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## Foraging Behavior of American White Pelicans *Pelecanus erythrorhyncos*

John Guy Thomas Anderson  
*University of Rhode Island*

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FORAGING BEHAVIOR OF AMERICAN WHITE PELICANS

Pelecanus erythrorhynchos

IN WESTERN NEVADA

BY

JOHN GUY THOMAS ANDERSON

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE

Approved REQUIREMENTS FOR THE DEGREE OF

Dissertation DOCTOR OF PHILOSOPHY

Major Professor IN

BIOLOGICAL SCIENCES

*James H. Schultz*  
*A. G. Arnold*  
DEAN OF THE GRADUATE SCHOOL

UNIVERSITY OF RHODE ISLAND

1987

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 flock size, reaching an asymptote at a flock size of  
 4. Analysis of the regurgitate of young birds revealed  
 that the pelicans' primary food source consisted of fish

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1987

## ABSTRACT

Foraging behavior by American White Pelicans (Pelecanus erythrorhynchos) was studied in the Lahontan Basin in western Nevada. Pelicans engaged in cooperative fish herding and in kleptoparasitism upon Double Crested Cormorants (Phalacrocorax auritus). Pelicans in groups of size 2 through 6 caught more fish than single birds. Mean strike number increased initially with increasing flock size but leveled off at a flock size of between 3 and 4. Strike efficiency (captures/bird/strike) declined with flock size, reaching an asymptote at a flock size of 4. Analysis of the regurgitate of young birds revealed that the pelicans' primary food source consisted of Carp (Cyprinus carpio) and Tui Chub (Gila bicolor). Analysis of flocks of pelicans arriving and departing from the colony on Anaho Island revealed a peak in total arrivals and departures between 1100 and 1300 hrs. This peak appeared to be constant throughout the season although the total number of birds arriving and departing increased into July. Mean flock size increased from April to July. Thermal flocks departing and arriving at higher altitudes were generally larger than low level counterparts. The evolutionary significance of cooperative foraging is briefly discussed.

## ACKNOWLEDGEMENTS

The studies leading to this dissertation have benefited enormously from the criticism, help, and support of a number of individuals and institutions. First of all I would like to thank the Tribal Council and members of the Pyramid Lake Paiute Tribe for allowing me to live and work at Pyramid Lake over the past seven years, for pulling me out of sand dunes when I had ventured too far off the beaten track, and for answering my many questions whenever our paths crossed. I would also like to thank Morris LeFever of the U.S. Fish and Wildlife Service for allowing me to work within the Stillwater Refuge, providing me with gate combinations and file access, and for dealing with me courteously and thoughtfully whenever I showed up unannounced out of the wild. I would also like to thank the staff of the Stillwater Refuge for helping me find addresses and permits and pelicans.

I owe a debt to my Major Professor, Frank Heppner, who has sponsored my research over the past five years and provided me with many stimulating conversations on a wide variety of topics. I also thank the members of my Committee Drs. Jim Heltsh, Bill Krueger, and Bob Shoop, each of whom put up with my flights of fancy, provided good council in time of need, and helped me gain new perspectives on the ways of Science.

I owe a special debt of gratitude to Dr. Sally Levings for provision of countless reprints, revision of countless



grant proposals, and most of all for teaching me to respect a degree of rigor in the scientific method. Much of this dissertation is the direct result of her suggestions and coaching.

I would also like to thank Paul Weiss, Caroline Stamato, Lee Raymond, Liz Strauss, Alexander, Jock, and Es Anderson, all of whom at one time or another were my companions and helpers in the Great Basin. I literally couldn't have done it without you.

I would also like to thank Pat Serrentino for many invaluable discussions, debates, and arguments all of which have contributed immeasurably to my development as a scientist. Bart Destasio provided a vital sounding-board for many of the ideas that appear here, and helped weed out the ones that belonged only in fantasy. Suzy Avazian and Alex Haro identified fish, proposed equations, handed out references, and gave me a lift when I needed one. Robin Gibbs and Adria Elskus provided tea and sympathy through four trying years of graduate school. Karen Wagner put up with my moods, plotted my charts, proofread and edited my manuscripts, and in general kept me together during the writing of this dissertation. Thanks to all.

Dan Anderson, S.K. Eltringham, Roger Evans, Mark Hart, Jim Keith, Fritz Knopf, Blair McMahon, and Ralph Schreiber all provided unpublished data, suggestions, ideas, and speculations on the ways of the Wonderful Bird. May we

all some day know how the hellican!

Last of all I would like to thank Dr. Pete August for the endless time and patience that he has put into trying to turn a brash, self-centered, and incredibly naive student into a scientist and an ecologist. Throughout my career as a doctoral student Pete has provided an example of all the reasons why I have wished to enter this profession. Faced with a confusing array of half-thought out research plans and half analysed data Pete's ability to get at root questions and provide new insights is nothing less than phenomenal. Time and again I have staggered into his office crying "it can't be done" only to emerge later with half a dozen new ideas to try. "Thanks" is certainly a gross underpayment of my debt, it's been fun Pete.

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LIST OF TABLES

P.

Table 1. Proportion of pelicans' diet consisting of Asiatic Carp (Cyprinus carpio) and Tui Chub (Gila bicolor).....13

Table 2. Analysis of the effects of group size on individual foraging success.....26

Table 3. Pelican responses to decoys.....35

Table 4. Monthly summary of pelicans arriving and departing to and from Anaho Island in different height classes..... 41

Table 5. Number of birds arriving and departing at and from Anaho Island daily and during peak periods..... 52



LIST OF FIGURES

White Pelicans (Haliaeetus leucorhynchus) near Pyramid Lake, Nev. P.

Figure 1. Map of study area showing Pyramid Lake, Stillwater Wildlife Management Area, and Carson Sinks..... 4

Figure 2. Diagram of pelicans feeding along shelving shorelines.....18

Figure 3. Diagram of feeding behavior by large groups of pelicans in open water.....20

Figure 4. Distribution of foraging flock sizes recorded during the study..... 24

Figure 5. Coefficients of variation for foraging success of individual birds feeding in flocks of size 1 to 10..... 28

Figure 6. Relationship of strike frequency to flock size for flocks of 1 to 10 birds..... 31

Figure 7. Strike efficiency for birds in flocks of size 1 to 10..... 33

Figure 8a-g. Distribution of numbers of birds arriving and departing at Anaho Island on selected dates..... 45

## INTRODUCTION

White Pelicans (genus Pelecanus) have been cited as examples of cooperative feeders (Rand 1954, Wrangham 1982, Alcock 1984, Welty 1986). At the present time the basis for claims of cooperative behavior rests on anecdotal accounts of fish herding (Goldsmith 1840, Goss 1888, Mills 1925, Cottam et al. 1942, Low et al. 1950), and although several authors (Behle 1958, Hall 1925, Woodbury 1966, Knopf and Kennedy 1980, for American White Pelicans (P. erythrorhyncos) and Din and Eltringham 1974a, 1974b for Great White Pelicans (P. onocrotalus) have made reference to pelican foraging behavior, no study has been directed specifically at feeding. It has not been demonstrated that cooperation occurs, or that group feeding results in a benefit to individual pelicans.

White Pelicans are good subjects for foraging studies because they are conspicuous, relatively tame birds, found throughout central and western North America (Palmer 1962). White Pelicans give a characteristic "head toss" upon capturing prey, similar to that observed in the Brown Pelican (Pelecanus occidentalis) by Orians (1969). It is thus possible to obtain an accurate count of prey captures.

The population of pelicans observed in this study consisted of birds breeding on Anaho Island, Pyramid Lake, Washoe County, Nevada. The pelican colony on Anaho Island is the second largest White Pelican colony in the United

states, and at present supports between 7000 and 8000 birds.

The White Pelican breeding season at Pyramid Lake begins in the last week of February, with peak numbers of birds nesting at the colony from mid-March to mid-June. Fledging of young generally begins in early June and extends into late August. The number of pelicans seen at Pyramid Lake usually starts to decline during the last week of July and the majority of birds are gone by the third week of August.

Prior to the 1986 breeding season there had been scattered reports of pelican sightings in the Lahontan Basin as late as December. Reports from U.S. Fish and Wildlife personnel at the Stillwater Refuge indicate that during the Winter of 1986 a number of pelicans may have overwintered in the basin, apparently taking advantage of the temporary increase in local food availability caused by declining water levels in the area.

All previous ethological studies of the Anaho pelicans (Hall 1925, Marshall and Giles 1953, Woodbury 1966, Anderson 1982) have focused on pelican behavior either on or in the immediate vicinity of the colony. Knopf and Kennedy (1980) provide valuable data on pelican foraging and loafing sites in western Nevada. Their study was conducted however immediately prior to the rise and subsequent decline of water levels in the Lahontan drainage system, and several of the areas that they report as suitable pelican habitat have been significantly



altered in the interim. In addition Knopf and Kennedy conducted the bulk of their observations from the air and therefore were unable to obtain precise information on actual pelican foraging patterns.

