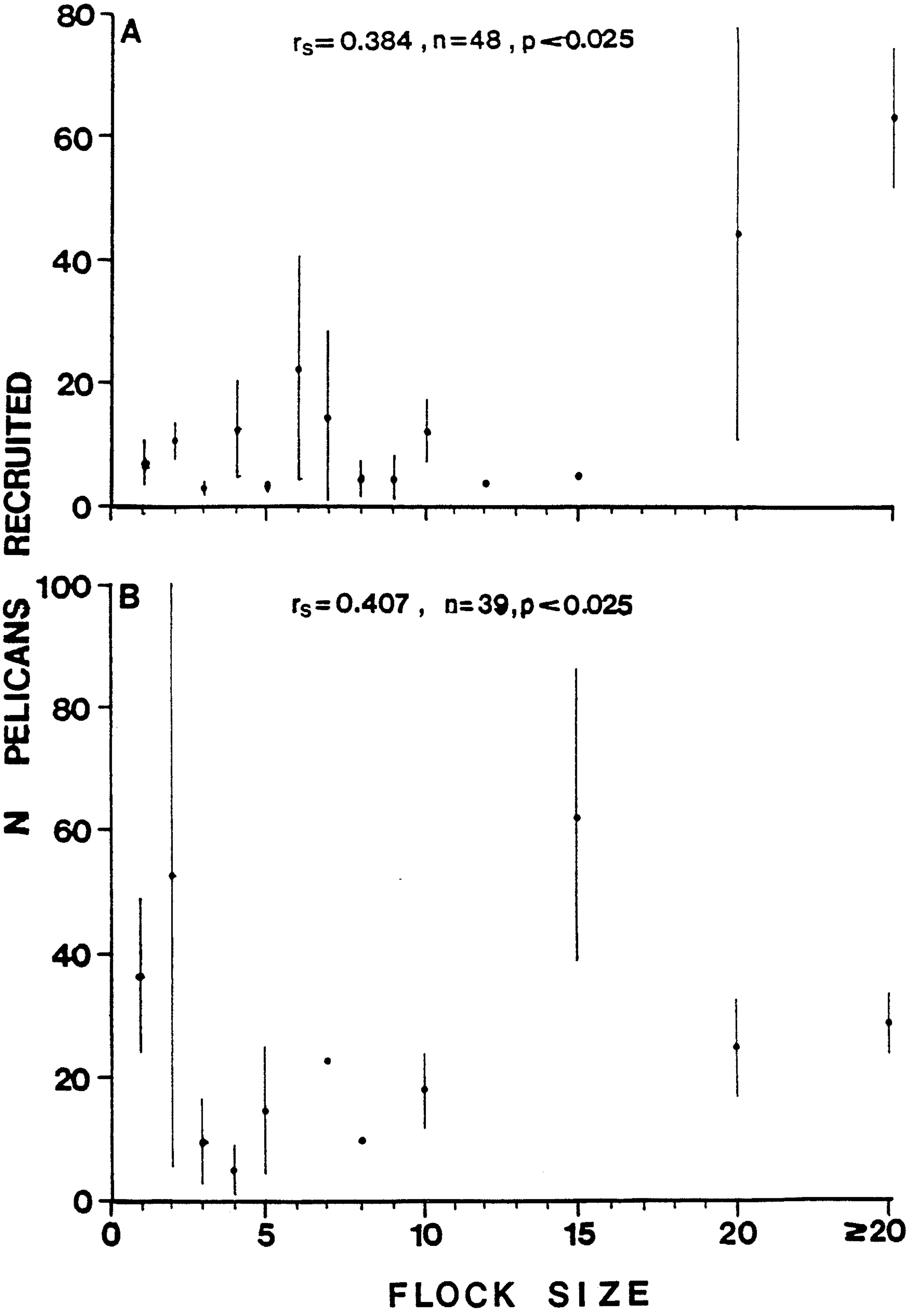
[1] Percentages given for ease of comparison. Statistics based on actual frequency of recruitment in (N) flocks.

night than during the day (Fig 7). Small flocks were thus more likely to increase in flock size. This difference reached statistical significance only for small flocks (Table 13).

Although a smaller proportion of large (≥10) flocks recruited pelicans, the total number attracted to flocks tended to increase with flock size during both day and night (Fig 8). Diurnal foraging flocks had a mean ± s.d. size of 9.9±10.44 (N=48) and recruited an average of 15.3±26.35 pelicans per flock. Nocturnal foraging flocks had a mean size of 17.0±17.42 (N=39) and recruited an average of 28.2±30.35 pelicans per flock. Significantly more pelicans were recruited by foraging flocks at night than during the day (K=4.75, $p<0.05$). However, this effect may be due to the presence of significantly larger flocks at night (K=5.06, $p<0.025$). No day-night difference in recruitment was discernable after controlling for the size of foraging flocks prior to attracting pelicans ($X^2=0.03$, df=1, $p>0.80$).

<u>Feeding success and recruitment</u>. It was predicted that an increase in a flock's feeding success (N prey captured x min^{-1}) should stimulate recruitment and hence the formation of larger flocks. To test this, a flock's feeding success was categorized into three groups according to the following criteria: 1)No feeding attempts were made (NF), 2)Bill dipping occurred but no prey were captured (BD), or 3)One or more prey were captured by any flock member (PC). In

Figure 8. Relationship between flock size and recruitment during the (A) day and (B) night, with associated Spearman's correlation coefficient (r_s). Diurnal foraging flocks had a mean ± s.d. size of 9.9±10.44 (N=48) and recruited 15.3±26.35 pelicans. Nocturnal foraging flocks had a mean size of 17.0±17.42 (N=39) and recruited 28.2±30.35 pelicans.


A
rs= 0.384 , n=48 , p<0.025
B
rs= 0.407 , n=39, p<0.025
N PELICANS RECRUITED
80
60
40
20
0
100
80
60
40
20
0
0
5
10
15
20
≥20
FLOCK SIZE

accordance with these categories, a flock's foraging success did not influence its probability of attracting at least one flock member (Table 14). There were also no differences in recruitment rates between day and night. Although foraging success had no effect on the probability of recruiting at least one flock member, more foragers were recruited when bill dipping and prey capture occurred. This effect was significant during the day (Table 15), when flocks that captured prey recruited significantly more pelicans than any other type of flock.

The influence that flock size had on frequency of recruitment varied with foraging success (Table 16). During the day, the probability of attracting at least 1 recruit was higher for small flocks, but this difference reached statistical significance only for flocks that were capturing prey. This preference for small, successful flocks provided the largest contribution explaining the disparity in recruitment among flock size shown in Table 13. At night, the size of flocks for those not attempting to feed did not appear to influence the frequency of recruiting at least one pelican (Table 16). However, smaller flocks were significantly more likely to attract at least one pelican if flock members were dipping their bills or capturing prey. Flocks not attempting to feed, especially large ones, were avoided by potential recruits during the day, but not at night.

Table 14. Percentage of flocks, having different foraging success, recruiting at least one pelican (N flocks in parenthesis).

	Foraging success[1]				
Period	NF	BD	PC	X^2	p
Day	18.5(54)	22.7(54)	17.1(187)	2.66	>0.20
Night	29.4(17)	20.6(102)	16.1(87)	1.79	>0.30
X^2;p	3.17;>0.05	0.27;>0.60	0.15;>0.60		

[1] NF=no bill dips; BD=bill dipping, but no prey captured; PC=bill dipping and prey capture. See Table 13, footnote, for description of values.

Table 15. Mean number of pelicans attracted per flock in relation to levels of foraging success (N flocks in parenthesis).

	Foraging Success[1]				
Period	NF	BD	PC	K	p
Day	3.3±4.87(9)^{a}	8.1±8.05(12)^{a}	22.4±33.07(27)^{b}	8.54	<0.025
Night	12.8±13.23(4)	23.8±24.81(24)	43.3±40.49(11)	4.97	<0.05
K; p	1.52;>0.20	3.05;>0.05	3.61;>0.05		

---

[1] Values in same row having different superscripts are significantly different at p=0.01 (Mann-Whitney U test). See Table 14, footnote, for description of categories

Table 16. Percentage of small (<10 pelicans) and large flocks having different foraging success that were joined by at least one pelican (N flocks in parenthesis).

Period	Flock size	Foraging success[1] NF	BD	PC	X^2	p
Day	1-9	10.6(47)^a	23.3(30)^b	36.4(55)^b	9.00	<0.025
	≥10	0.0(10)	8.3(24)	9.1(132)	1.00	>0.50
X^2; p		0.22;>0.60	1.88;>0.10	18.48;<0.001		
Night	1-9	27.3(11)^a	81.8(11)^b	46.2(13)^{a,b}	6.78	<0.05
	≥10	33.3(6)	13.2(91)	10.8(74)	2.53	>0.20
X^2; p		——[2]	24.23;<0.001	7.78;<0.025		

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[1] Values in same row having different superscripts are significantly different at p=0.05(2 x 2 X^2 tests). See Table 14, footnote.

[2] Insufficient sample size for 2 x 2 X^2 test.

Sign tests were used to determine whether or not prey capture (PC) influenced the size of flocks that subsequently formed in the same area. Focal PC flocks that were preceded by at least a 30 min period in which no other flock had captured prey were identified. The initial size of flocks that foraged within 5 min before and 5 min after these PC flocks were then compared. The mean ± s.d. size of foraging flocks was significantly higher after than before prey capture during the day (30.0±37.67 vs. 8.7±10.40 pelicans, N=17; $X^2=9.00$, $p<0.005$), but not at night (39.1±33.23 vs. 26.1±18.34 pelicans, N=20; $X^2=1.80$, $p>0.20$).

Flock breakup

The breakup and subsequent dispersal of flocks was observed for 43.0% (N=272) and 68.3% (N=183) of forays during day and night, respectively. Flocks often dispersed immediately after the cessation of bill dipping by all flock members. Foraging flocks lasted an average of only 157.0±92.53 secs (N=272) during the day and 129.9±58.55 secs (N=183) at night. Prior to dispersal, some pelicans usually began to swim away from the foraging flock, resulting in an increase in the average distance separating foragers ie. flock density decreased. Most flocks decreased in density prior to breakup during both day (66.2% of flocks, N=145; $X^2=15.23$, $p<0.001$) and night (60.0%, N=130; $X^2=5.20$, $p<0.025$).

Flocks lasted slightly but not significantly longer during the day than at night (Table 17). During the day, flocks that captured prey (PC) lasted significantly longer than flocks which were unsuccessful during bill dipping (BD). Neither group lasted significantly longer than those that made no attempt to feed (NF)(Table 17). At night, PC flocks lasted longer than either BD or NF flocks, and BD flocks lasted significantly longer than NF.

Foragers occasionally left flocks while other flock members were still foraging. This occurred during 20.8% (N=250) and 12.0% (N=183) of forays observed during day and night, respectively. Sign tests were used to determine whether the departure of one or more flock members coincided with periods, within forays, in which the rates of bill dipping and prey capture had dropped off. During both day and night, bill dipping was significantly lower within 30 secs of departure than for the preceding period (Table 18). Capture rates 30 sec before departure were significantly lower than for preceding periods during the day, but not at night. Rates of bill dipping and prey capture were therefore declining well before departure.

Table 17. Percentage of flocks, having different foraging success, that lasted longer than 2 min (N flocks in parenthesis).

	Foraging success[1]				
Period	NF	BD	PC	X^2	p
Day	62.7(51)^{a,b}	54.8(31)^{b}	74.7(186)^{a}	6.67	<0.05
Night	16.7(6)^{a}	37.8(90)^{b}	69.0(84)^{c}	20.06	<0.001
X^2;p	2.98;>0.05	2.10;>0.10	0.68;>0.40		

[1] See Table 16, footnote[1]

Table 18. Changes in rates of bill dipping and prey capture before one or more foragers left a flock (N flocks in parenthesis).

Variable[1]	Period	>30 sec Before Departure	30-0 sec Before Departure	%[2] Decreased	X^2	p
Dip Rates	Day	8.3±6.33(47)	5.0±4.78(56)	87.1(31)	17.06	<0.001
	Night	12.7±7.34(23)	8.7±6.44(23)	84.2(19)	8.89	<0.01
Capture Rates	Day	0.5±0.80(47)	0.4±1.50(56)	96.2(26)	22.15	<0.001
	Night	0.1±0.09(23)	0.0±0.08(23)	63.6(11)	0.41	>0.50

[1] Dip rates = N bill dips x bird^{-1} x min^{-1}; Capture rates = N prey captured x bird^{-1} x min^{-1}

[2] See Table 13, footnote; Percentage of (N) forays in which values were smaller within 30 sec of departure than at any time before departure

DISCUSSION

Flock development

Avian species that feed on inconspicuous prey that are clumped and/or unpredictable in distribution are commonly attracted to birds of the same or similar species and apparently use the presence of others as indicators of food location (Kushlan 1977, Caldwell 1981). Mixed species seabird flocks are frequently formed when a "catalyst" species, usually a large and conspicuous bird such as Black-legged Kittiwakes (*Rissa tridactyla*) or Glaucous-winged Gulls (*Larus glaucescens*), locate food and provide visual cues that attract others to the site of prey capture (Sealy 1973, Hoffman *et al.* 1981, Grover and Olla 1983). Birds that watch for and join others that capture prey benefit through having reduced search times and increased capture rates (Krebs *et al.* 1972, Krebs 1974, Brown 1988). To maximize foraging success on ephemeral and temporarily clumped prey, piscivorous birds such as terns immediately approach conspecifics that capture prey (Gochfeld and Burger 1982, Safina and Burger 1985).

Diurnally active American White Pelicans at Dauphin River showed a strong preference for joining foraging flocks that were capturing fish and avoiding ones containing pelicans that were not dipping their bills. Qualitatively, successful foragers were normally joined by one or more conspecifics within approximately 30 sec of prey being captured.

None of these recruits (N=9 observations) captured prey 30 to 120 sec prior to joining a successful flock. Since fish are ephemeral and disperse quickly upon detection by predators, pelicans should benefit from an immediate approach to the site of ongoing prey capture.

At night, pelicans did not selectively join flocks that were capturing prey over those not attempting to feed. This may suggest that reduced visual acuity of pelicans at night does not allow proper assessment of whether or not a flock was capturing prey. Flocks that were small and actively bill dipping for prey, but without prey capture, had the highest recruitment frequencies at this time.

In his study on House Sparrows (Passer domesticus), Barnard (1980b) suggested that larger flocks form where prey densities are highest because foragers remain longer at these sites. Since foraging flocks capturing prey lasted longer than those dipping unsuccessfully (Table 17), a probabilistic model predicts that if they are selected at random they should have the higher frequency of recruitment, which they did (Table 15). However, successful flocks were no more likely than unsuccessful flocks to recruit pelicans (Table 14), which suggests that selection of foraging flocks was based on properties other than their duration. Selection by duration also can not explain the greater recruitment to PC than to NF diurnal flocks, since their durations did not differ.

Studies on Rooks (Corvus frugilegus) and Glaucous-winged Gulls suggest that larger flocks had higher probabilities of attracting conspecifics (Waite 1981, Porter and Sealy 1982). O'Malley and Evans (1984) provided evidence suggesting that American White Pelicans arriving at Grand Rapids joined foraging and loafing flocks that were larger than if selected at random. At Dauphin River, the total number of pelicans recruited also increased with foraging flock size. Greater recruitment to large flocks should be an adaptive foraging tactic if such flocks form where prey densities and capture rates are highest (Waite 1981). At Dauphin River, the high probability of small flocks that captured prey recruiting at least one conspecific suggests that pelicans are sufficiently opportunistic to take advantage of social foraging cues other than flock size (eg. foraging success).

Flock Breakup

The Marginal Value Theorem (Charnov 1976) predicts that an optimal forager will leave a patch of food when its expected net gain drops to a level equivalent to the gain expected from the habitat as a whole. Capture rates attained by a pelican, and surrounding flock members, should provide a general estimate of patch quality and could be used in the decision whether to stay or leave. In support of this interpretation, declining rates of bill dipping and prey capture were closely related to the departure of pelicans from foraging flocks during the day. At night, departure of foragers from flocks correlated with declining rates of dipping, but did not correlate with capture rates (Table 18). In agreement with flock recruitment (see above), these results suggest that pelicans foraging at night are better able to monitor bill dipping than capture rates of nearby flock members, perhaps due to the louder noise of dipping compared to swallowing. Bill dipping provides unambiguous evidence that flock members are at least actively foraging, and to that extent should provide useful information to a forager in determining whether to remain with or leave a nocturnal flock.

Improper assessment of patch quality may also occur, and could partly explain observed departures of pelicans from many flocks that had stable or increasing rates of prey capture. Alternatively, pelicans that departed at such times may have been individuals that were satiated or had little or no success and left regardless of prey capture rates in neighbouring birds.

CHAPTER 3. FORAGING STRATEGIES OF AMERICAN WHITE PELICANS

INTRODUCTION

American White Pelicans (Pelecanus erythrorhynchos) normally feed by floating on a water surface and dipping, or striking, their bill into the water. Observed in both monospecific and mixed-species flocks, these pelicans are also kleptoparasites (food thieves) and scavengers of food (Skinner 1917, Koonz 1981, O'Malley and Evans 1983, Anderson 1987). They feed primarily on fish, from minnows to Carp (Cyprinus carpio) and Cui-ui suckers (Chastmistes cujus) exceeding 2 kg in weight and 500 mm in length (Hall 1925, Cottam and Williams 1939, Bond 1940, Alcorn 1943, Lingle and Sloan 1980). They have also been shown to take frogs and salamanders on occasion (Lingle and Sloan 1980, Godfrey 1986).

Many researchers have described "cooperative" feeding flocks in which American White Pelicans form a half-circle formation and drive fish into shore, or surround a school of fish on the open water of a lake and form an ever-contracting circle that traps fish (Goss 1888, Hall 1925, Cottam *et al*. 1942, Anderson 1987). American White Pelicans have also been observed making aerial dives into water from a height of 5 m (Hall 1925). Skinner (in Hall 1925) reported seeing a pelican that floated on a water surface, then dove in and was completely submerged in water. Pelicans have also been observed wading into shallow water in search of prey (Godfrey 1986).

Flock size, activity patterns and forager location are three factors which may influence the amount of search effort and prey captured by pelicans. Anderson (1987) demonstrated that increasing flock size was associated with increasing rates of bill dipping and decreasing efficiency of prey capture by American White Pelicans. In contrast, capture efficiency in the Great White Pelican (P. onocrotalus) increased with flock size (Wirtz 1986). To maximize prey intake rates, American White Pelicans should also forage whenever prey are abundant and accessible. Foraging activity for these pelicans is highest around morning and evening twilight, and possibly during portions of the night (O'Malley and Evans 1984). These authors suggested that the periodicity in foraging activity of pelicans at Grand Rapids, Manitoba, coincided with the activity cycles of fish in the area. Pelicans also show a strong preference to forage in shallow water during the breeding season (Knopf and Kennedy 1980, Lingle and Sloan 1980); this preference is apparently due both to higher abundances of prey near the shoreline of lakes and to pelicans being restricted to capturing prey located less than 1 m from the top of the water column.

The purpose of this study was to provide a detailed examination of the various ways American White Pelicans obtain food (foraging strategies) at a riverine site during day and night. Surveys and focal animal samples were used to describe and to quantify the differences between strategies and factors influencing their selection. This information was used to determine whether or not pelicans enhanced foraging success by most often using those strategies having the highest rates of prey capture. Rate and duration of bill dips were used to test the prediction that search effort increases after prey capture. Search paths were examined to test the prediction that foragers would stay longer in areas of recent prey capture, a phenomenon known as area restricted search (Tinbergen _et al_. 1967). An examination of the influence of flock size on dip rates, independent of capture rates, was used to test for the existence of social facilitation, i.e. contagious behaviour where the action of one animal releases identical behaviour in another (Thorpe 1956, Turner 1965). If social facilitation was operative, then an action such as bill dipping should increase with flock size. The following factors were also examined to see whether or not they influenced search effort and/or prey capture: time of day, number and location of foragers, flock density, location within flocks and fish accessibility.

MATERIALS AND METHODS

Focal animal samples

Diurnal and nocturnal foraging of American White Pelicans were studied at Dauphin River, Manitoba, Canada between 0 and 4 km from the river mouth. (see Chapter 1, Figs 1&2). This area was divided into Downriver (0 to 2.9 km from river mouth) and Intermediate (3 to 4 km from river mouth) river sections. The behaviour of individuals selected from various sized flocks (focal bird samples) were recorded during the periods of 31 May to 10 June and 23 August to 5 September in 1985. Focal group samples were based on the behaviour of the majority of pelicans in a flock and were collected from 11 to 28 May in 1986. Observations were conducted during: A)Diurnal hours - from 0429-2232 hrs (CDT) in spring 1985, 0606-2102 hrs in summer 1985, and 0451-2206 hrs in spring 1986, and B)Nocturnal hours - the period mutually exclusive of daylight hours.

Depending on the amount of illumination and distance of a flock from the observer, 10x50 Bushnell binoculars, a 16-36x50 Bushnell spotting scope or a Javelin (model #325) infrared scope were used in data collection. Continuous verbal accounts of relevant data were recorded into a Sony cassette deck throughout each observation. Information from focal bird and group samples was transcribed from tape onto a 20 channel Esterline Angus event recorder.

Individual pelicans were selected by randomly directing the spotting scope towards a previously unsampled foraging flock. For this portion of the study, the operative definition of flocks included solitary foragers (O'Malley and Evans 1982a, 1982b). Focal bird samples lasted either until the designated foragers departed from an area visible to the observer, or until a maximum time limit of five minutes was reached. Date, time, and location of a flock in relation to the river mouth (to nearest 100 m) were noted prior to each observation.

Foraging strategy, size and density of a flock were noted at the onset and end of each focal bird sample. Foraging strategies were defined on the basis of search methods, including presence or absence of flocking, of locomotion, shape of flock, and relative degree of coordination of movements among flock members. Foraging strategies were classed into: Sit-and-Wait, Mobile Individual, Aggregation, Following, Nucleus, and Semicircle. Pelicans also scavenged fish and used kleptoparsitism; in the present study, these are classed as prey capture techniques rather than foraging strategies.

Group density was based on the following operational scale: 1)Very dense - neighboring flock members were within one bill length of each other, 2)Dense - inter-pelican distance was between a pelican's bill and body length, 3)Moderate density - one to two body lengths between pelicans, 4)<u>Low density</u> - two to three body lengths between pelicans and 5)<u>Very low density</u> - distance between neighbouring flock members exceeded three body lengths.

Orientation of the focal bird was classed as being either upstream, downstream or towards northern or southern river shore (the river flows from west to east). Any 90° change in orientation was classed as a turn. For example, a forager that was facing upstream made two turns when it rotated 180° and faced downstream. Both forager orientation and its distance from the nearest shore (to nearest 10 m) were estimated whenever changes occurred.

Continuous records were kept of when the focal bird dipped its bill into the water and when prey were captured. The words "dip" and "up" were spoken into the cassette deck when the bill struck and was subsequently raised from water; time (secs) between these events is referred to as "dipping time". If a pelican's head was raised in a swallowing motion, the word "capture" was spoken and denoted the exact moment when prey entered the esophagus. The period extending from the moment that the bill was raised completely out of the water to when prey were swallowed was referred to as "swallowing time". Captured fish were classed into five groups: Fish less than 1/4 the length of a pelican's bill (<u>Very small</u>), fish that were 1/4 to 1/2 (<u>Small</u>), 1/2 to 3/4 (<u>Medium</u>), 3/4 to bill length (<u>Large</u>), and fish exceeding bill length (<u>Very large</u>). Small fish were often hidden in a pelican's gular pouch. In these cases, fish size was estimated by examining the amount and shape of gular pouch distention. Instances where fish size could not be reliably determined were excluded from subsequent analysis.

Preliminary observations suggested that, at this site, foraging flocks were usually active for approximately 2 min before flying to a new location. Focal group samples taken in 1986 lasted a maximum of 2 min during the day. At night, observations ended either when flocks passed beyond visual range or when 50% of foragers left a flock. All areas within randomly selected flocks were scanned continuously. Any changes in foraging strategy, size, density or orientation of a flock were recorded. Foraging strategy, flock size and density measurements were taken in the same way as those measurements taken in 1985. Flock orientation was based on the direction faced by the highest percentage (majority) of foragers in a flock. Distance from center of each flock to the nearest shore (to nearest 10 m) was assessed approximately every 15 seconds. Prior to recording bill dipping, the binoculars or infrared scope were directed randomly to a segment of a preselected flock. The word "dip" was recorded the moment that the cumulative number of pelicans striking the water with their bills exceeded 50% of those under observation. Number of bill dips performed within these sections were used to estimate mean dip rates for individual flock members. There was sufficient time between bill dips within sections to scan the flock and record the total number and size of prey captured by other foragers.

Rates of bill dipping (N bill dips x $bird^{-1}$ x min^{-1}) were used as a measure of search effort. Capture rates (N prey captured x $bird^{-1}$ x min^{-1}) and, where appropriate, capture efficiency (N prey captured x N bill $dips^{-1}$) were used as measures of foraging success. Turn rates (N turns x min^{-1}) were used as a measure of search path movement patterns. Analysis of changes occurring to foraging strategies, flock size and density during observations were based entirely on focal group samples taken in 1986. Information on size, abundance, and distribution of each type of foraging strategy were supplemented by data (not included in Chapter 1) obtained during surveys performed along the Dauphin River study site in 1985 and 1986 (methods described in Chapter 1). Foraging strategy, flock size and density were recorded for each forager observed during surveys. Forager location was classed into one of four habitats: downriver, intermediate, rapids and upriver (see Chapter 1, methods). In the present study, the term "foray" refers to a period of foraging occurring in one location; after a foray the flock flew to another site, usually 100 or more meters away.

Film analysis of foraging flocks

Foraging flocks were filmed to assess whether or not dipping rates, capture rates or capture efficiency differed between locations within flocks. Filming occurred between 1730 and 2140 hrs, from 13 to 24 May in 1986. A Sony Video Camera (90-230 mm lens) was used in conjunction with a reel to reel videorecorder. Flocks located from 2.5 to 4.5 km upstream from the mouth of Dauphin River were filmed. Flocks were filmed for 97±39.3 (mean ± s.d.) seconds. Date, time, duration of observations, and distance of the flock from shore were noted at the time of filming.

Videorecordings from 40 flocks were played back onto a 300 mm wide television screen. Each flock was first categorized into a front, middle and back sections. The front section was defined as the leading third of the flock. Data were then collected from an equal number of pelicans (10.2±6.86, range=2 to 20) in each section. When no clearly discernible middle section could be identified, as commonly occurred in flocks having fewer than 15 pelicans, data were collected only from one to three individuals located in the leading and trailing portion of the flock. Data taken from films included: foraging strategy, flock size and density, number of bill dips and number and size (relative to bill length) of prey captured. This information was collected from every individual sampled within preselected flock sections. To determine fish size more accurately, the film was stopped during playback and a magnifier was used to enhance the image. Dip rates, capture rates and capture efficiency were calculated and used in analysis.

Statistical analysis

ANOVA and Student's t-tests were used for testing whether or not variables such as turn rates and group density varied between populations. For each test, normal probability plots were produced to check the assumption of normality, and either Bartlett's or Hartley's Fmax tests were used to test for equality of variances (Neter and Wasserman 1974). Upon attaining a statistically significant result through ANOVA, multicomparison tests (Duncan's or Scheffe's tests, Berenson *et al*. 1983) were used. Whenever variance-stabilizing transformations were ineffective, a nonparametric Kruskal-Wallis rank test (K) was employed. When results were statistically significant, the Mann-Whitney U test was used to make all paired comparisons; this procedure required adjustment of the acceptable p level in accordance with the number of comparisons made, ie. 0.05 / N comparisons. Chi-squared tests were used when comparing frequency data and different events occuring at the same time and place. The Poisson distribution and runs tests were used in determining the dispersion pattern of prey captures. The Runs test employed a binomial probability distribution comparing the frequency at which sequential groupings (runs) of two events occurred (Mendenhall and Reinmuth 1982). Where two events such as bill dipping without prey capture (A) and bill dipping with prey capture (B) occur in the following order 'AAABBAAAAB', there is said to be four runs.