The purpose of this dissertation is to present an analysis of pelican foraging behavior under a variety of conditions, with special attention to possible cooperative activity. I also present data on pelican flight-flock sizes and the timing of arrivals and departures from a breeding colony and attempt to relate this information to the birds' foraging and breeding biology.

#### STUDY AREA AND METHODS

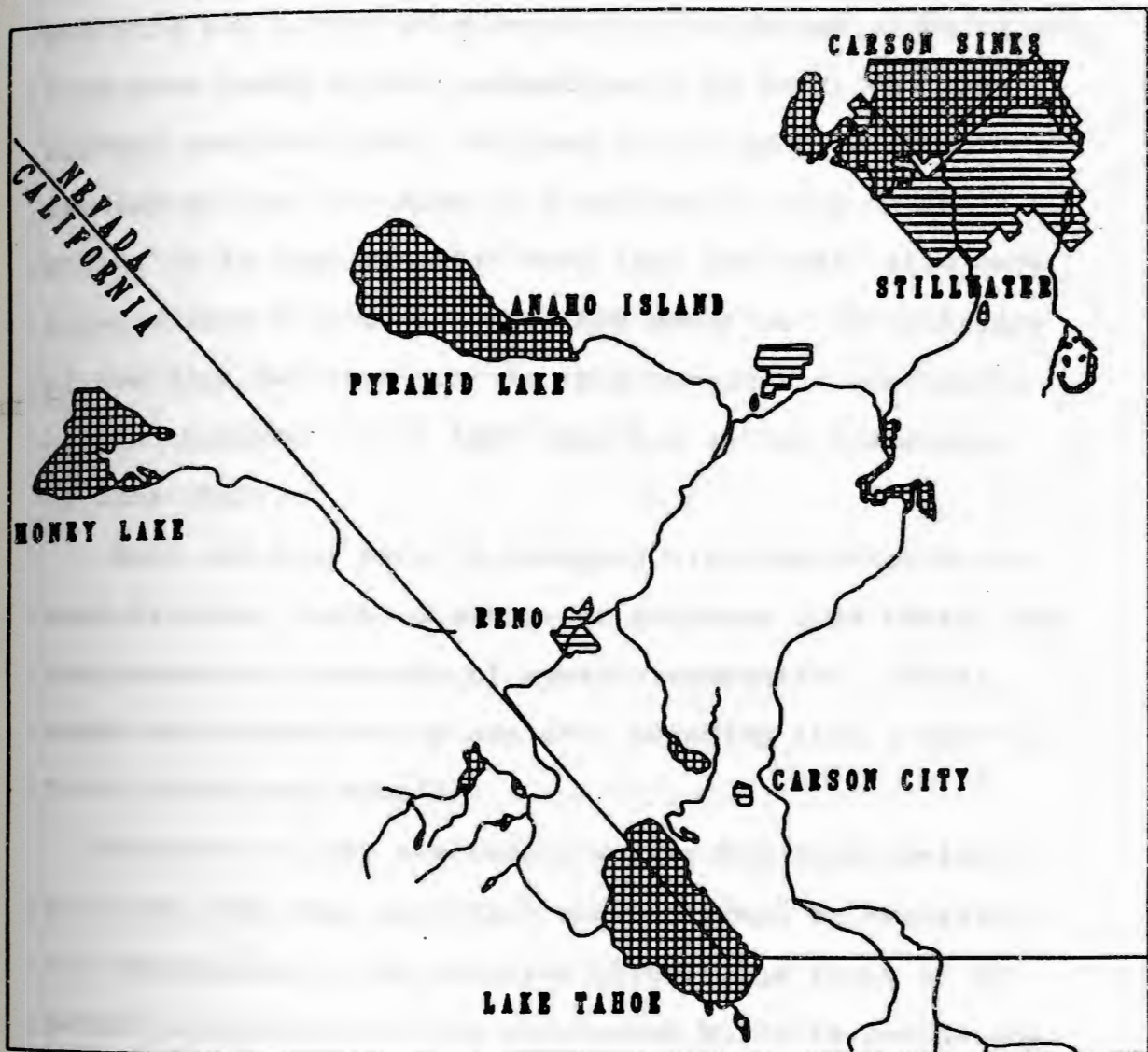
The study was conducted at Pyramid Lake, Washoe County, Nevada, the Stillwater Wildlife Refuge, and Carson/Humboldt Sinks, Churchill County, Nevada. All three of these areas lie within the Lahontan drainage basin and serve as the terminal outlets of the Truckee, Carson, and Humboldt Rivers respectively (Fig. 1). Increased rainfall and resultant river flow during 1981-1985 resulted in a significant increase in water levels throughout the basin and the temporary fusion of the Humboldt and Carson Sinks.

Observations were conducted from June through August of 1984, February through August of 1985, and in August of 1986. All observations were conducted using 7x35 mm binoculars and a Celestron 1000 mm spotting scope. Selected behavioral sequences were filmed with a Beaulieu

Fig. 1. Map of the study area showing location of breeding colony on Anaho Island; Pyramid Lake; the Humboldt and Carson Sinks; and the Stillwater Marshes.







super 8mm movie camera for later analysis.

Foraging group size, strikes per minute, and captures per bird per minute were recorded. Estimated captures per bird were based on the assumption of at least one fish capture per head toss. Because of the suction effect created by the expansion of a pelican's pouch during a strike it is possible that more than one small fish were taken during a successful capture sequence. The estimate of one fish per head-toss is thus somewhat conservative but is consistent with that reported in the literature (Orians 1969).

Note was also made of foraging site characteristics such as water depth, distance of pelicans from shore, and the presence or absence of aquatic vegetation. Water depth was determined by use of a sounding line a Loranz fish finder echo sounder.

Censuses of prey availability were conducted using a gill net, and prey selection was confirmed by analyzing the regurgitate of 50 startled birds. The terms of my permit to work within the Stillwater Wildlife Refuge and agreements with the Pyramid Lake Paiute Tribal Council precluded my either taking adult pelicans or entering actual breeding areas prior to the departure of the bulk of the nesting population. These restrictions placed distinct limits on my ability to obtain information on prey taken early in the season.

The regurgitation response of pelicans is well known

and has been used in a number of studies (Hall 1925, Gromme 1930, Marshall and Giles 1953, Behle 1958, Woodbury 1966) as an alternative to or in addition to more destructive methods of sampling stomach contents. During the first week of August 1985, while moving between observation points on the west side of Anaho Island I encountered a group of approximately 75 young pelicans. All of these birds had the majority of their flight feathers, and I estimate that they were within one week of fledging. The time of the encounter was approximately one hour after a large group of adult birds had arrived at the colonies and fed their young.

The majority of the young birds responded to my presence by regurgitating their stomach contents in discrete piles before retreating over the shoulder of the island's northern ridge. The contents of each pile of regurgitate consisted of whole, largely undigested fish. Each fish was measured using dial calipers and weights were estimated by applying recorded lengths to a weight/length regression line derived from fish netted in the Stillwater Marshes.

The size of the area covered by the foraging pelicans precluded a comprehensive survey of all possible feeding areas. Preliminary observations during a previous study (Anderson 1982) permitted the establishment of a list of likely pelican foraging sites that were accessible by either truck or on foot.



Observations were made on an opportunistic basis. Each day I awoke between 0400 and 0630 hours and drove or walked to areas where pelicans had previously been observed or which had been listed as potential foraging habitat. If pelicans were encountered as expected I would remain, recording observations until dark (1900 -2100 hours) If no birds were present when I arrived, but the area looked promising I would remain, otherwise the next area on my list would be visited.

For night observations a blue 1975 Datsun pickup was positioned at dusk within 5 m of sloughs where pelicans had been seen during the day. The camper shell of the truck served as a blind and the pelicans appeared to ignore my presence provided no lights were shown. Areas visible from the truck were checked for signs of foraging pelicans at two hour intervals. Observations were recorded on a portable tape recorder for later transcription.

#### TESTS WITH DECOYS

In addition to passive observation, a series of experiments were performed at both Pyramid Lake and the Stillwater Wildlife Refuge to determine the effect of group size and distribution on pelican feeding behavior. I constructed a number of pelican decoys using commercial White-fronted Goose (Anser albifrons) floater decoys as a base. The bill of each decoy was replaced with a beak/pouch assembly carved from blocks of styrofoam, and the entire decoy was then painted to resemble a pelican in

breeding plumage. In the latter portion of the season (June to August) I repainted the decoys' white crowns black to simulate birds in the post-nuptial molt (Knopf 1975). Unmodified goose decoys served as controls for each experiment. During static tests each decoy was anchored by a 1 kg concrete weight attached to a 2-3 m monofilament tether. Decoys were deployed in groups of 1 to 7, and distributed in both crescent and haphazard patterns.