RESULTS

Prey capture techniques

Bill dipping. The period between when a pelican's bill struck and was subsequently raised above the water, referred to as dipping time (Dt), normally ranged from one to two seconds. For unsuccessful prey capture attempts, Dt was significantly longer at night than during the day (Table 19). Conversely, dipping time during prey capture was longer during the day than at night (Table 19). Dipping times were also significantly longer for successful than unsuccessful prey capture attempts during the day (Kruskall-Wallis K=83.29, p<0.001), but not at night (K=0.18, p>0.60). The period between when prey were brought to the surface and subsequently swallowed, or swallowing time (St), was similar in duration to Dt, but was significantly longer at night (Table 19). Prey handling time, which presumably includes portions below and above the water surface, was estimated as St above water plus a portion of Dt below water. Below-water handling time was estimated as Dt during prey capture minus Dt when no prey were captured. This estimate of below-water handling time assumes that time to dip the bill down and return it to the surface, exclusive of handling time, was the same for successful and unsuccessful dips. The resulting estimates for handling time below-water and total handling time were 0.7 and 1.9 sec during day and 0.2 and 2.1 sec at night. An estimated 37% and 10% of the time

Table 19. Mean ± s.d. dipping time and swallowing time of pelicans foraging during the day and night in 1985 when no prey were captured (N unsuccessful prey capture attempts in parenthesis) and prey were captured (N prey captures in parenthesis).

Foraging[1] success	Variable	Day	Night	K	p
BD	Dipping time	1.3±0.71(1131)	1.6±0.83(4814)	191.17	<0.001
PC	Dipping time	2.0±0.96(140)	1.8±1.67(46)	5.33	<0.025
PC	Swallowing time	1.2±0.91(140)	1.9±1.18(46)	17.69	<0.001

[1] BD = Bill dipping without prey capture; PC = Bill dipping with prey capture. Note that swallowing time is not relevant for BD

spent handling prey occurred below the water surface during the day and night, respectively.

Kleptoparasitism. When a pelican captured fish, neighbouring flock members sometimes jabbed at or grasped its head and bill in an attempt to force the successful forager to drop or disgorge its catch. Kleptoparasitism, or food theft, was a fortuitous method of prey capture that occurred in only 8 of 469 (1.7%) monospecific flocks observed along Dauphin River in 1986. Such kleptoparasitism was primarily observed during the day, with only 25% of all cases observed at night. Intraspecific kleptoparasitism occurred in flocks having 3 to 500 pelicans (mean ± s.d.= 87.0±170.70, N=8).

Kleptoparasitism attempts were only directed towards conspecifics that captured fish larger than about 20 cm in length. Attempts at food theft usually occurred only after an extended period (30.0±34.18 min, N=5) in which no prey were captured. The kleptoparasite and host were normally less than 5 m apart at the time of prey capture by the host. Large fish were evidently hardest to handle. Of those attempts where fish size and success of the kleptoparasite were observed, three large fish (35 to 50 cm in length) were stolen while three smaller fish (25 to 33 cm) were not. Pelicans that captured very large prey always swam or flew away from the flock, pursued by conspecifics.

Scavenging. Forty pelicans scavenged fish being thrown out of a commercial fishing boat docked 2.5 km from the river mouth on 6 May, 1985. After slowly approaching and picking up a discarded fish, a pelican would immediately fly away from the flock. Flock members chased and attempted to steal prey from any pelican that secured a large fish (>25 cm long). A large flock of Ring-billed gulls (*Larus delewarenses*) soon entered the area. Both species remained at this site until approximately 5 min after the last fish had been taken.

Foraging strategies

Foraging strategies were categorized on the basis of presence or absence of grouping, locomotion, and on shape and relative degree of coordination of movements among flock members. Flock size, speed of movement, duration of forays (foraging activity restricted to one place and time), flock density and feeding technique (bill dipping, kleptoparasitism or scavenging) were all considered to be attributes of a given strategy. By these criteria monospecific flocks used six readily identifiable foraging strategies:

Sit-and-Wait: These were solitary, sedentary foragers. Only 4 instances were seen at Dauphin River. In each case, a pelican positioned itself in shallow water less than 5 m from shore. These pelicans remained motionless for 5 to 20 minutes (8.5±2.78 min), and rarely turned their bodies (Table 20). The neck and head were raised well above the water surface, occasionally being extended forward and subsequently withdrawn. A side to side motion of the head was common (2.2±1.11 head turns x min^{-1}) and prevailed throughout forays. Two of four pelicans that used this strategy were within 5 m of an actively foraging Great Blue Heron (Ardea herodias).

Mobile Individual: This involved solitary foragers, farther than 5 m from the nearest conspecific, that were in nearly constant motion. Individuals moved at the same speed as pelicans employing group strategies, but turned significantly more frequently (Table 20). Erratic movement patterns were typical of Mobile Individuals, giving them the appearance of random searchers (Fig 9A).

Aggregation: These foraging flocks contained two or more pelicans, located within five meters of the nearest flock member, that oriented neither towards each other nor in the same direction (Fig 9B). This was a strategy that appeared to involve uncoordinated individual foragers gathered in a loosely organized flock. Turn rates were relatively low and flock speed similar to other group strategies (Table 20). One to three

Table 20. Mean ± s.d. turn rate, speed of swimming, and time between bill dipping sequences for pelicans using each foraging strategy (N flocks in parenthesis).

	Foraging Strategy[1]							
Variable	Sit-and-Wait	Individual	Aggregation	Following	Nucleus	Semicircle	K	p
Turns x min^{-1}	0.3±0.00(1)	3.2±2.20(50)^{a}	1.7±1.34(15)^{b}	2.1±1.51(161)^{b}	2.2±1.21(732)^{b}	2.4±1.26(46)^{b}	11.44	<0.025
Speed(m x sec^{-1})	0.0±0.00(4)	1.5±0.00(1)	2.2±0.00(1)	1.7±0.82(10)	2.4±0.96(241)	2.2±0.84(7)	5.97	$= 0.05$
Inter-dip[2] duration	—	2.9±2.22(5)^{a}	2.2±1.52(9)^{a}	2.4±2.27(32)^{a}	2.5±2.53(194)^{a}	4.3±4.55(166)^{b}	33.82	<0.001

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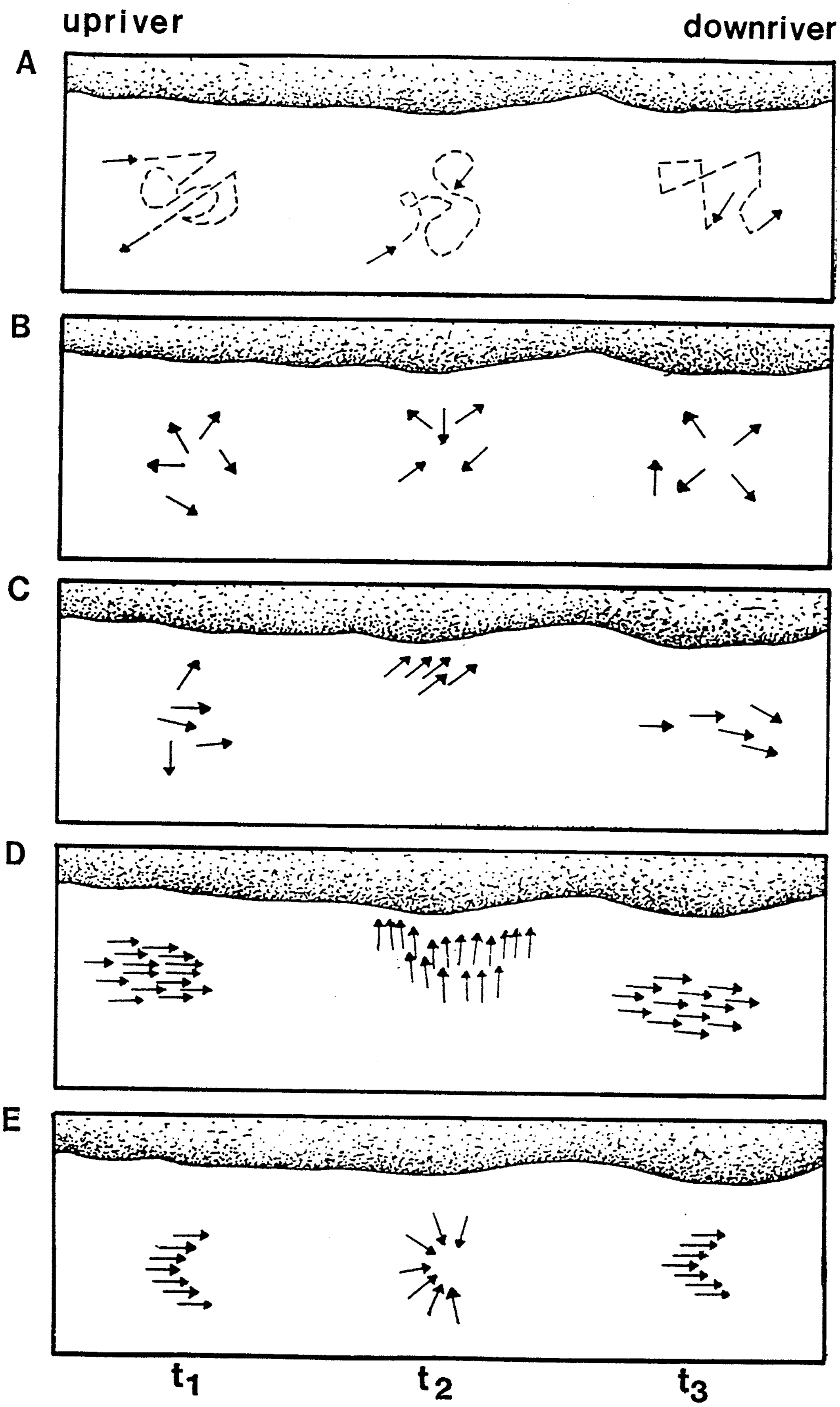
[1] Values in same row having different superscripts are significantly different at p=0.01 (Mann-Whitney U test). Variables having a sample size of less than 5 are not included in analysis.

[2] Time (sec) from the end of one dipping sequence to the onset of the next

Figure 9. Diagramatic representation of changes that typically occurred over time (t_i) in the structure and orientation of foraging flocks employing five different strategies: A) Mobile Individual, B) Aggregation, C) Following, D) Nucleus, and E) Semicircle. Sit-and-Wait foragers lack appreciable movement and were excluded. The stiples in "A" represent a typical search path for a solitary forager. In each diagram, river current flowed from left to right.


upriver
downriver
A
B
C
D
E
t_1
t_2
t_3

body lengths (Low and Moderate densities) separated flock members 96.6% of the time (Table 21).

Following: This stragegy was characterized by sporadic periods of coordinated movements and bill dipping among flock members. Foragers usually moved in the same direction for short periods, after which some moved in separate directions and later reformed with the flock (Fig 9C). Turn rate and flock speed were similar to other strategies containing two or more pelicans (Table 20). Flock density varied widely during most forays (Table 21). There was a significant difference ($X^2=91.14$, $df=8$, $p<0.001$) in flock density among the three coordinated foraging strategies (Following, Nucleus, Semicircle), lower densities being most common in Following. Directional changes and bill dipping were always initiated by foragers in the leading edge of the Following flocks that were filmed. Near synchronization of bill dipping occurred when dipping by foragers in the front of flocks was almost immediately copied by neighbouring pelicans. Such synchrony rarely occurred and was only maintained for two to five successive bill dips.

Nucleus: Movement patterns and bill dipping were more highly coordinated for Nuclei than Following. Though normally a dense circular flock, Nuclei also formed an elliptical shape prior to moving towards and encom-

Table 21. Number of forays in which each flock density predominated for the four strategies having more than one pelican (percentage of total time that each strategy was at each density is provided in parenthesis).

Flock[1] Density	Foraging Strategy			
	Aggregation	Following	Nucleus	Semicircle
Very Low	0 (0)	9 (10.4)	8 (4.9)	0 (0.5)
Low	2 (36.2)	35 (29.3)	24 (12.0)	0 (2.8)
Moderate	3 (60.4)	32 (33.3)	31 (15.8)	3 (18.5)
Dense	0 (3.7)	31 (25.0)	143 (43.6)	14 (44.8)
Very High	0 (0)	1 (1.9)	69 (23.7)	4 (33.4)
Total Time[2]	6.9	213.5	639.3	45.2

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[1] See Methods for definiton of density categories

[2] Total Time (min) that each foraging strategy was observed

passing a portion of the shore (Fig 9D, t_2). Pelicans in Nuclei turned at similar rates and moved faster, but not significantly so, than other group strategies (Table 20). Distance between flock members was normally less than one body length (Dense to Very High density) and varied little during forays (Table 21).

Near synchronization of bill dipping in Nuclei was manifested as a sequential wave of descending heads, initiated at the front and moving towards the rear of the group. This occurred in 21.6% (N=37) of the Nuclei filmed. Synchrony in these instances was maintained among most members of the flock for up to approximately 20 dips, then dipping became asynchronous. Nuclei containing 100 to 2000 pelicans usually had one to three subsections of 5 to 30 foragers located in the leading-downstream edge of the flock. Bill dipping within these subsections was synchronous, but out of phase with the rest of the flock.

Semicircle: This was the most highly coordinated strategy. Movement patterns, flock speed and bill dipping were almost perfectly synchronized among all flock members throughout forays. Pelicans usually maintained a half-circle formation, but occasionaly formed a closed circle prior to the onset of bill dipping (Fig 9E). Unlike other strategies, positional changes among flock members were never observed. Turn rates and flock speed were similar to other group strategies (Table 20). Distance between foragers, normally less than one body length (dense or very high density), varied little during forays (Table 21). During synchronized bill dipping, an individual would raise its head, slowly extend its neck and remain in that position until all other flock members were positioned in like fashion; all flock members would then strike the water simultaneously with their bills. Flock members then realigned themselves into a half-circle prior to the next bill dipping sequence. The time between dips was significantly longer for Semicircles than for other strategies (Table 20), but the degree of dipping synchronization was much greater. Dipping often became asynchronous when one or more foragers captured prey. Foragers then made one to five rapid dips prior to reforming into a highly coordinated flock.

Frequency of occurrence of foraging strategies. The mean number of foraging pelicans observed during surveys of Dauphin River varied significantly among strategies (Table 22). Sit-and-Wait was the rarest foraging strategy. Though never observed during surveys, it represented 4 of 1026 (0.4%) flocks sampled during focal bird and group samples. Most (75%) were seen at night. During spring surveys, few pelicans foraged as Mobile Individuals or within nocturnal

Table 22. Mean ± s.d. number of foragers per survey using different strategies during surveys of Dauphin River in the day and at night.

			Foraging Strategy[1]						
	Period	N surveys	Mobile Individuals	Aggregation	Following	Nucleus	Semicircle	K	p
Spring '85	Day	18	2.6 ± 3.29^{a}	11.5 ± 47.07^{b}	9.3 ± 10.04^{c}	24.0 ± 34.90^{d}	2.6 ± 6.99^{a}	21.46	< 0.001
	Night	9	1.1 ± 0.60^{a}	0.0 ± 0.00^{b}	3.7 ± 5.32^{a}	154.4 ± 78.42^{c}	1.4 ± 2.96^{a}	30.02	< 0.001
	K(p)[2]		1.19(>0.20)	1.04(>0.30)	2.13(>0.10)	15.05(<0.001)	0.02(>0.80)		
Summer '85	Day	16	76.7 ± 119.19^{a}	4.8 ± 9.73^{b}	23.5 ± 23.90^{a}	194.3 ± 272.36^{a}	0.0 ± 0.00^{c}	34.52	< 0.001
	Night	9	55.2 ± 82.65^{a}	$141.0 \pm 195.03^{a,b}$	22.2 ± 33.69^{a}	403.7 ± 394.04^{b}	0.0 ± 0.00^{c}	34.52	< 0.001
	K(p)[2]		0.12(>0.70)	9.36(<0.005)	0.21(>0.60)	5.20(<0.025)	—		
Spring '86	Day	28	4.8 ± 3.48^{a}	8.4 ± 20.77^{b}	34.4 ± 42.74^{c}	58.4 ± 66.42^{c}	1.3 ± 3.94^{a}	63.64	< 0.001

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[1] See Table 20, footnote; Sit-and-wait foragers were never observed during surveys

[2] Day-night comparisons were for the areas extending from 0 to 4 km and 12 to 17 km from the river mouth

Aggregations or Semicircles (Table 22). Pelicans frequently used Following, especially in 1986, but Nuclei predominated during most surveys. In spring, only Nuclei demonstrated significant temporal variation and contained more foragers at night than during the day. Remaining strategies were slightly, but not significantly, more abundant during the day. In summer, most pelicans foraged within Nuclei. Semicircles were never observed in summer. Significantly more summer foragers participated in Aggregations and Nuclei at night than during the day (Table 22). Mobile Individuals and Following contained slightly, but not significantly, more pelicans during the day.

Foraging strategy and flock sizes. Flock size also varied significantly among foraging strategies (Table 23). Flock size for Mobile Individuals was, by definition, always equal to one. Mobile Individuals were the most frequently seen flock, while flocks employing Sit-and-Wait, Aggregation and Semicircle strategies were the rarest. Flock sizes for Following tended to be smaller than for Aggregations or Semicircles and were always significantly smaller than Nuclei. Nuclei and Aggregations usually had the largest flocks. Only Aggregations demonstrated significant day-night variation in flock size, and then only in summer (Table 23). The range of flock sizes for Aggregations (2-900), Following (2-100) and Nuclei (2-2000) were large in comparison with Semicircles (2-30).

Table 23. Mean ± s.d. flock size of foraging strategies observed during surveys of Dauphin River in the day and at night (N flocks in parenthesis).

		Foraging Strategy[1]						
Season	Period	Mobile Individual	Aggregation	Following	Nucleus	Semicircle	K	p
Spring '85	Day	1.0±0.00(46)	103.5±136.47(2)	4.9±2.90(34)^{a}	36.0±31.23(12)^{b}	11.5±8.70(4)	26.41	<0.001
	Night	1.0±0.00(10)	—	3.7±1.58(9)^{a}	47.9±44.04(29)^{b}	6.5±2.12(2)	22.98	<0.001
	K(p)[2]	—	—	1.16(>0.20)	0.72(>0.30)	—		
Summer '86	Day	1.0±0.00(1227)	12.8±8.75(6)^{a}	8.5±6.42(44)^{a}	194.3±255.70(16)^{b}	—	33.38	<0.001
	Night	1.0±0.00(497)	90.6±72.12(14)^{a}	7.7±8.98(26)^{b}	88.6±112.68(41)^{a}	—	43.36	<0.001
	K(p)	—	5.07(<0.025)	2.72(>0.05)	2.29(>0.10)	—		
Spring '86	Day	1.0±0.00(135)	14.7±15.93(16)	5.5±5.67(176)^{b}	29.2±32.68(56)^{c}	12.3±2.52(3)	101.54	<0.001

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[1] See Table 20, footnote; Mobile Individuals not included in analysis; Sit-and-Wait foragers were never observed during surveys

[2] See Table 22, footnote[2]

Formation and restructuring of foraging strategies. From 12% to 92% of foraging flocks recruited at least one pelican during a foray (Table 24). Recruitment frequencies, defined as the percentage of flocks attracting pelicans, did not differ significantly among foraging strategies during the day. At night, Following had the significantly highest recruitment frequency. Recruitment frequencies for Nuclei did not differ significantly ($X^2=1.42$, $p>0.20$) between day and night. Recruitment frequencies for Following were significantly higher ($X^2=29.45$, $p<0.001$) at night (Table 24).

Mean number of pelicans recruited by Nuclei during daytime forays was significantly higher than for any other strategy. At night, mean number of pelicans attracted to Nuclei was significantly higher than for Following but similar to Mobile Individuals. Semicircles recruited the fewest number of pelicans during both day and night (Table 24). All foraging strategies attracted more pelicans at night than during the day; statistical significance was reached for Mobile Individuals ($t=3.26$, $df=8$, $p<0.025$), but not Following ($t=1.61$, $df=30$, $p>0.05$) or Nucleus strategies ($t=0.49$, $df=42$, $p>0.30$).

Foraging strategies were occasionally formed through the restructuring of existing flocks (Table 25). The frequency with which this restructuring, or strategy switching, occurred during forays differed significantly among strategies ($X^2=55.53$, $p<0.001$). Strategy switching rarely

Table 24. Recruitment of pelicans to each type of foraging strategy during the (A) day and at (B) night in 1986 (N flocks in parenthesis).

Variable[1]	Foraging Strategy[2] Mobile Individual	Aggregation	Following	Nucleus	Semicircle	Test	p
A							
Initial flock size	1.0±0.00(8)^{a}	20.0±0.00(1)	4.1±1.45(20)^{b}	14.9±10.56(22)^{c}	6.7±1.53(3)	K=39.94	<0.001
Percent recruiting	24.2(33)	12.5(8)	18.2(110)	14.1(156)	15.8(19)	X^2=2.40	>0.05
N recruited	7.1±10.20(8)^{a,b}	6.0±0.00(1)	6.3±8.16(20)^{a}	26.8±34.94(22)^{b}	2.0±1.00(3)	K=11.52	<0.01
B							
Initial flock size	1.0±0.00(2)	—	4.1±2.35(12)^{a}	32.2±23.40(22)^{b}	9.3±5.13(3)	K=21.03	<0.001
Percent recruiting	33.3(6)^{a}	—	92.3(13)^{b}	13.4(164)^{a}	33.3(9)^{a}	X^2=48.03	<0.001
N recruited	36.5±17.68(2)	—	21.5±41.28(12)^{a}	31.2±23.01(22)^{b}	9.7±5.51(3)	K=6.69	<0.01

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[1] Initial flock size = mean ± s.d. flock size prior to recruitment; Percent recruiting = proportion of flocks of a given strategy attracting at least one pelican during a foray; N recruited = mean ± s.d. number of pelicans recruited per foray

[2] Values in same row having different superscripts are significantly different at $p=0.01$ (Mann-Whitney U test) and at $p=0.05$ (2 x 2 X^2 test)

Table 25. Frequency of changes between foraging strategies during forays.

Strategy Changed to:	Initial Strategy: Mobile Individual	Aggregation	Following	Nucleus	Semicircle
Mobile Individual	(27)[1]	0	4	0	0
Aggregation	2	(3)	4	0	0
Following	6	4	(113)	13	6
Nucleus	4	1	12	(303)	2
Semicircle	0	0	5	4	(20)
% Change(N)[2]	30.8(39)[a,b]	62.5(8)[a]	18.1(138)[b]	5.3(320)[c]	28.6(28)[a,b]

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[1] Values on the diagonal represent N forays in which foraging strategy did not change

[2] Proportion of flocks of a given strategy that changed from one type to another during a foray (total number of flocks of specified strategy in parenthesis); See Table 24, footnote[2], for description of alphabetical superscripts

occurred for Following and Nuclei (Table 25), while Aggregations and to a lesser extent Mobile Individuals had the highest frequencies of strategy switching. The combined frequency of strategy switching for uncoordinated flocks (Mobile Individual, Aggregation) was significantly higher than for all coordinated strategies combined (36.2%, N=47 vs. 10.3%, N=486; $X^2=23.82$, $p<0.001$).

Whereas Following flocks reorganized into all other strategies, Nuclei switched only to Following and Semicircles. The percentage of uncoordinated flocks forming Semicircles was significantly lower than the percentage forming either Following or Nuclei (0.0%, N=9 vs. 31.3%, N=48; $X^2=5.10$, $p<0.025$). Restructuring of flocks thus appeared to occur along a continuum: Flocks lacking coordination did not form Semicircles, Following flocks could be restructured into any other strategy, and the two most highly coordinated strategies did not become uncoordinated Mobile Individuals or Aggregations (Table 25).

New foraging strategies sometimes formed immediately after pelicans either departed from or were recruited to a flock. This occurred in 26.9% (N=52) of all flocks during the day and 7.7% (N=13) at night. A significantly higher percentage of foraging flocks switched strategies during daytime forays than at night (32.2%, N=326 vs. 16.2%, N=207; $X^2=5.46$, $p<0.001$).

Positional changes among flock members that did not produce a change in foraging strategy were common in Following and Nuclei whenever many fish were captured. At these times, individuals located near the rear of the flock often swam into and sometimes displaced birds directly in front of them. As the flock approached shore, many foragers near the rear would move to the leading-downstream edge of flocks by rapidly swimming around other flock members. Almost constant flying of foragers from rear to front of Nuclei containing more than 100 pelicans was common whenever many large fish were being captured. This "leap-frogging" frequently occurred in the early afternoon and around dusk in summer.

Factors influencing foraging effort and success

Search effort, how intensely a forager sought out food, was estimated from rates of bill dipping. Foraging success was based on prey capture rates and, when appropriate, capture efficiency.

Foraging strategies. Rates of bill dipping differed significantly among foraging strategies (Table 26). Sit-and-Wait foragers and Mobile Individuals seldom dipped their bills, while Aggregations and Following flocks usually had intermediate rates of dipping. In spring, Nuclei and Semicircles consistently maintained the highest rates of dipping during both day and night. This trend was also present during summer nights.

Table 26. Mean ± s.d. rate of (A) bill dipping and (B) prey capture per foray for each foraging strategy (N forays in parenthesis).

		Foraging Strategy^{1}							
Season	Period	Sit-and-Wait	Mobile Individual	Aggregation	Following	Nucleus	Semicircle	K	p
A^{2}									
Spring '85	Day	1.21±0.00(1)	1.42±2.86(4)	—	0.70±1.79(12)^{a}	4.29±3.28(57)^{b}	4.50±1.77(2)	18.93	<0.001
	Night	0.39±0.24(2)	0.00±0.00(4)	—	2.23±2.96(10)^{a}	8.60±4.02(166)^{b}	7.73±2.64(11)^{b}	32.64	<0.001
	K;p	—	—	—	0.81;>0.30	44.73;<0.001	—		
Summer '85	Day	—	0.80±0.71(3)	0.10±0.20(4)	2.96±2.30(2)	3.10±3.21(47)	0.33±0.00(1)	—	—
	Night	0.00±0.00(1)	1.00±1.67(5)	2.15±3.40(4)	1.29±1.71(3)	4.08±3.88(142)	3.04±1.27(5)	9.14	<0.025
	K; p	—	—	—	—	2.28;>0.10	—		
Spring '86	Day	—	1.62±2.79(29)^{a}	4.11±3.87(7)^{b}	3.59±4.24(102)^{b}	6.41±3.18(152)^{c}	7.84±2.36(19)^{c}	74.72	<0.001
	Night	—	1.82±3.08(6)^{a}	3.64±0.00(1)	4.87±4.45(26)^{a}	6.98±3.81(161)^{b}	6.82±3.31(9)^{a,b}	15.23	<0.005
	K; p	—	0.00;>0.90	—	2.21;>0.10	1.85;>0.10	1.02;>0.30		
B^{2}									
Spring '85	Day	0.40±0.00(1)	0.00±0.00(4)	—	0.02±0.09(12)^{a}	0.63±0.81(57)^{b}	0.27±0.38(2)	13.64	<0.001
	Night	0.15±0.05(2)	0.00±0.00(4)	—	0.08±0.25(10)^{a,b}	0.07±0.25(166)^{a}	0.19±0.35(11)^{b}	18.63	<0.001
	K; p	—	—	—	0.04;>0.80	60.71;<0.001	—		
Summer '85	Day	—	0.00±0.00(3)	0.00±0.00(4)	0.00±0.00(2)	0.11±0.32(47)	0.00±0.00(1)	—	—
	Night	0.00±0.00(1)	0.00±0.00(5)	0.00±0.00(4)	0.00±0.00(3)	0.02±0.13(142)	0.00±0.00(5)	0.65	>0.70
	K; p	—	—	—	—	9.89;<0.005	—		
Spring '86	Day	—	0.14±0.44(29)^{a}	0.29±0.50(7)^{b}	0.24±0.49(102)^{b}	0.31±0.31(151)^{c}	0.38±0.35(19)^{c}	56.76	<0.001
	Night	—	0.00±0.00(6)	0.00±0.00(1)	0.09±0.26(26)	0.02±0.05(161)	0.05±0.07(9)	6.92	>0.05
	K; p	—	0.66;>0.40	—	1.72;>0.10	131.08;<0.001	10.76;<0.001		

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[1] See Table 20, footnote

[2] Dip rate = N bill dips x bird^{-1}x min^{-1}; Capture rate = N prey captured x bird^{-1}x min^{-1}

Capture rates also differed among strategies, but differences were significant only in spring (Table 26). Capture rates were usually highest for coordinated strategies during both day and night. There were few exceptions to this rule.