Each test lasted for 45 minutes. The closest approach by pelicans to the decoys was noted as was any activity by other birds in the vicinity of the decoys. A test was considered over if a pelican approached to within 2 m of a decoy, because at that point the "flock" might be regarded as decoys plus real pelican, thus affecting its possible attractiveness. Control and experimental decoys were alternated in successive trials to remove possible temporal effects on sociality, and equal numbers and patterns of both controls and experimentals were used in each test. A total of 30 experimental tests of anchored decoys consisting of 3-5 replicates of 1 to 7 decoys were run during the 1985 season. A positive response to a decoy group was recorded in the event of an approach by a pelican to within 2 m of a decoy. In addition I noted if pelicans executed a tight wheeling flight low over the decoys in an apparent prelude to landing. Similar criteria are described in Barnard and



Thompson (1985).

The anchors were removed for herding simulations and the decoys were linked above the waterline by single monofilament lines. The outside decoys were then linked to additional lines held by assistants on either side of a slough or stream. An array of 1 to 3 decoys could be drawn through the water in linear or crescent formations. Two additional tests of a single moving decoy were conducted in 1986.

A series of three simulations using one, two, and three decoys connected above the waterline by 30 cm of monofilament line was conducted to test the response of fish to a herding situation. Each set of decoys was drawn through the water by assistants standing approximately 5 m on either side of a slough in the Stillwater Refuge. As a control measure observers walked along both sides of the slough at equivalent distances to those maintained during the herding simulation. In each case the responses of fish were recorded by an observer standing on the embankment above the slough.

The carcasses of 5 adult pelicans found dead at Pyramid Lake and in the Stillwater Marshes were obtained for morphological data and analysis of stomach contents. Measurements of neck and bill length were made using dial calipers and a meter stick.

Counts of birds moving to and from the breeding colony on Anaho Island were made from a hillside approximately 1

km southeast of the island. From this position all arrivals and departures to and from every sub-colony on the island could be observed. Observations began either at first light (approximately 0430 - 0500 hours) lasting until mid afternoon, or in mid morning lasting until dark (approximately 1900 to 2100 hours). All observations were made using 7x35 mm binoculars. During peak activity periods a running commentary on the number of arriving or departing flocks was recorded on a portable tape recorder for later transcription.

Observations were conducted on April 22 and 23, May 27, June 13, 28 and 29 and July 12 1985. Total observation time was 60 hours, with the longest continuous sequence lasting 11 hours (May 27) and the shortest 4 hours (July 12).

The time, direction of departure or arrival, and the number of birds seen approaching or leaving the colony were recorded during one min intervals. In addition note was made whether the birds arrived or departed below or above the observation point, which was located approximately 200 m above the surface of Pyramid Lake. Evidence of the use of thermal vortices in soaring was recorded.

Statistical analysis was performed using the SYSTAT (Systat Inc. 1986) SAS (SAS Institute 1987) and MINITAB (Ryan et al. 1986) statistical packages. In cases where variances differed significantly and/or populations were



not normally distributed appropriate transforms (Sokal and Rohlf 1981) were performed and tests of significance were performed on the transformed data. Levels of significance for statistical tests were obtained from Rohlf and Sokal (1981).

## RESULTS

### COMPOSITION OF PREY SPECIES AND FOOD REQUIREMENTS

All studies to date agree that the major food source for White Pelicans in the Pyramid Lake region consists of the Asiatic Carp Cyprinus carpio and the Lahontan Tui Chub Gila bicolor (Table 1). Although estimates are based on food fed to birds-of-the-year it seems reasonable to suggest that this is also representative of the adults' diet.

Analysis of the regurgitate of near-fledging young pelicans on Anaho Island immediately after feeding revealed that these birds had been fed a mean of 9.9 fish (4.3 S.D., range 1-17, n = 50). Mean weight of individual fish found in the regurgitate of the young pelicans was estimated at 138 g. (84.3 g. S.D., range 51.4-663.1 g. n= 364). Mean total weight of fish in regurgitate was 1199.9 g. (414.6 g. S.D). There was a significant negative correlation between fish size and total number fed ( $r = -0.25$ ,  $p < 0.01$ ,  $n = 357$ ).

### FORAGING LOCATIONS AND HABITAT

Pelicans were observed throughout the Lahontan Basin, but foraging activity during the period of February



Proportion chub + carp in Pelicans diet			
By Number (%)	By Weight (%)	N	Source
96.8	98.1	2897	Hall (1925)
50.2	88.9	211	Bond (1940)
87.0	-	-	Marshall & Giles (1953)
65.8	-	-	Woodbury (1966)
85.0	98.3	384	This Study



through mid-May was concentrated in the southeastern portion of the Carson Sink, and along the lower reaches of the Humboldt River (Fig 1). 87% (n= 4762) of all pelicans observed foraging during this period were seen in the Stillwater region. Although this estimate is biased in favor of areas with easy ground-access, it is in good accord with earlier, more systematic surveys (Knopf and Kennedy 1980).

From mid-May until early August large numbers of pelicans switched to foraging at Pyramid Lake, apparently in response to the inshore movement of chub. Discussion with Stillwater Refuge personnel revealed that less than 200 birds were regularly seen on the refuge during this period. Large numbers of birds continued to use the Humboldt Sinks region south of Interstate 80 throughout the season. By mid-August the numbers of pelicans seen near Stillwater increased again, though never approaching the numbers observed at the beginning of the season. Many of these birds were juveniles, and the Stillwater region must be regarded as a critical component in the pelicans' post-breeding dispersal.

Increases in rainfall and river flow during 1981-1985 caused a massive growth in the total submerged area within the Sinks and a resultant enlargement in suitable foraging habitat. Censuses of sloughs in the Stillwater Refuge in 1984 and 1985 and discussions with the staff of the Stillwater Refuge suggest a substantial increase in local

carp populations.

Preferred foraging habitat during daylight hours away from Pyramid Lake consisted of open water 0.03 to 2.5 m deep. Water clarity throughout the Lahontan Basin is minimal, however the turbulence patterns created by carp and chub while feeding and swimming rapidly are clearly visible to seated human observers at distances of over 15 m. Pelicans frequently probed at the base of partially submerged vegetation and it seems likely that the birds are using a combination of tactile and visual cues in locating prey.

Pelicans used low mud islands for loafing areas between feeding bouts. Several of these islands appeared to serve as assembly areas, both for feeding groups and for flights assembling for the return trip to Anaho Island. Groups of up to several hundred birds might gather on islets in the Stillwater Marshes before taking off together and spiralling slowly off in the direction of the colony.

#### FORAGING BEHAVIOR

No evidence of diving activity was recorded during the course of the study. Groups of pelicans feeding in the Stillwater Marshes and along the Humboldt River foraged almost exclusively in water less than 2 m deep.

Measurements of dead pelicans found at Stillwater revealed a mean neck plus bill length of 85.5 cm (15.2 cm S.D. n = 5). Partial submersion during a vigorous strike



adds several centimeters to this effective length, thus White Pelicans appear to be restricted to foraging on prey in the upper 1.25 m of the water column.

Group foraging behavior fell into two general forms. In the first (Fig. 2), performed in areas with a slowly shelving shoreline and in shallow creeks and sloughs, members of the flock formed a line or arc facing the shore and moved in toward the bank. As the birds reached the shallows it was often possible to see the disturbance caused by fish swimming ahead of the flock. On two occasions I saw carp driven out of the water onto the bank where they were seized by members of the driving flock.

In the second form of group feeding (Fig. 3), usually performed in open water or in areas with a sharp drop-off near shore, flocks would move in double or treble file, occasionally probing with their bills. The rear segment of the flock would then sweep round to one side, and gradually move around and ahead of the leaders. The leaders would fan out in a line or arc, still oriented in the original direction of movement, at which point the breakaway section would turn to face them. As the groups moved together, both segments would commence probing and striking. In some cases the groups would disintegrate after a brief interval of striking, in others the whole group would reform and repeat the sequence.

Schools of carp responded to the approach of the decoys by bunching up and moving away. It proved possible with

Fig. 2. Foraging behavior by groups of pelicans along shelving shorelines. Ovals represent individual birds, arrows indicate direction of travel.