Search effort and foraging success were compared between Semicircles and all other strategies seen foraging at approximately the same time (±15 min) and place. Neither dip rates nor time required to capture the first prey item during a foray were significantly different between strategies (Table 27). Mean rates and efficiency of capture were also similar, but were greater for Semicircles than other strategies in a significant proportion of forays (Table 27). Since this positive effect was not due to increased search effort (dip rate) or to a reduction in foraging time required to locate prey, foragers in Semicircles were evidently more often faster and more efficient at prey capture after prey were located. Semicircles were not only the most highly coordinated strategy, but remained as a cohesive flock for significantly longer than other strategies (Table 27).

Video recordings revealed that flock movements and bill dipping were also highly coordinated in many Nuclei. Near synchronization of bill dipping occurred in 21.6% (N=37) of all Nuclei. These more highly coordinated Nuclei had higher dip rates than other Nuclei (6.0±3.81, n=8 vs. 3.3±2.46 bill dips x $bird^{-1}$ x min^{-1}, n=29; $t=2.43$, $p<0.025$). Capture

Table 27. Mean ± s.d. values for foraging parameters between semicircles and other types of flocks foraging at the same time (±15 min) and location (N forays in parenthesis).

Variable[1]	Semicircles	Other strategies	% Sc[2] higher	X^2	p
Dip rate	6.50±2.90(37)	6.50±4.15(138)	54.3(162)	1.21	>0.10
Capture rate	0.18±0.29(37)	0.17±0.37(138)	65.7(108)	10.71	<0.005
Capture efficiency	0.03±0.05(37)	0.03±0.08(138)	63.2(117)	8.21	<0.01
First capture_t	40.1±48.90(26)	35.3±43.81(99)	43.3(104)	1.88	>0.10
Foray duration	195.0±123.94(28)	153.5±91.24(153)	63.9(147)	11.44	<0.001

[1] Dip rate = N bill dips x bird^{-1} x min^{-1}; Capture rate = N prey captured x bird^{-1} x min^{-1}; Capture efficiency = N prey captured x N bill dips^{-1}; First capture_t = time (secs) from onset of foray until first prey captured, where flock formation observed; Foray duration = time (secs) from onset of foray to departure of flock

[2] Percentage of (N) forays in which Semicircles had higher values, for a given foraging variable, than other flocks foraging at the same time and place

rates for the highly coordinated Nuclei were not significantly different from other Nuclei (1.6±2.13, n=8 vs. 1.1±1.37 captures x bird^{-1} x min^{-1}, n=29; t=0.81, p>0.40). This evidence thus suggests that the amount of synchronization of bill dipping in Nuclei does not influence the amount of prey captured. However, only highly coordinated Nuclei captured large fish.

Effects of prey capture on search effort. It was predicted that intensity of search would increase whenever prey were captured. This hypothesis was tested by comparing bill dipping of the focal bird immediately before and after the initial capture of prey during a foray. Both dipping time and inter-dip intervals were shorter significantly more often immediately after than before prey capture (Table 28). Pelicans thus responded to prey capture by dipping faster and more frequently. There was, however, no long term difference in dip rates extending from 30 seconds before and after prey capture (Table 28). Increased search effort immediately following prey capture was therefore maintained for only a short period.

Flock size and social facilitation. The influence of flock size on dip rates as an indicator of social facilitation was tested using flocks in which no forager captured prey. During both day and night, dip rates tended to increase with flock sizes up to about 100 (±20), then reached an asymptote or declined (Fig 10). A weak (low r^2

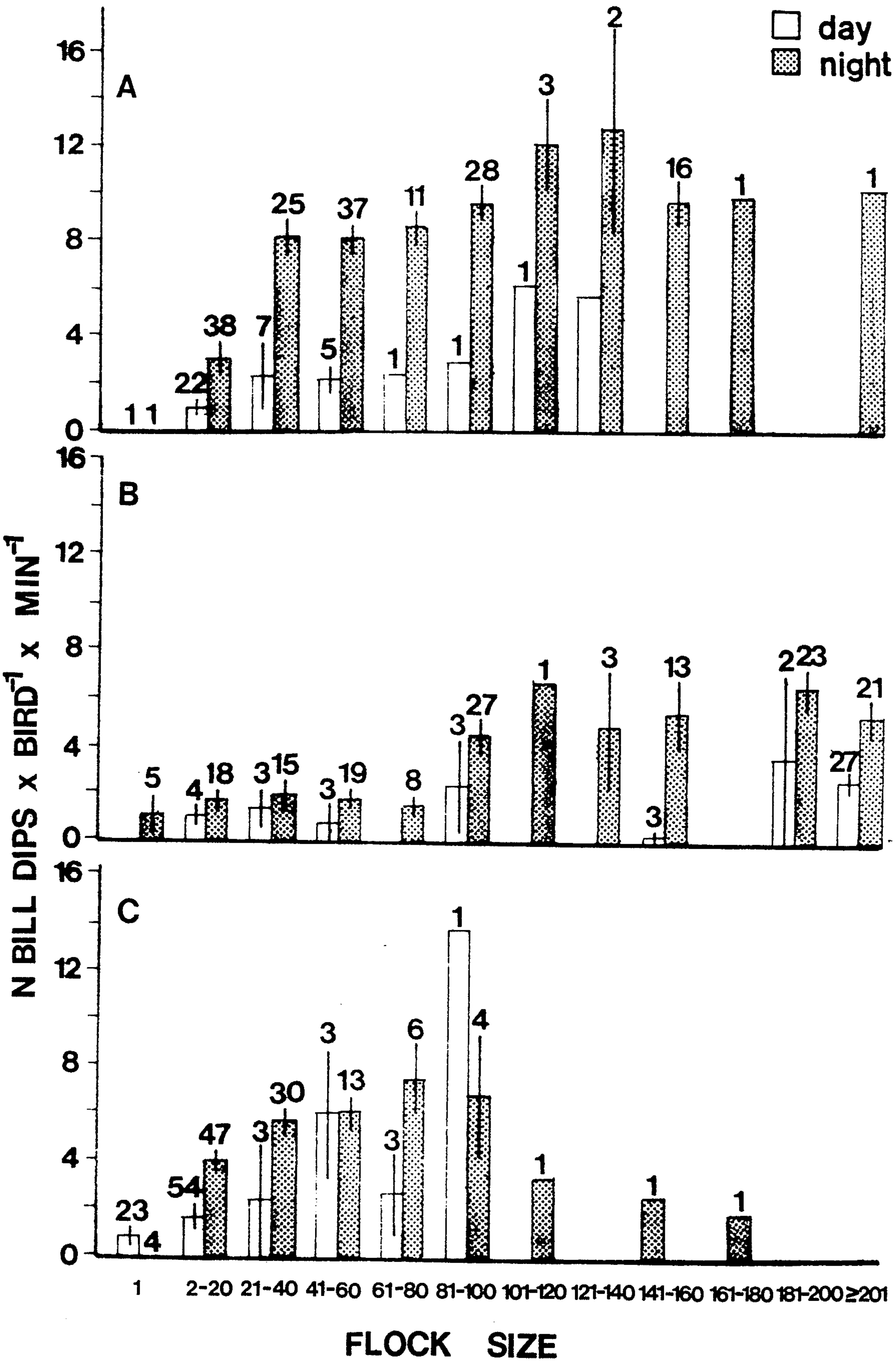
Table 28. Influence of prey capture on bill dipping. Based on the first prey captured during forays in 1985.

Variable[1]	Period	N forays	Before capture	After capture	% decreased[2]	X^2	p
Dipping time	Day	67	1.4±0.72	1.2±0.81	65.4(81)	7.72	<0.01
	Night	46	1.5±0.80	1.3±0.73			
Inter-dip interval	Day	67	3.0±3.77	2.9±3.69	64.1(103)	8.17	<0.005
	Night	43	2.5±3.15	2.0±4.13			
Dip rate	Day	36	8.9±3.90	9.5±5.02	47.5(59)	0.15	>0.60
	Night	27	15.1±8.01	14.6±7.99			

[1] Dipping time = period (secs) in which the bill was struck into and subsequently raised from the water; Inter-dip interval = period (secs) from end of one dip to onset of next; Dip rate = N bill dips x $bird^{-1}$ x min^{-1}, 30 sec before and after first prey capture

[2] Percentage of (N) forays in which single values, for each variable, were smaller immediately after than before first prey capture; day and night combined for X^2 test

Figure 10. Relationship between flock size and mean ± s.e. dip rates for forays in which no prey were captured by any flock member during (A) spring '85, (B) summer '85, and (C) spring '86.



day
night
A
B
C
N BILL DIPS x BIRD^{-1} x MIN^{-1}
0
4
8
12
16
FLOCK SIZE
1
2-20
21-40
41-60
61-80
81-100
101-120
121-140
141-160
161-180
181-200
≥201
1 1
22
38
7
25
5
37
1
11
1
28
1
3
2
16
1
1
5
4
18
3
15
3
19
8
3
27
1
3
13
3
2
23
27
21
23
4
54
47
3
30
3
13
3
6
1
4
1
1
1

values) but statistically significant positive relationship existed between flock size and bill dipping throughout both spring seasons and during summer nights (Table 29). This relationship between flock size and dip rates was stronger at night than during the day. Taken collectively, these results suggest a positive effect of group size on dip rates, as predicted by the social facilitation hypothesis.

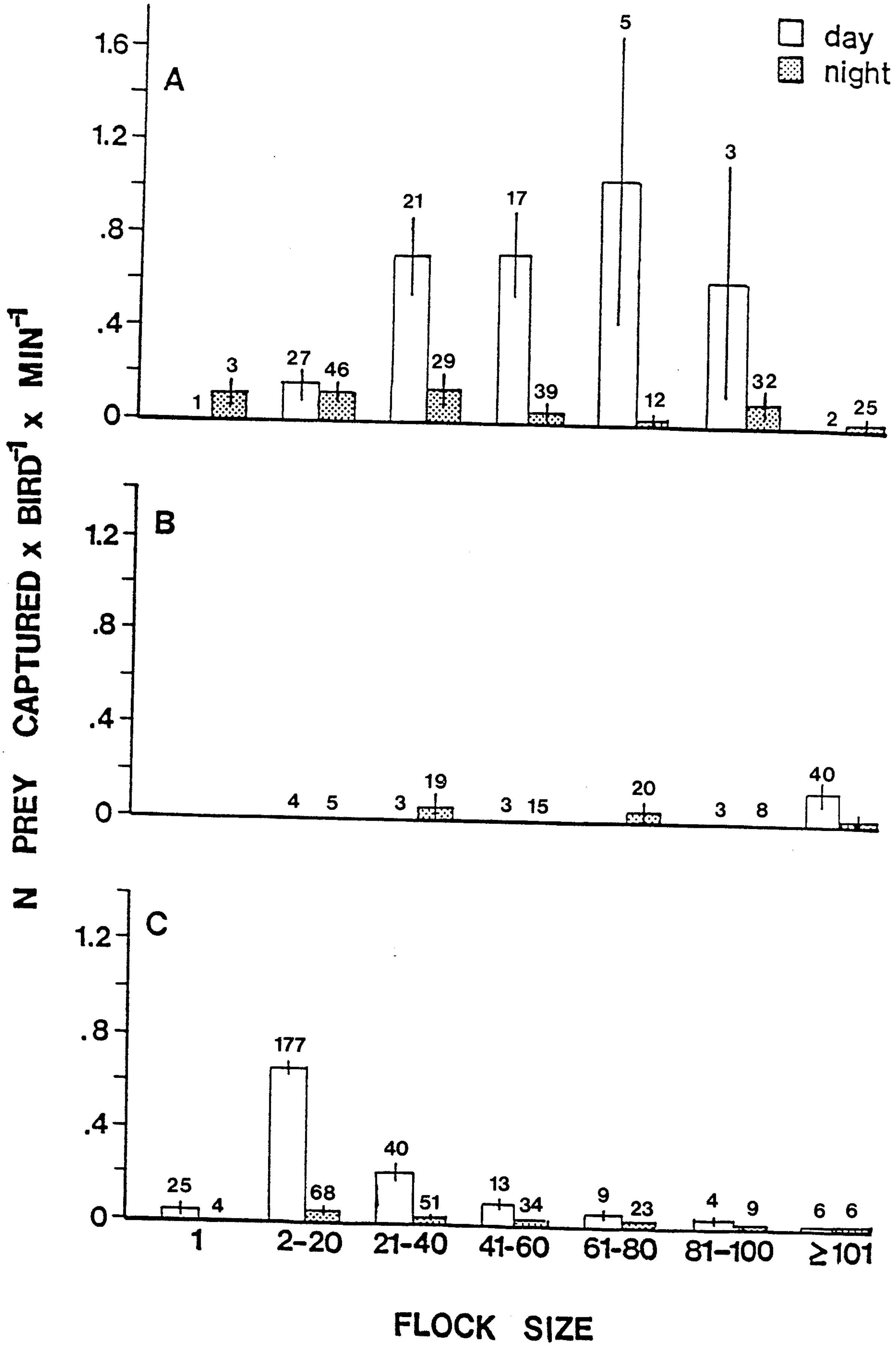
Effects of flock size on capture rates were more variable (Fig 11). In spring, daytime capture rates were highest for flocks containing 21-100 foragers in 1985 and 2-20 foragers in 1986. There was no detectable relationship between flock size and capture rates at night.