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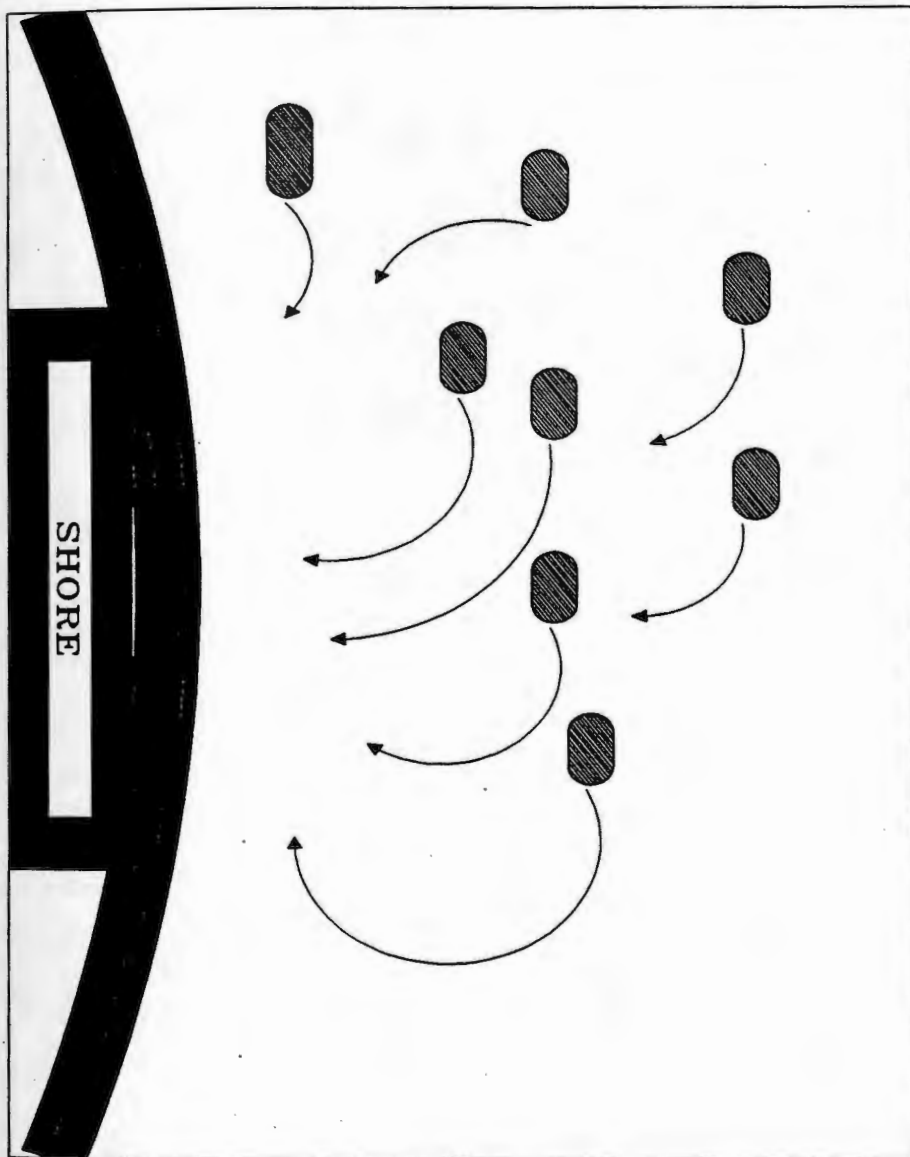
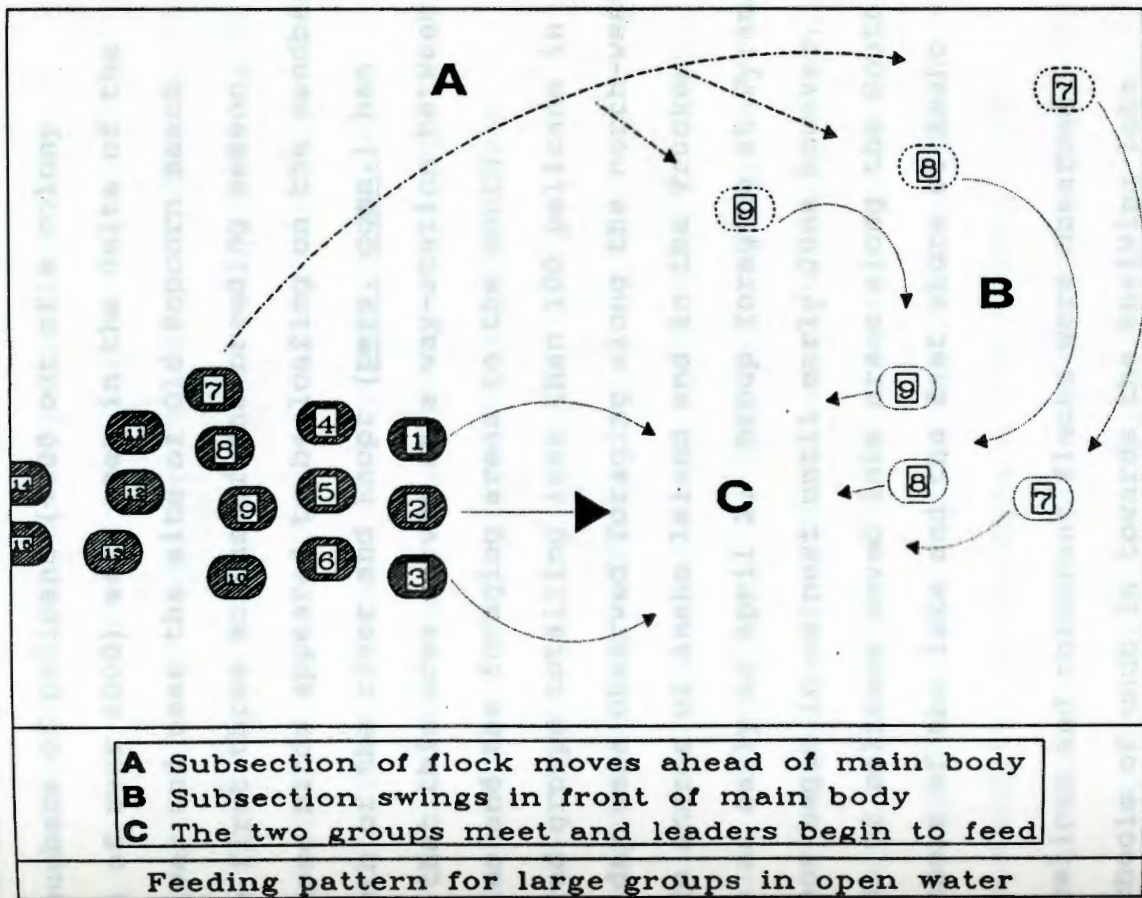


Fig. 3. Foraging behavior by large (usually > 20) groups of pelicans in open water. Ovals represent individual birds, numbers identify the same bird throughout, Letters (A,B,C) refer to three distinct phases of the entrapment operation, arrows indicate direction of travel.







the "flock" of three decoys to steer the school into such shallow water that individual carp were exposed to the air as they pushed past each other. These responses were not observed when observers simply walked parallel to the slough without decoys.

Small numbers of pelicans (<400 out of a colony population of over 8000) were seen in the delta of the Truckee River and near the site of Old Popcorn Beach during the first three months of the breeding season. Many of these birds appeared to be loafing on the sandbars at the mouth of the river and Knopf (pers. comm.) has suggested that this area serves as a way-station between the colonies and the foraging areas to the south.

Scattered groups totalling less than 100 pelicans in any given day were observed foraging along the north-west and eastern shores of Anaho Island and in the Truckee Delta area as early as April 2. Group foraging at Pyramid Lake did not begin in earnest until early June however, when groups of pelicans moved into areas along the South and West shore of the lake and the East shore of Anaho Island.

Mixed pelican and cormorant flocks were observed herding schools of chub in towards the shelving lake shorelines, beginning their drive in water over 7 m deep. Other flocks performed apparent encirclement maneuvers at the southeastern end of the lake in water over 15 m deep.

Pelicans were never observed foraging along the

southern half of the West side of Anaho Island. Measurements with an echo sounder revealed that the island drops steeply away to depths of over 70 m along this shore making the area unsuitable as a spawning ground and rendering herding-to-shore impractical.

Herding groups generally consisted of less than 10 birds (Fig. 4) but on occasion I observed flocks of up to 150 birds at Stillwater and over 300 birds at Pyramid Lake engaged in coordinated fishing activity. The tendency of large groups (>50 birds) to rapidly sub-divide and reform into local clusters precluded an accurate estimate of effective group size, especially when the flock was feeding among partially submerged vegetation in the Stillwater Marshes.

#### GROUP SIZE AND FORAGING SUCCESS

Analysis of foraging success as a function of group size revealed a significant difference in individual capture success (Table 2). There was no evidence that a particular position within a flock affected foraging success and all members of a given flock appeared to have an equal probability of catching a fish during a given time interval. Single birds did significantly worse than members of groups of sizes 3-6 ( $F = 4.89$  Fisher's LSD test  $p < 0.05$ ). Fig. 5 presents the coefficient of variation ( $[S.D. \times 100]/\text{mean}$ ) corrected for bias (Sokal and Rohlf 1981) for foraging success in flocks of size 1-10.



Fig. 4. Distribution of flock numbers and total birds in flocks of given size seen feeding in the Lahontan Basin during the course of the study. Solid bars indicate the number of flocks in a given size-class (left vertical axis) while hatched bars represent the total number of birds seen in that size class (right axis).