Search paths. The rate at which pelicans turned during a foray provided a measure of the straightness of search paths and of area restricted search. A forager was said to have made one turn when it changed its orientation by 90°, moving either downstream, upstream, or towards either shore. It was predicted that pelicans would concentrate their foraging around the site of prey capture (area restricted search) by increasing their rate of turning. During daylight hours in both years, mean time between turns was much higher after than before prey capture (29.4±18.12 vs. 12.4±11.58 sec, N=105). In 84.6% (N=104) of all cases, duration between turns increased immediately after prey capture (X^2=49.85, df=1, p<0.001). At night, duration between turns was also higher after than before prey capture (45.5±32.79 vs.

Table 29. Regression of dip rate on flock size.

Season	Period	N	Equation of line	F	r^2	p
Spring '85	Day	39	$y = 0.71 + 0.03x$	4.72	0.208	<0.025
	Night	163	$y = 5.77 + 0.03x$	20.10	0.200	<0.001
Summer '85	Day	37	$y = 1.08 + 0.00x$	2.38	0.102	>0.10
	Night	97	$y = 2.70 + 0.01x$	14.57	0.163	<0.001
Spring '86	Day	89	$y = 1.51 + 0.01x$	6.71	0.135	<0.005
	Night	106	$y = 3.81 + 0.03x$	12.46	0.195	<0.001

Figure 11. Relationship between flock size and mean ± s.e. capture rate during forays in (A) spring '85, (B) summer '85, and (C) spring '86.



N PREY CAPTURED x BIRD^{-1} x MIN^{-1}
A
1.6
1.2
.8
.4
0
day
night
1
3
27
46
21
29
17
39
5
12
3
32
2
25
B
1.2
.8
.4
0
4
5
3
19
3
15
20
3
8
40
C
1.2
.8
.4
0
25
4
177
68
40
51
13
34
9
23
4
9
6
6
1
2-20
21-40
41-60
61-80
81-100
≥101
FLOCK SIZE

14.69±12.74 sec, N=72). In 91.7% (N=72) of all cases, time between turns was longer after prey capture ($X^2=50.00$, df=1, $p<0.001$). In contrast to the prediction, pelicans responded to prey capture by turning less frequently, and thus did not exhibit area restricted search.

Time of day. Dip rates peaked around dusk, and were significantly higher at night than during the day in the spring of 1985 (t=8.34, df=265, $p<0.001$) and 1986 (t=4.37, df=475, $p<0.001$)(Fig 12A,C). Capture rates, in contrast, were relatively low throughout the night and significantly higher during the daytime in the spring of 1985 (t=6.39, df=265, $p<0.001$) and 1986 (t=8.65, df=474, $p<0.001$). In summer, major peaks in bill dipping occurred around 1100 hrs, 1900 hrs and from 2100 hrs to 0300 hrs (Fig 12B). Summer capture rates were not high at night, and peaked in daylight at approximately 1100 hrs and 1900 hrs. Dip rates in summer were similar between day and night (t=1.73, df=210, $p>0.05$); capture rates were significantly higher during the day (t=2.24, df=210, $p<0.05$). Figure 12 suggests that a strong positive relationship existed between dip and capture rates during the day, but not at night.

Location along the river. Mean rates of bill dipping and prey capture were always higher in the intermediate river habitat than downriver (Table 30). Rate of bill dipping usually increased as foragers approached shore (Table 31), and was always highest within 10 m of shore. Capture rates

Figure 12. Relationship between time of day and mean ± s.e. rates of bill dipping and prey capture in (A) spring '85, (B) summer '85, and (C) spring '86.

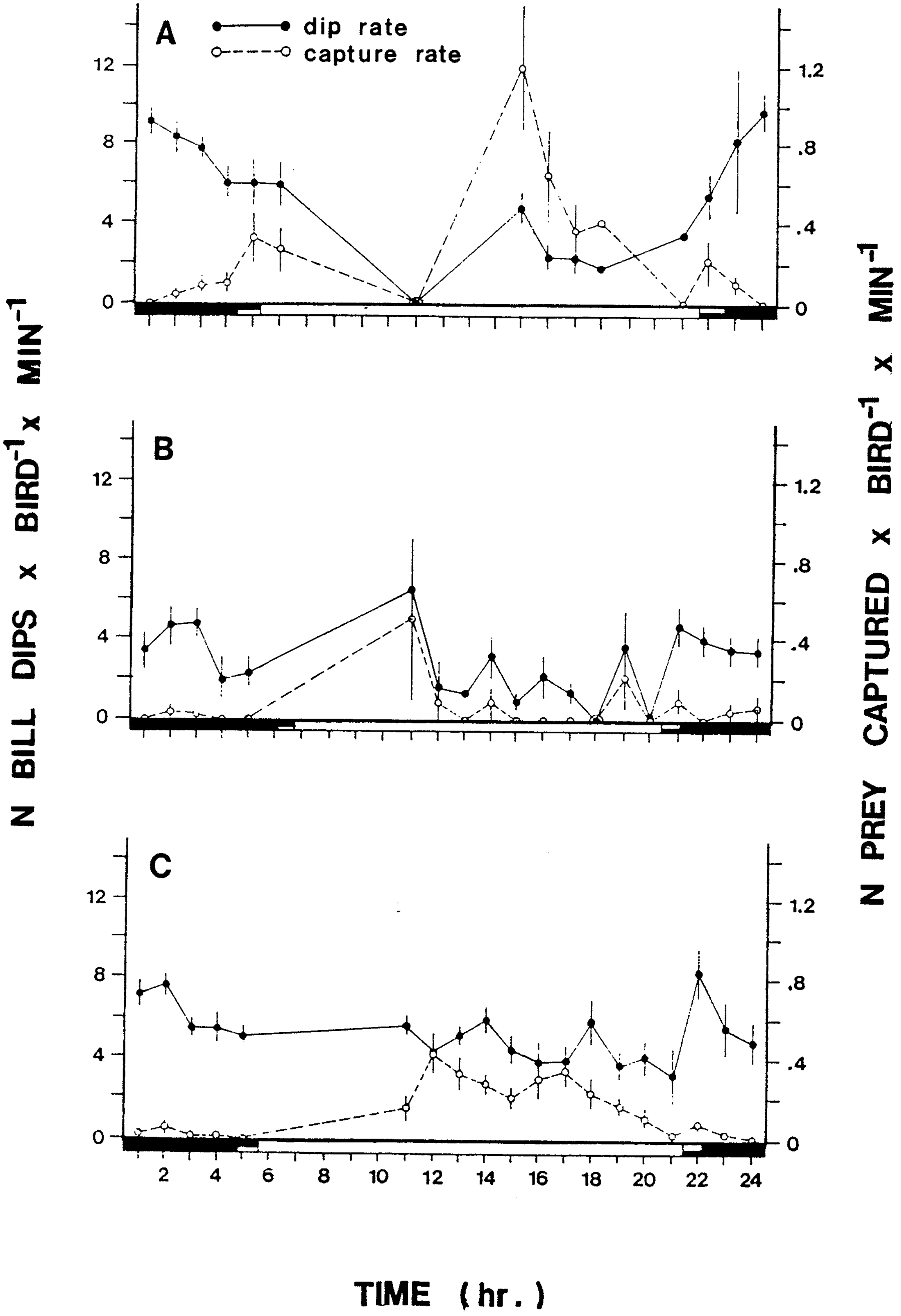

A
B
C
dip rate
capture rate
N BILL DIPS x BIRD^{-1} x MIN^{-1}
N PREY CAPTURED x BIRD^{-1} x MIN^{-1}
0
4
8
12
0
.4
.8
1.2
2
4
6
8
10
12
14
16
18
20
22
24
TIME (hr.)

Table 30. Mean ± s.d. rate of bill dipping and prey capture in downriver and intermediate habitats during the day (N forays in parenthesis).

		River habitat[2]			
Variable[1]	Season	Downriver	Intermediate	K	p
Dip rate	Spring '85	0.04±0.09(9)	4.11±3.24(63)	17.53	<0.001
	Summer '85	1.94±0.00(1)	2.77±3.16(53)	—	—
	Spring '86	1.53±3.14(34)	5.51±3.68(240)	33.93	<0.001
Capture rate	Spring '85	0.00±0.00(9)	0.58±0.79(63)	8.32	<0.005
	Summer '85	0.00±0.00(1)	0.10±0.30(53)	—	—
	Spring '86	0.07±0.24(34)	0.30±0.40(240)	28.10	<0.001

---

[1] See Table 26, footnote[2]

[2] See methods for definition of habitats

Table 31. Mean ± s.d. rate of (A) bill dipping and (B) prey capture in relation to distance of flock from shore.

			Distance from shore (m)							
	Season	Period	0-9	10-19	20-29	30-39	40-49	N	r	p
A[1]	Spring '85	Day	4.0±3.45	1.1±2.45	0.6±2.37	0.0±0.00	0.0±0.00	158	-0.454	<0.001
		Night	10.7±17.14	7.4±4.90	5.1±5.44	4.6±5.61	4.0±6.51	405	-0.208	<0.001
	Summer '85	Day	5.4±4.92	3.2±4.06	1.4±2.11	1.2±2.51	0.9±2.69	164	-0.369	<0.001
		Night	8.8±5.40	5.6±5.79	3.5±4.31	1.7±3.69	1.3±3.32	348	-0.449	<0.001
	Spring '86	Day	6.4±4.08	0.7±2.75	0.1±1.29	0.2±0.94	0.3±1.00	564	-0.562	<0.001
		Night	10.2±4.08	2.9±3.39	1.6±4.05	0.4±1.31	0.3±1.18	485	-0.639	<0.001
B[1]	Spring '85	Day	59.7±83.20	20.1±95.77	11.2±40.82	0.0±0.00	0.0±0.00	158	-0.269	<0.01
		Night	9.5±34.91	10.3±43.30	4.0±26.63	0.0±0.00	0.0±0.00	405	-0.103	>0.20
	Summer '85	Day	16.2±43.19	11.0±35.76	1.8±11.72	0.0±0.00	5.1±23.38	164	-0.163	>0.10
		Night	3.0±16.17	2.2±20.85	0.9±8.74	0.0±0.00	0.0±0.00	348	-0.081	>0.60
	Spring '86	Day	33.2±41.23	1.7±10.89	0.0±0.00	0.0±0.00	0.1±0.39	563	-0.401	<0.001
		Night	4.0±15.12	0.4±2.29	0.2±2.00	0.0±0.00	0.0±0.00	485	-0.157	<0.001

---

[1] See Table 26, footnote[2]

also increased as foragers approached shore; this relationship was significant during daylight hours in spring 1985 and both day and night in 1986 (Table 31). Most prey were captured close to shore, in water less than 1 m in depth during the day (99.4%, N=2374) and night (94.8%, N=421).

Flock density. Changes in flock density occurred during 73.5% (N=215) of forays sampled in the day and 68.0% (N=172) at night. At the onset of forays, flock density was normally moderate to very low. Foragers normally tried forcing their way from the rear to the front of Nuclei and Following flocks that were approaching shore. This caused flock members to congregate into a progressively smaller space. Flock density increased immediately prior to, and during, bill dipping and decreased rapidly following the cessation of dipping by the entire flock. During both day and night, dip rates increased with flock density (Table 32). Only for low and moderate densities were dip rates significantly higher at night than the day. Capture rates also increased with flock density (Table 32). Daytime capture rates were significantly higher than at night for moderately dense to very dense flocks.

Location within flocks. Following and Nucleus strategies containing 5 to 300 pelicans (62±66.0 pelicans, N=40 flocks) were filmed. Dip rates were significantly higher in the front than either the middle or back section of these flocks (Table 33), and dip rates in the middle were significantly

Table 32. Mean ± s.d. rate of (A) bill dipping and (B) prey capture of different flock densities in 1986 (N flocks in parenthesis).

	Flock density[1]						
Period	Very low	Low	Moderate	Dense	Very dense	K	p
A[2] Day	0.67±1.56(29)^{a}	0.39±1.09(72)^{a}	2.79±3.64(67)^{b}	7.78±4.04(119)^{c}	9.94±4.22(44)^{d}	186.04	<0.001
Night	0.00±0.00(12)^{a}	1.36±2.32(34)^{b}	4.30±3.95(47)^{c}	7.49±4.50(103)^{d}	12.08±4.78(59)^{e}	116.99	<0.001
K(p)	3.37(>0.05)	10.77(<0.001)	4.49(<0.05)	0.48(>0.40)	3.42(>0.05)		
B[2] Day	0.03±0.15(29)^{a}	0.00±0.01(72)^{b}	0.16±0.41(67)^{a}	0.39±0.40(119)^{c}	0.44±0.42(44)^{c}	149.38	<0.001
Night	0.00±0.00(12)^{a}	0.00±0.00(34)^{a}	0.01±0.04(47)^{a,b}	0.02±0.06(103)^{b}	0.04±0.07(58)^{c}	49.23	<0.001
K(p)	1.78(>0.10)	0.28(>0.50)	5.31(<0.025)	85.90(<0.001)	31.02(<0.001)		

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[1] See Table 20, footnote; flock density categories are defined in methods

[2] See Table 26, footnote[2]

Table 33. Mean ± s.d. values for foraging variables in the front (N=40), middle (N=26), and back (N=40) sections of flocks filmed in 1986.