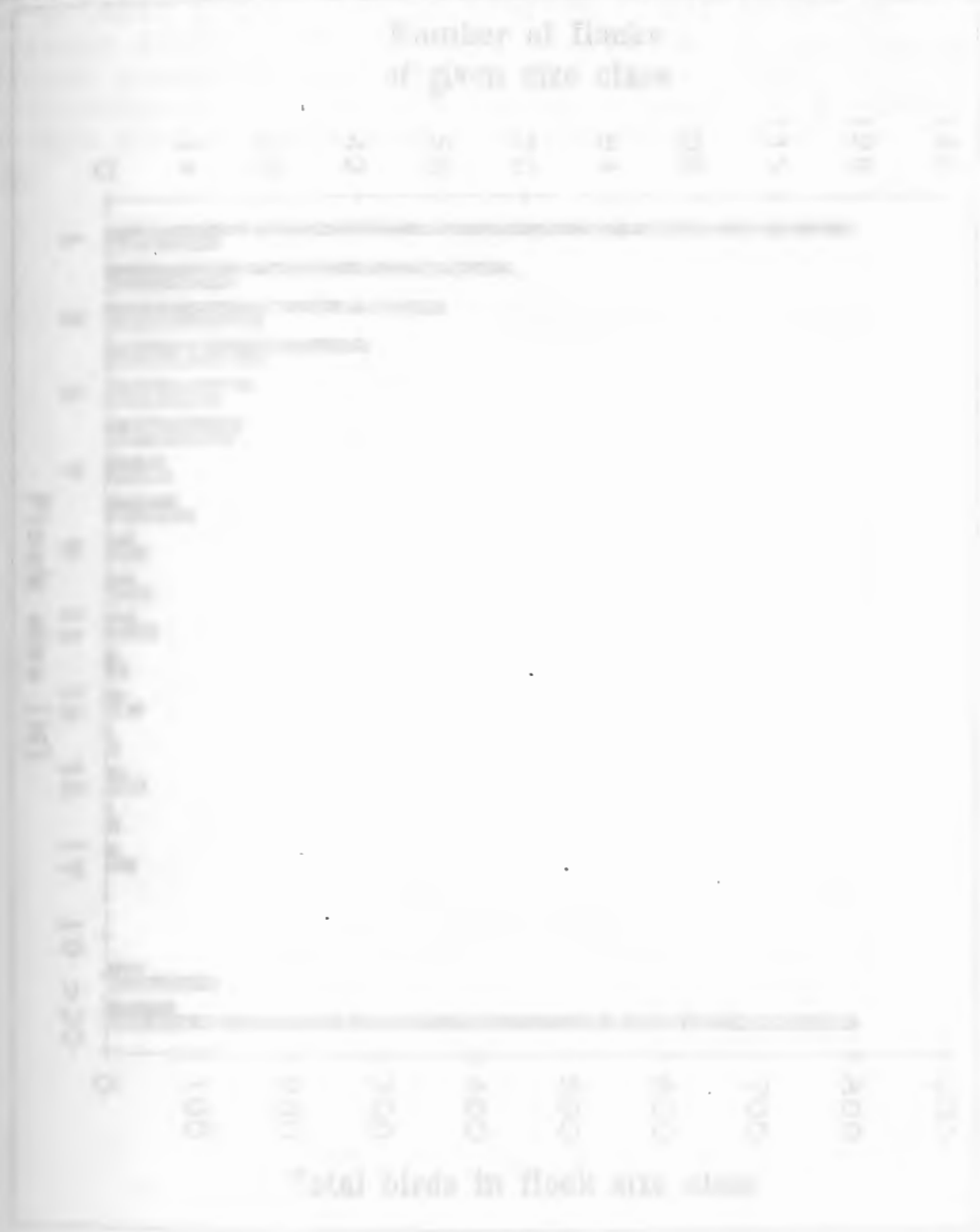




Table 2. Analysis of pelican foraging success. Numbers refer to head-tosses per bird per minute in flocks of a given size. The data were analyzed under the SAS General Linear Models procedure (SAS Institute, 1987). Analysis of variance revealed a significant difference within the data set ( $F = 4.89, p < 0.0001$ ). Means separation using Fisher's least significant difference test revealed significant differences between flocks of single birds and flocks consisting of two, three, five, and six birds (indicated by \* in the table). Values for flocks of three were also significant. In general, the more flocks of two...

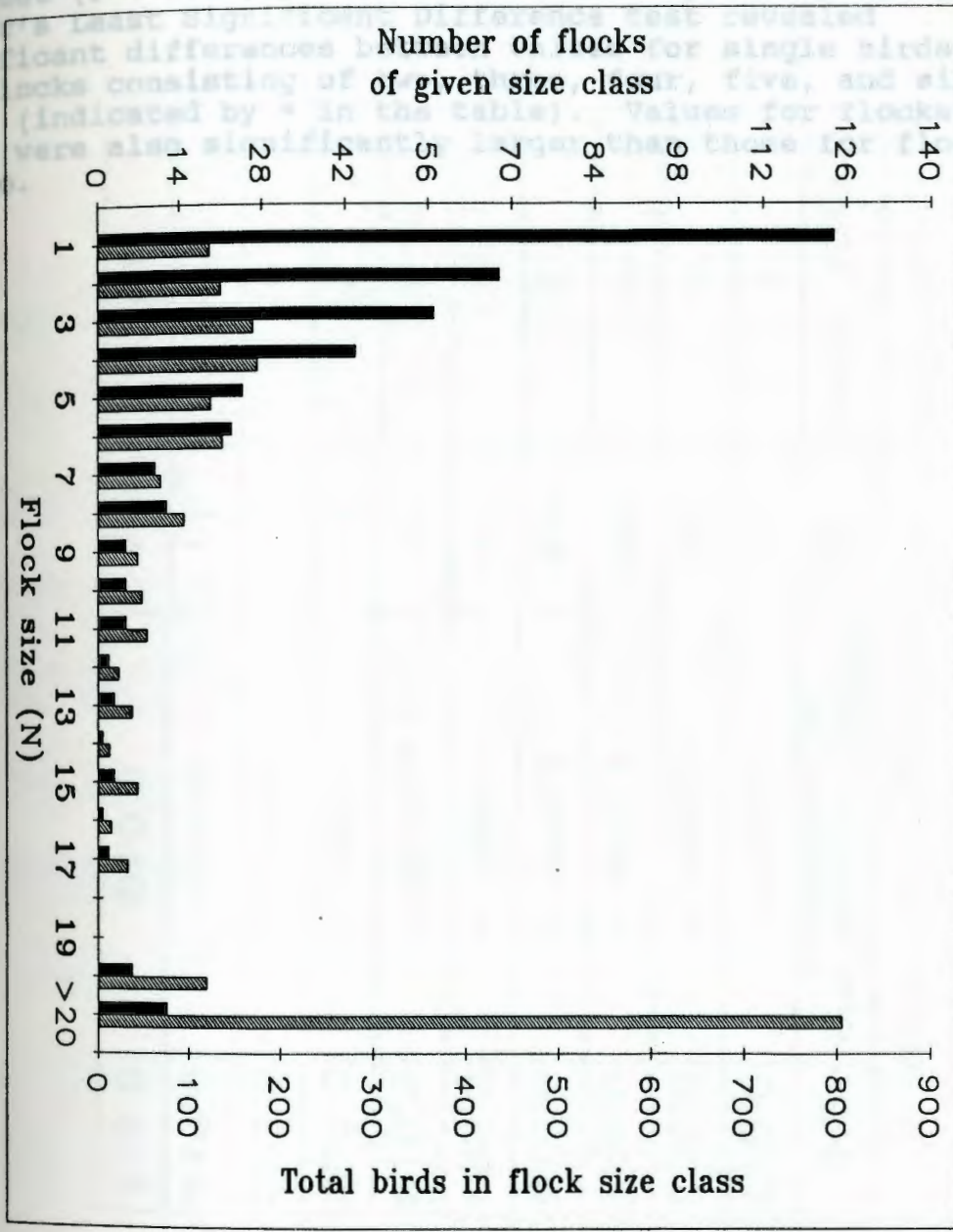


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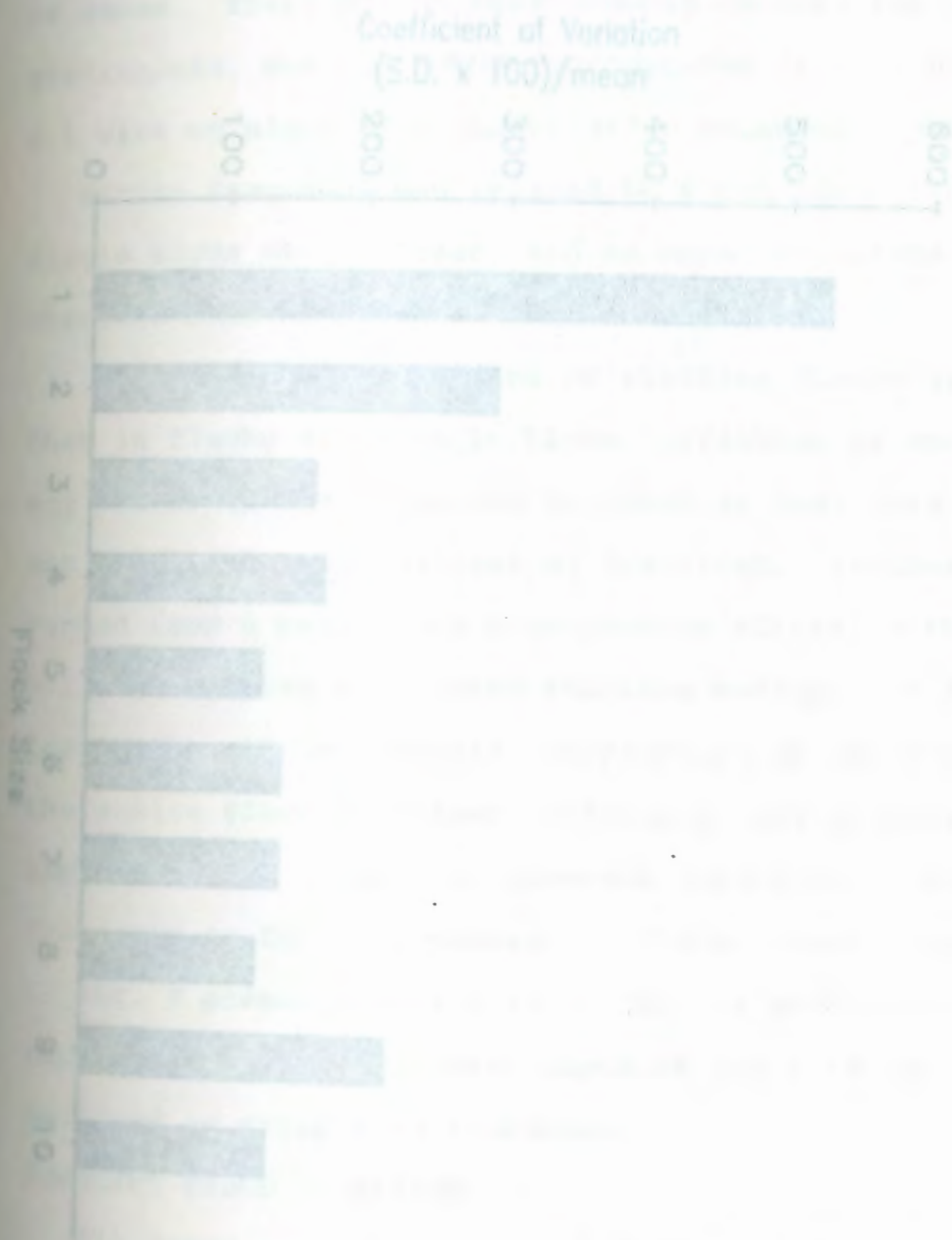
Pelican foraging success			
Flock Size	N	Mean Captures/Min. by Individual	S.E.
1	115	0.035	0.017
2	81	0.055 *	0.025
3	39	0.128 *	0.034
4	58	0.078 *	0.018
5	51	0.097 *	0.023
6	18	0.056 +	0.018
7	14	0.063	0.023
8	14	0.063	0.022
9	11	0.020	0.014
10	14	0.040	0.015

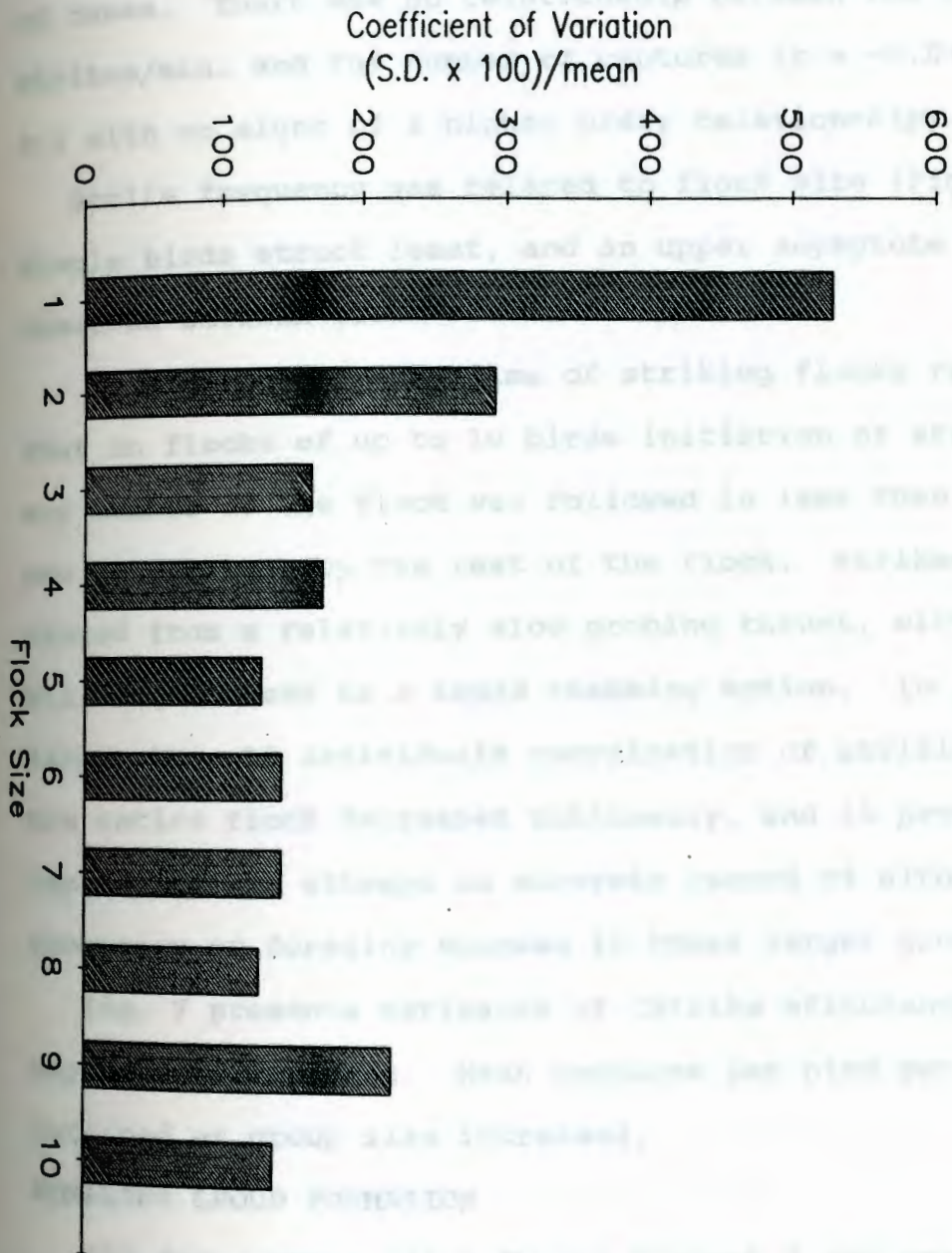
Fig. 9. Coefficient of variation (variance divided by mean squared) for foraging success of individual birds while members of a flock of given size class.

Pelican foraging success			
Flock Size	N	Mean Captures/min. by individual	S.E.
1	115	0.035	0.017
2	61	0.065 *	0.025
3	39	0.128 *	0.034
4	58	0.078 *	0.018
5	31	0.097 *	0.023
6	16	0.056 *	0.018
7	14	0.063	0.023
8	14	0.063	0.022
9	11	0.020	0.014
10	14	0.040	0.015



Fig. 5. Coefficient of variation (Sokal and Rohlf 1981) for foraging success of individual birds while members of a flock of given size class.





Contrary to Low et al. (1950), probing and striking (which I assume to be synonymous with Low et al.'s "dipping") did not result in prey capture in the majority of cases. There was no relationship between the number of strikes/min. and the number of captures ( $r = -0.03$ ,  $p > 0.1$  with no signs of a higher order relationship).

Strike frequency was related to flock size (Fig. 6). Single birds struck least, and an upper asymptote was observed between flock sizes of 3 and 4.

Examination of the films of striking flocks revealed that in flocks of up to 10 birds initiation of striking by any member of the flock was followed in less than 3 sec by striking by the rest of the flock. Strikes ranged from a relatively slow probing thrust, with the bill held closed to a rapid stabbing motion. In flocks larger than 10 individuals coordination of striking within the entire flock decreased noticeably, and it proved impractical to attempt an accurate record of either strike frequency or foraging success in these larger groups.

Fig. 7 presents estimates of "strike efficiency" or captures/bird/strike. Mean captures per bird per strike declined as group size increased.

#### FORAGING GROUP FORMATION

All decoy group sizes from 1 through 5 and one group of 7 resulted in a positive response (Table 3). Any doubts that the pelicans would regard the decoys as other than pelicans were dispelled at the beginning of the season



Fig. 6. Strikes per bird per minute for flocks of size 1 to 10. Bars indicate  $\pm 1$  standard error.