	Location in flock[2]				
Variable[1]	Front	Middle	Back	X^2	p
Dip rate	6.00 ± 4.00^a	3.49 ± 2.38^b	3.81 ± 3.37^c	43.87	<0.001
Capture rate	0.26 ± 0.43^a	0.05 ± 0.08^b	0.15 ± 0.34^b	20.76	<0.001
Capture efficiency	0.04 ± 0.05^a	0.01±0.02	0.02 ± 0.04^b	10.13	<0.001

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[1] See Table 27, footnote[1]

[2] Sign tests were used to compare foraging variables between sections of same flock. Values in same row having different superscripts are significantly different at p=0.05

lower than at the back. Capture rates were significantly higher in the front than in the other two sections but did not differ between the middle and back sections of flocks (Table 33). Capture efficiency was significantly higher at the front than the back section of flocks. Compared to the back section, foragers at the front were faster and more efficient at capturing fish. The strongest correlation between dip and capture rates ($r=0.747$, $n=39$, $p<0.001$) occurred within the back section of flocks. Prey capture also increased significantly with dip rates in the front section ($r=0.410$, $n=40$, $p<0.001$), but not the middle of flocks ($r=0.184$, $n=27$, $p>0.30$).

Prey size

The proportion of captured fish in the very small category were significantly different ($X^2=36.29$, $df=3$, $p<0.001$) for Aggregations (100%, N=11), Following (87.8%, N=106), Nuclei (66.7%, N=895) and Semicircles (50.6%, N=83). The prey of pelicans using coordinated strategies consisted of a higher proportion of large fish than for those employing uncoordinated strategies ($X^2=3.88$, $p=0.05$). Prey captured by Semicircles consisted of a significantly greater proportion of large fish than for either Following ($X^2=29.66$, $p<0.001$) or Nuclei ($X^2=8.00$, $p<0.005$). Increased ability to find and/or capture large fish may thus be one of the main benefits of coordinated strategies.

During the day, the proportion of captured fish classed as very small that were obtained in water less than 0.5 m in depth (67.6%, N=1039) was not significantly different (X^2=0.62, $p>0.30$) from the proportion in deeper water (73.3%, N=60). At night, significantly more (X^2=3.57, $p<0.05$) very small fish were captured in shallow than in deep water (18.9%, N=132 vs. 0.0%, N=9).

Frequency of prey capture increased with decreasing prey size (Table 34). Relative number of captures of varying sized fish differed significantly between day and night (X^2=220.26, df=4, $p<0.001$). Significantly more small and very small fish were captured during the day than at night (X^2=20.03, $p<0.001$). The percentage of unidentifiable prey was significantly higher at night than during the day (X^2=16.58, $p<0.001$), due presumably to a reduction in visual acuity at night.

Video recordings revealed that a forager's position within a flock had a significant effect on the number of different sized prey that were captured (3 x 5 contingency analysis; X^2=25.85, df=6, $p<0.001$)(Fig 13). The proportion of fish captured in the front that were very small (94.4%) was higher than in the middle (62.5%) or back (85.7%) sections of flocks. In contrast, large and very large fish were only captured in the middle and back sections of flocks (Fig 13).

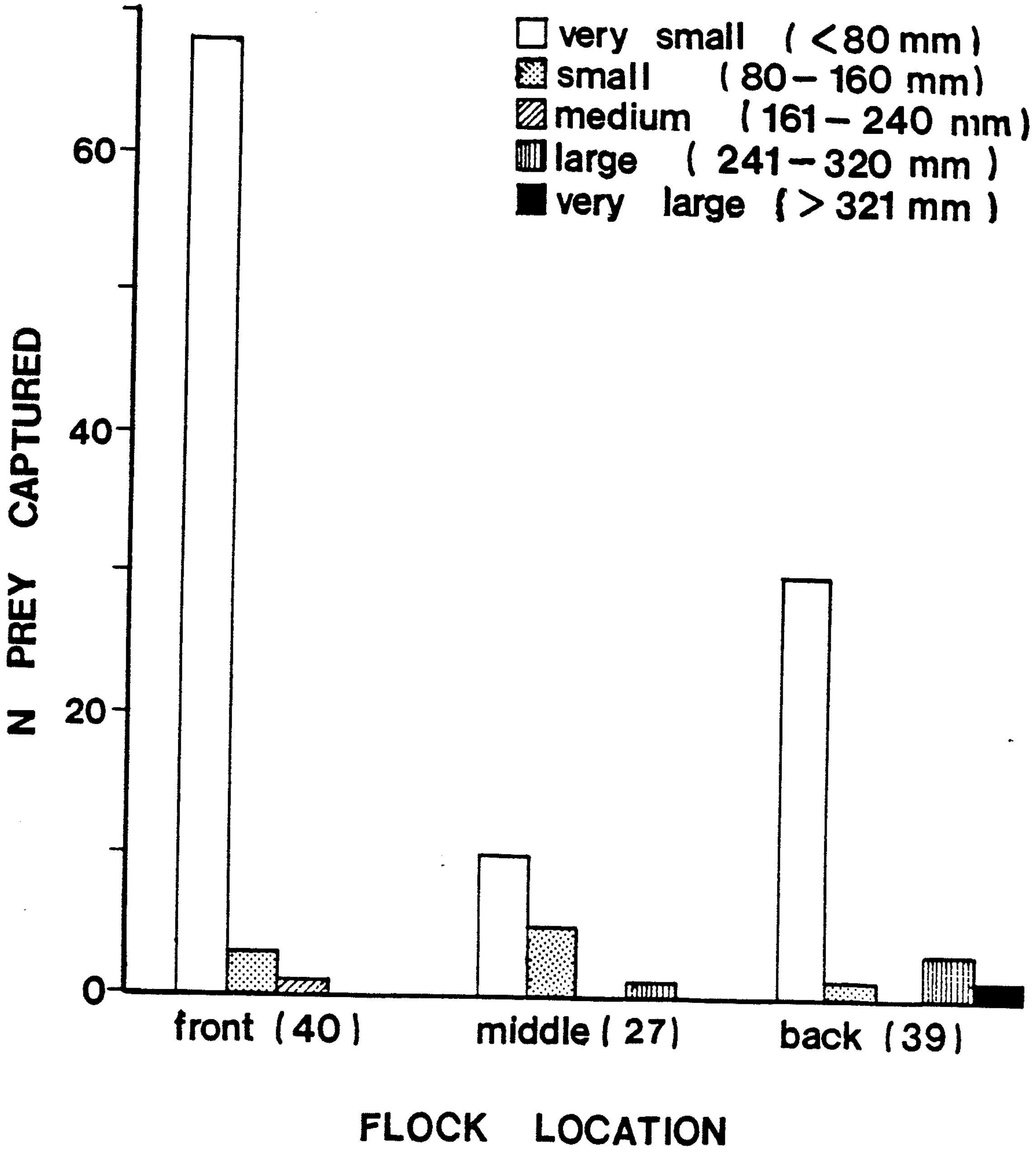
Table 34. Frequency of capture of different prey sizes during the day and night in 1986.

	Prey size[1]					
Period	Very small	Small	Medium	Large	Very large	unknown
Day	67.1(722)	23.2(250)	8.0(86)	1.5(16)	0.2(2)	54.5(2363)
Night	17.7(25)	59.6(84)	5.0(7)	8.5(12)	9.2(13)	65.4(408)
Total	61.4(747)	27.4(334)	7.6(93)	2.3(28)	1.2(15)	56.1(2771)

---

[1] N prey captures of each size expressed as a percentage of total N captures identified (N prey of each size captured in parenthesis). See methods for definition of prey sizes

Figure 13. Number of prey of various sizes captured at the front, middle and back sections of flocks (N flocks in parenthesis).



□ very small (<80 mm)
▩ small (80-160 mm)
▨ medium (161-240 mm)
▥ large (241-320 mm)
■ very large (>321 mm)
N PREY CAPTURED
0
20
40
60
front (40)
middle (27)
back (39)
FLOCK LOCATION

Temporal dispersion of prey captures

To determine whether or not the number of prey captures by flocks were randomly distributed in time, total number of prey captured within each of the 477 forays observed in 1986 were compared to a Poisson distribution. Within most forays, fish were either captured in large numbers or not at all, especially during the day (Fig 14). Significant nonrandomness in prey capture was present during both day and night. A variance to mean ratio test (Elliot 1977) further suggested a contagious distribution of fish captures during both the day (Index of dispersion (I)=13.37; $X^2=3757.86$, df=9, $p<0.001$) and at night (I=30.758; $X^2=5970.63$, df=4, $p<0.001$).

Runs tests were employed to determine if prey captures occurred at random time intervals within forays. Comparisons involved tabulation of the number of runs of unsuccessful and successful bill dips, one run being the number of sequential bill dips not resulting in prey capture, the other run being the number of sequential bill dips resulting in prey capture. During forays, initial prey capture was often followed by successive captures. Runs tests revealed that prey captures were significantly clumped within forays during both day and night (Table 35A). A runs test was also used to test for randomness in the sequence of successful forays occurring within 30 min of each other. During the day, there were 1 to 20 min-long periods of foraging in

Figure 14. Frequency distribution of the number of forays in which 0, 1, 2....n prey were captured during the (A) day and (B) night.

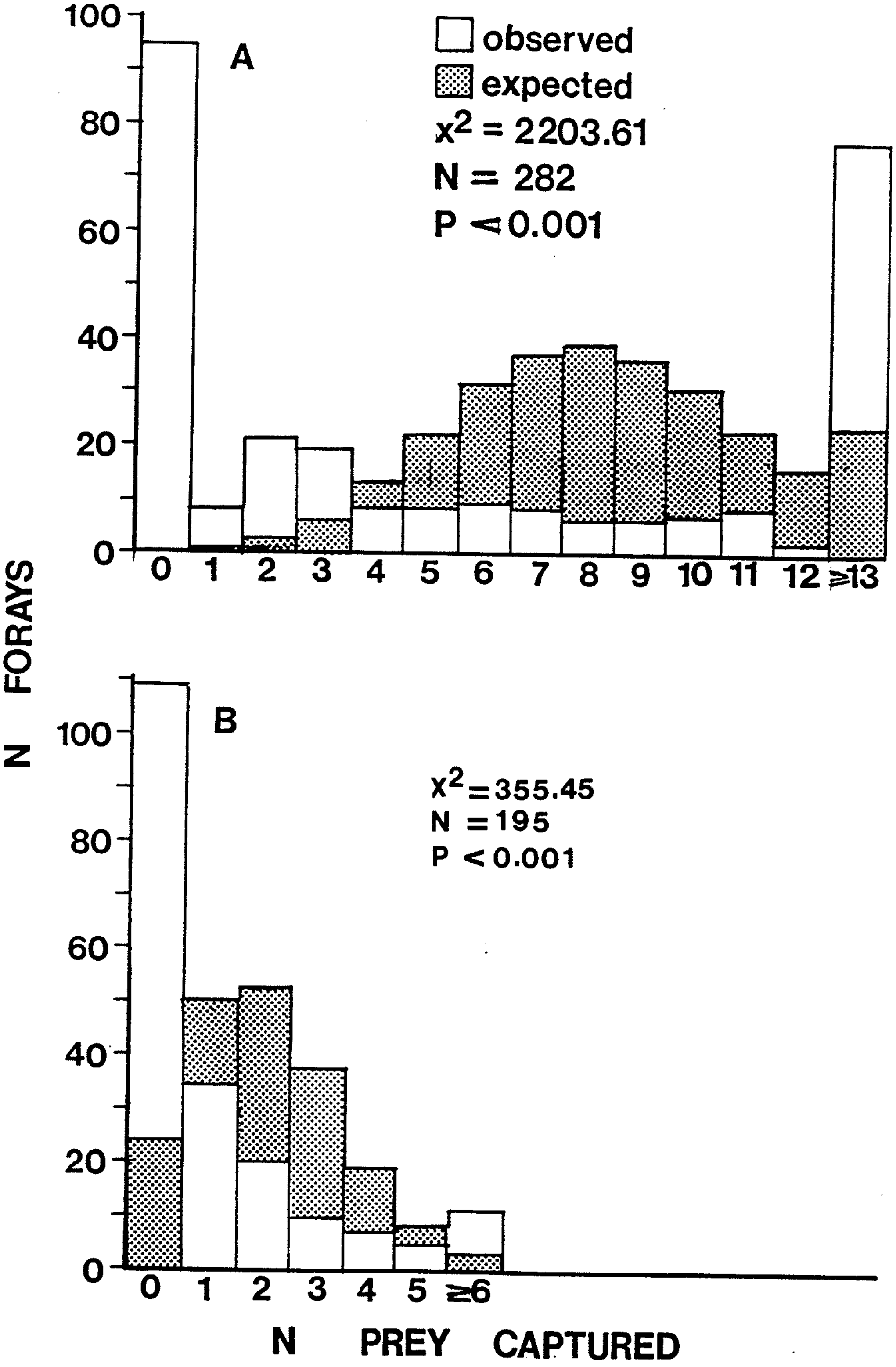

A
observed
expected
$x^2 = 2203.61$
N = 282
P < 0.001
100
80
60
40
20
0
0 1 2 3 4 5 6 7 8 9 10 11 12 ≥13
N FORAYS
B
$x^2 = 355.45$
N = 195
P < 0.001
100
80
60
40
20
0
0 1 2 3 4 5 ≥6
N PREY CAPTURED

Table 35. Number of runs of (A) bill dips, during forays, without and with prey capture and (B) successive forays in which flock members do not and do capture prey.

	Period	N_j[1]	N_k	Runs[2]	Z	p
A						
	Day	36	90	42 (52.4)	2.28	<0.025
	Night	85	52	63 (65.5)	0.46	<0.30
B						
	Day	478	279	146 (353.3)	16.20	<0.001
	Night	312	86	89 (135.8)	6.94	<0.001

---

[1] (A) N_j = total number (N) dips without prey capture, N_k = N prey captured

(B) N_j = N forays without prey capture by any flock member, N_k = N forays with prey captured

[2] Observed N runs of prey capture plus no capture (expected N runs provided in parenthesis)

which no prey were captured by any flock. These periods were followed by the rapid and abundant harvest of fish by several flocks in succession. This was reflected in a significant clumping of successful and unsuccessful forays during the day, but not at night (Table 35B).