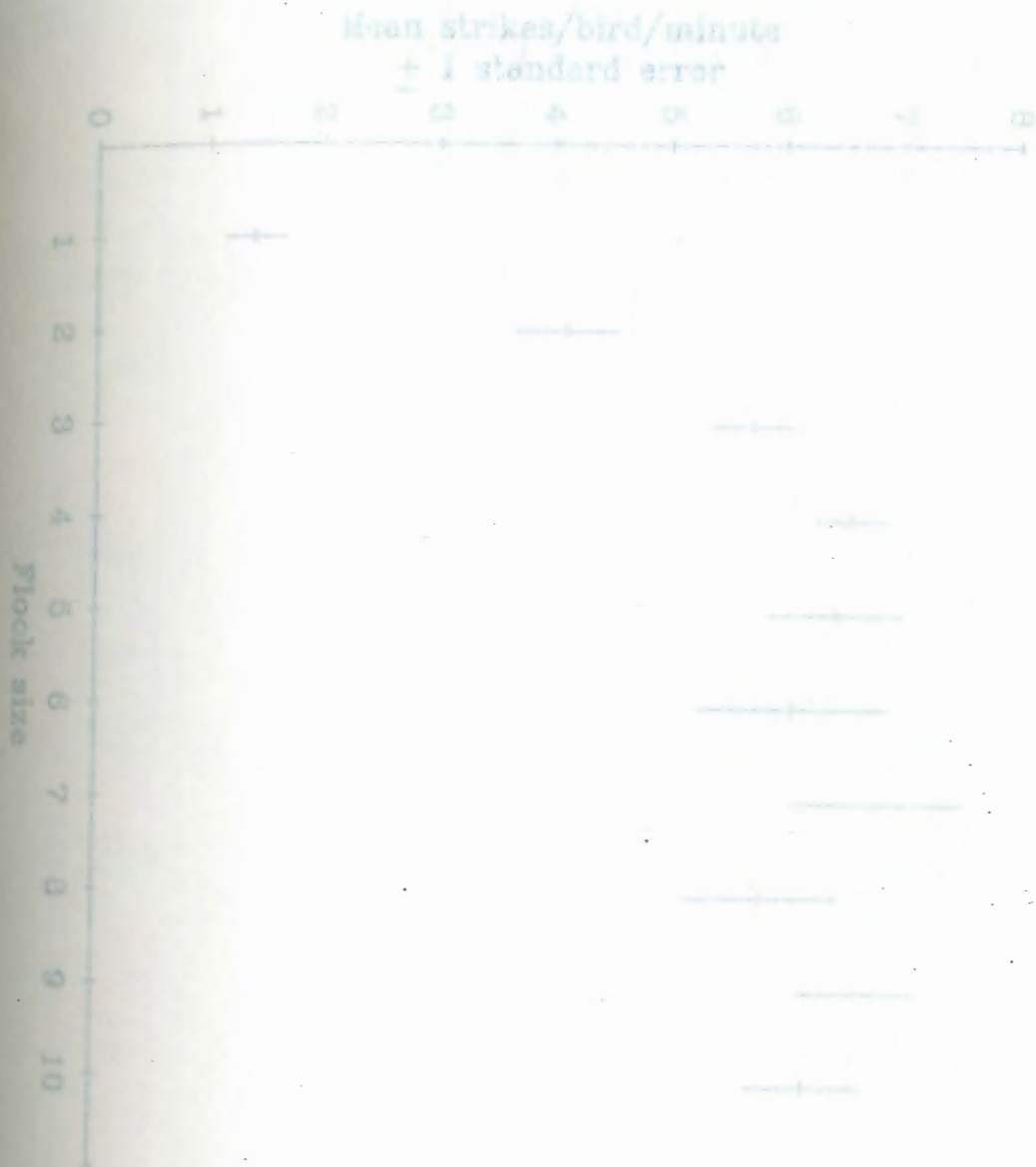


Fig. 7. Mean strike efficiency for birds in flocks of sizes 1 to 10 plus or minus one standard error.

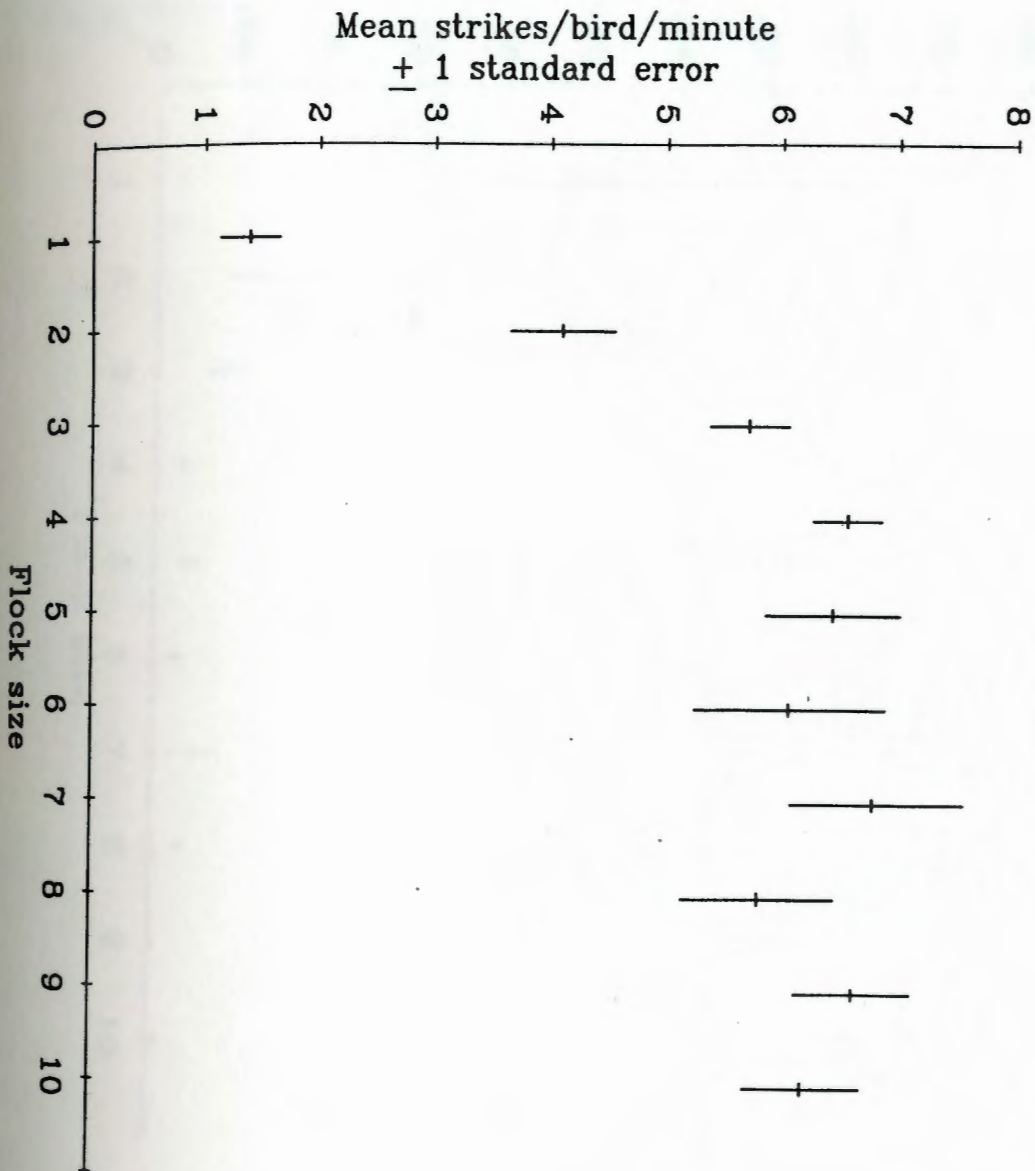


Fig. 7. Mean strike efficiency for birds in flocks of sizes 1 to 10 plus or minus one standard error.