Discussion

Prey capture techniques

American White Pelicans usually captured prey by dipping, or striking, their bill into the water, but other techniques, including kleptoparasitism and scavenging, were also noted. Kleptoparasitism is common to many species of birds (Rand 1954, Brockman and Barnard 1979). Most common are cases of interspecific kleptoparasitism, with gulls or terns being species which commonly steal prey from piscivorous hosts (Schnell et al. 1983, Hoffman et al. 1981). Intraspecific kleptoparasitism has been reported for Double-crested Cormorants, numerous Peruvian seabirds and American White Pelicans (Bartholomew 1942, Duffy 1980, O'Malley and Evans 1983).

Both scavenging and intraspecific kleptoparasitism appeared to be fortuitous feeding methods rarely used by pelicans at Dauphin River. Kleptoparasitism attempts primarily occurred when large fish were captured by a potential host. A relatively high probability of parasitism may partly explain why pelicans always turned or flew away from their foraging flock immediately after capturing a large fish. As at Dauphin River, few instances of intraspecific food theft were found for pelicans at Grand Rapids (O'Malley and Evans 1983).

Foraging strategy continuum

American White Pelican foraging strategies fell along a continuum of coordination from single birds to Semicircles. Aggregations involved grouping by 2 or more birds, but there was no coordination of movements or bill dipping among pelicans using this strategy. Individuals searched for food in the same general area, but were not otherwise oriented with respect to each other. Following flocks showed more coordination among participating members, in that pelicans followed each other and the flock moved in one direction, sometimes with coordinated dipping. High stability in flock structure and near synchronization of activities in Nuclei and Semicircles suggests that these strategies were more highly coordinated than Following. Semicircles achieved the highest level of coordination, exemplified by highly synchronized dipping.

Intensity of search appeared to vary inversely with level of coordination in foraging strategies at Dauphin River. Dispersal of uncoordinated, independently searching foragers presumably allowed a larger area to be searched. These individual foragers had the highest turn rates, suggesting a high level of localized food searching. Rates of bill dipping and prey capture were also lower for uncoordinated strategies, which suggests they were searching for rather than harvesting prey. When the availability and/or size of prey increased, the most highly coordinated strategies were favoured. Nuclei and Semicircles had the highest rates of bill dipping and prey capture. Pelicans using these strategies also captured the largest prey. Following, which was less coordinated than Nuclei, had a prey capture rate similar to Aggregations.

Strategy switching also fell along the same continuum. Mobile Individuals and Aggregations seldom restructured into Nuclei or Semicircles. Following frequently changed into all other strategies. Although Nuclei and Semicircles frequently reformed into Following flocks, they never reformed into uncoordinted flocks. Strategies generally switched from less to more coordinated after prey were captured. This relationship supports the idea that more coordinated strategies were more effective at harvesting prey. The shift to less coordinated flocks occurred after prey capture rates dropped off. Pelicans could thus shift from one flock type to another depending on the food resource. The continuum of foraging strategies thus extended from single birds, best suited to searching a large area for prey, to Semicircles which were the most efficient at capturing prey.

One objective of this study was to assess the hypothesis that the most effective strategies would be the most common. Some support of this view was obtained. Most pelicans foraged in Nuclei, which had the highest capture rates and recruited the most new foragers. Conversely, Semicircles were rare but had high capture rates. The infreqency of occurrance of this strategy suggests the possibility that these flocks formed and functioned optimally only under rare and specific conditions. In the cases where formation of Semicircles were observed, flock initiators were pelicans that had been foraging, within approximately the previous 10 min, in that area. From recent foraging experience, pelicans may be able to assess prey characteristics such as their abundance and distribution. Learning about prey abundance or location is a common attribute of foraging in many species (Krebs 1978). The rarity and high success of Semicircles could thus be due to the occurrence of special conditions of prey clumping at the time of their formation, but further work is required.

Cooperative foraging

Cooperation occurs when participating members of a group benefit from the presence of each other (Brown 1975). Cooperation is thought to be especially important in securing resources normally unobtainable to individuals (Grier 1984). Social carnivores like African Hunting Dogs (Lycaon pictus) and wolves (Canis lupus) cooperate in the capture of large prey items (Kuhme 1965, Mech 1970, 1975, Zimen 1975, 1981). Prey herding is also thought to involve a degree of cooperation and functions to concentrate prey into an area where they can be easily captured. Bartholomew (1942) reported seeing large "U" shaped flocks of Double-crested Cormorants that drove large fish schools forward. In pelicans, Semicircles, with their high degree of synchronization and high success rates, represented the most highly cooperative foraging strategy observed. The efficiency and rate of prey capture were much higher for Semicircles than any other type of flock. Pelicans in Semicircles also captured larger fish than those using other strategies.

Studies by Goss (1888) and Cottam _et al_. (1942) also provide accounts of cooperation in which pelicans form a line or semicircle and drive fish into shallow water or trap prey by forming an ever-decreasing circle around a school of fish. The ability of a semicircular formation to trap fish was demonstrated by Anderson (1987); pelican models were aligned into a semicircle and were used in concentrating carp into progressively smaller schools that were driven to shore. African White Pelicans also formed semicircles which are similar in shape and size to those used by pelicans at Dauphin River. Wirtz (1986) discovered that Great White Pelicans using semicircles were five fold more efficient at prey capture than were solitary foragers. At Dauphin River, Nuclei were also highly coordinated, although less so than Semicircles. Nuclei sometimes spread into an elliptical shape when moving through the shallows towards shore, suggesting they also functioned on occasion for driving fish. Following appeared to represent a much less well developed example of cooperative foraging.

Nocturnal foraging

Significantly more pelicans foraged at Dauphin River at night than during the day. Nocturnal foragers were usually concentrated into a few large Nuclei. Unlike daytime, when solitary foragers were common and dispersed along the river, Mobile Individuals were not common at night and foraged for only short periods. During daytime, solitary foragers could watch each other and join flocks that were successfully catching fish. At night, darkness probably prevented foragers from seeing each other and joining together over large distances by means of local enhancement. Under these conditions, any benefits of group foraging would be best achieved by maintaining large, dense flocks.

Sit-and-Wait was the rarest foraging strategy used by pelicans at Dauphin River and was mainly observed at night. The back and forth head movements of these foragers suggest that they were constantly scanning the water surface for prey. Lowered light levels at night and the lack of body movement presumably provided effective camoflauge for foragers using a Sit-and-Wait strategy. High efficiency of prey capture at night suggests that these foragers were able to see their prey prior to bill dipping. Sit-and-Wait is thought to be adaptive for capturing mobile prey (Huey and Pianka 1981, Toft 1981). Great Blue Herons, Snowy Egrets (*Egretta thula*) and Northern Shrikes (*Lanius exubitor*) all use Sit-and-Wait foraging techniques (McNicholl 1972, Des-Granges 1979, Owen 1980, Itzkowitz and Makie 1986).

Pelicans dipped their bills more frequently and for longer periods at night than during the day. This form of probing appeared to function as an effective search strategy when prey were not readibly visible. Since most pelicans infrequently turned their heads in a searching manner, it appears they were not using visual means to locate prey at night. The Wood Ibis (*Mycteria americana*) also uses a form of probing in capturing inconspicous prey when hunting in very turbid waters (Owen 1980). As with other probing birds, it should be beneficial to capture prey rapidly after contact is made. Estimated handling time below water for pelicans was (0.2 sec) 3.5 times shorter at night than during the day (0.7 sec).

Factors influencing foraging effort and success

Effect of prey capture on search effort. A predator that uses area restricted search concentrates its foraging around an area where prey have been captured (Tinbergen *et al*. 1967). Smith (1974a,b) demonstrated that area restricted search was a strategy adapted to feeding on clumped prey and that the benefits procured would increase with prey abundance. Area restricted search has been documented in coccinelid beetles (*Adalia decempunctata*) and grazing stream insects (*Baetis tricaudatus*) (Dixon 1959, Chandler 1969, Kohler 1984).

In contrast to the predictions of area restricted search, turn rates for pelicans decreased after the initial capture of prey. Unlike species showing area restricted search, most pelican flocks captured prey after they had turned and started moving towards shore. To be effective, area restricted search requires that prey be sedentary. The adoption of linear, rather than area restricted, paths after prey capture would seem more adaptive when herding mobile fish prey. Forward search paths would essentially move pelicans up a gradient of increasing prey abundance as fish were concentrated into successively smaller spaces near shore. Thus, a form of mobile search, correlating with the changing location of mobile prey, appears to be a better description of pelican foraging after prey capture than simple area restricted search, which is mainly relevant for sedentary prey.

Prey capture can also affect other aspects of searching. For example, woodcocks (Scolopax minor) used shallow, widely spaced "exploratory" probes prior to contacting prey (Rabe et al. 1983). Upon capturing an earthworm, woodcocks rapidly probed their bills more deeply into soil adjacent to the site where prey were captured. Pelicans similarly changed the periodicity of bill dips. Immediately following prey capture, the frequency of bill dips increased and the duration decreased. Since prey were clumped in space and time (Fig 15, Table 35), the probability of capturing a second fish should have increased after the first one was secured. By changing their pattern of bill dipping, pelicans in effect concentrated their immediate search in or near the area where prey were captured. The concentration of bill dipping combined with forward motion after prey capture suggests a nonrandom foraging pattern designed to maximize the utilization of aggregated but mobile prey.

Flock size and social facilitation. Some benefits commonly associated with foraging in groups include increased food-finding ability (Krebs *et al.* 1972, Pitcher *et al.* 1982), increasing prey availability as with the herding of fish (Bartholomew 1942), increasing capture efficiency (Zimen 1975, 1981, Bertram 1978) and increased ability to capture larger prey (Pimlott 1967, Mech 1975). For pelicans at Dauphin River, spring capture rates were highest for flock sizes of 2 to 80 during the day and 2 to 40 at night. Low capture rates observed for exceedingly large flocks may have been largely due to increased competition for a limited resource. Individuals that joined such large flocks may have done so at the expense of lowered foraging success in the remaining flock members. Hatch (1975) found that Laughing Gulls (*L. atricilla*) which joined conspecifics that were chasing and attempting to steal fish from terns (*Sterna spp.*) benefited at the expense of flock initiators.

Flock size and density may also affect the intensity with which foragers search for prey. Thorpe (1956) described social facilitation as contagious behaviour where the action of one animal elicits the same behaviour in another. Since the frequency of occurrence of a socially facilitated behaviour is dependent on the proximity of other animals, an increase in its rate of expression is expected to occur when the number or density of participating animals increases. In agreement with the social facilitation hypothesis, dip rates of pelicans at Dauphin River increased with both flock size and density. Dip rates increased with flock size up to flock sizes of 120, then declined sharply (Fig 11). The decline in dip rates for very large flocks may suggest a behavioural limit to socially facilitated bill dipping.

Time of day. Although rate of bill dipping was lowest during daylight hours, frequency of prey capture was highest at this time. High visual acuity during daylight may partly account for low dip rates and high capture rates at this time. Diurnal foragers were frequently seen moving their heads as though scanning the water surface prior to striking the water with their bill; such behaviour suggests pelicans were searching for and able to locate prey visually during the day. High capture rates during the day may also reflect relatively high abundances of small fish. Yellow perch, darters and minnows form many small schools that are most active in shallow water during spring days (Emery 1973, Hall and Werner 1977).

Forager location. The foraging success of pelicans varied among habitats, in relation to water depth, and with forager location within flocks. Rates of bill dipping and prey capture were both higher in the intermediate than the downriver habitat. Pelican abundance was also greater in the intermediate habitat (Chapter 1), suggesting that pelicans readily discriminated between foraging habitats and concentrated where foraging success was highest. Many other species are known to concentrate their search in areas of highest prey densitites (Goss-Custard 1970, Smith and Dawkins 1971, Smith and Sweatman 1974, Barnard 1980a, Barnard and Stephens 1981). Smith and Sweatman (1974) also demonstrated that Great Tits (_Parus major_) increased the amount of prey captured by selectively searching in areas having the highest prey densities.

The present study demonstrates that an inverse relationship existed between distance from shore and foraging success of pelicans. When located farther than 10 m from shore, no flock member attempted to capture prey. As pelicans approached shallow water near shore, both dip and capture rates rose suddenly. The presence of larger numbers of foragers in shallow water (see Chapter 1) may be largely explained by relatively high foraging success in these areas. Previous studies have provided qualitative evidence which suggests that pelicans prefer to forage near shore (Hall 1925, O'Malley and Evans 1984). Anderson's (1987) study further suggests that shallow water benefits pelicans by allowing them to concentrate fish and drive them towards shore where they can be more readily captured. For pelicans at Dauphin River, it was not possible to determine whether prey abundance was higher near shore and/or foraging flocks were herding fish into the shallows. However, the systematic movement patterns of Nuclei suggested that prey herding may have been operative: Nuclei occupying a 10 m^2 area would suddenly spread out into a 20 to 50 m long line and individually orient perpendicular to shore, then move towards and encompass a large portion of the shore.

Disparity in foraging success within coordinated strategies also occurred between the front, middle and back sections of flocks. Pelicans located near the front of foraging flocks had the highest rates of bill dipping and prey capture. In these flocks, pelicans located near the rear often moved around conspecifics in order to obtain forward positions. In flocks capturing large numbers of fish, such as those in the summer, pelicans frequently flew from the rear to leading edge of the flock. Such movement patterns were similar to the "leap frogging" described for P. erythrorhynchos by Anderson (1987) and for P. onocrotalus by Murray (1969). Pelicans apparently attempted to maximize their rate of prey intake by positioning themselves near the front of flocks.

Despite having lower capture rates, pelicans located near the rear of coordinated foraging flocks captured a higher proportion of large fish than pelicans located near the front. Potential foraging benefits, in terms of prey biomass captured, at the rear of flocks may to some extent have offset higher rates of capture of small fish at the front of flocks.

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