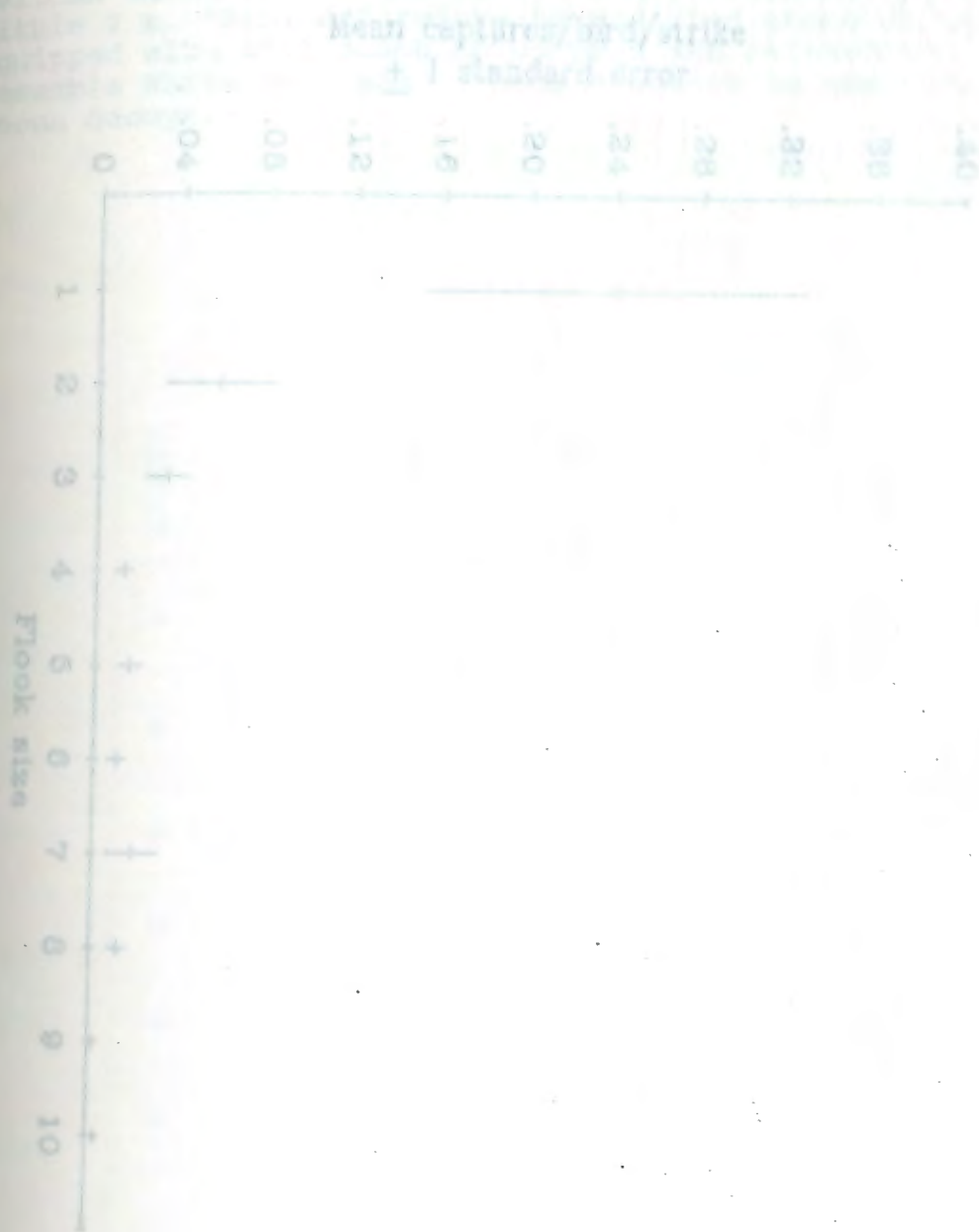




Table 3. Pelican responses to decoys. A flyover was recorded if one or more birds banked low over the decoys but did not land. A "close approach" consisted of a pelican landing near the decoys and/or approaching to within 2 m. "Pelican captures" were recorded if decoys equipped with bill pouches were struck. Decoys painted to resemble White Pelicans were used in addition to unmodified goose decoys.

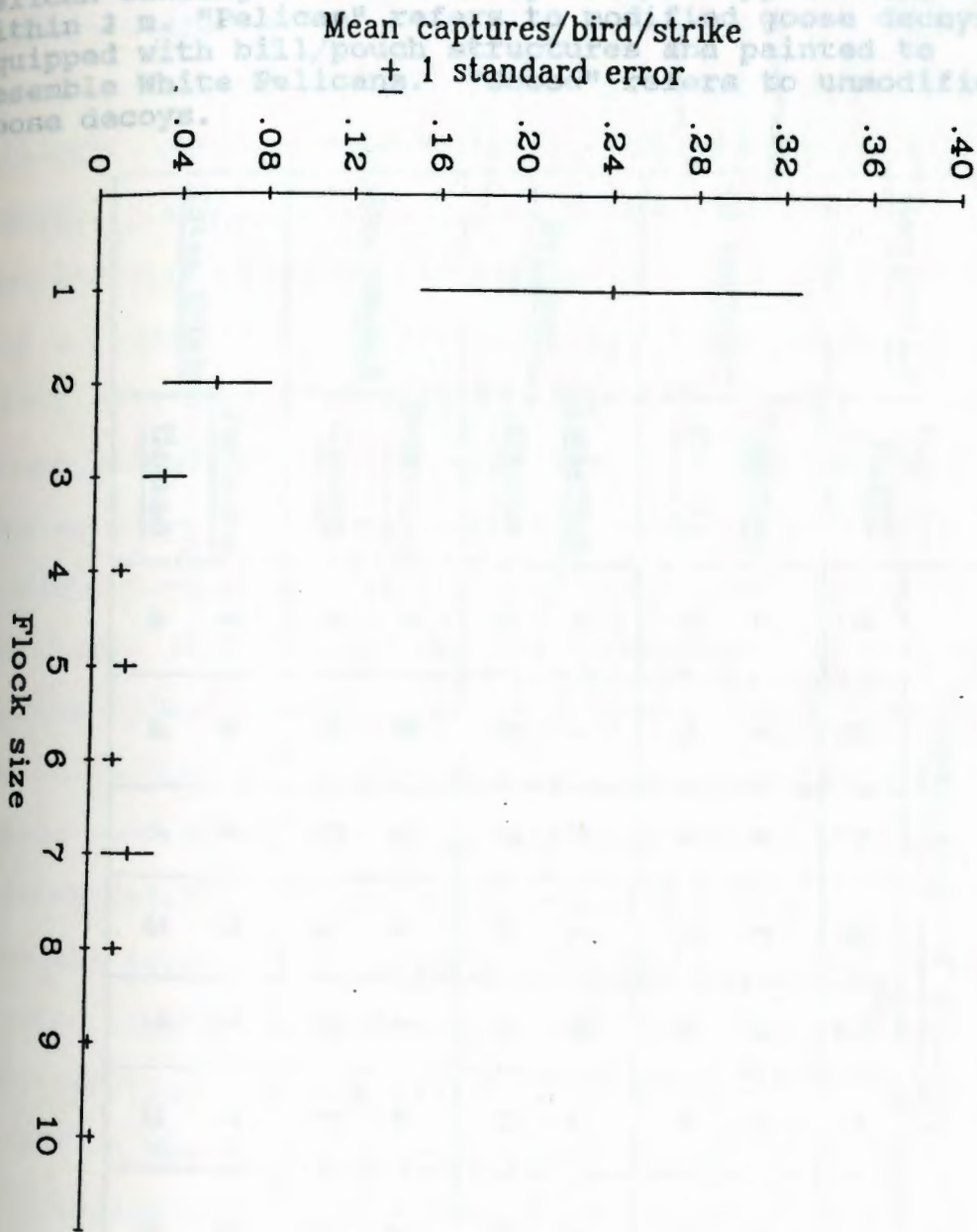


Table 3. Pelican responses to decoys. A flyover was recorded if one or more birds banked low over the decoys but did not land. A "close approach" consisted of a pelican landing near the decoys and/or approaching to within 2 m. "Pelican" refers to modified goose decoys equipped with bill/pouch structures and painted to resemble White Pelicans. "Goose" refers to unmodified goose decoys.

Response	Decoy Type	Number of Decoys						
		1	2	3	4	5	6	7
No Response	Pelican	1	1	1	1	0	2	0
	Goose	4	4	4	3	3	2	1
Flyover	Pelican	1	1	1	1	2	0	1
	Goose	0	0	0	0	0	0	0
Close Approach	Pelican	2	2	2	1	1	0	1
	Goose	0	0	0	0	0	0	0
Total Trials	Pelicans	4	4	4	3	3	2	2
	Gooses	4	4	4	3	3	2	1

<u>Response</u>	<u>Decoy Type</u>	<u>Number of Decoys</u>						
		<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>
<u>No Response</u>	<u>Pelican</u>	1	1	1	1	0	2	0
	<u>Goose</u>	4	4	4	3	3	2	1
<u>Flyover</u>	<u>Pelican</u>	1	1	1	1	2	0	1
	<u>Goose</u>	0	0	0	0	0	0	0
<u>Close Approach</u>	<u>Pelican</u>	2	2	2	1	1	0	1
	<u>Goose</u>	0	0	0	0	0	0	0
<u>Total Trials</u>	<u>Pelican</u>	4	4	4	3	3	2	2
	<u>Goose</u>	4	4	4	3	3	2	1



when single decoys placed along the West shore of Anaho Island became the objects of apparent courtship behavior by male pelicans. The persistence of the decoys' attractiveness away from the breeding site and throughout the season rules out reproduction as the sole cause of sociality. Late in the season it proved possible to induce immature birds-of-the-year to follow moving decoys and to approach to within 2 m of a partially submerged observer if a decoy was also present. Similarly, adult pelicans landed in closer proximity to my vehicle when decoys were deployed than when they were absent. At no time did pelicans respond to the control goose decoys. Large flocks (> 20 birds) feeding at Pyramid Lake in July were clearly attractors, with birds often leaving loafing areas to join in a foraging session.

There was no evidence of groups of pelicans actively resisting joining by additional members although individual birds occasionally struck at each other during a herding session. Individuals belonging to different groups foraging in the same general area would frequently haul out on nearby mudbanks and then join another group or form a new unit upon returning to the water.

#### PIRACY

During April 1985 I frequently saw flocks of up to 350 pelicans swimming near the junction of the Truckee River and Pyramid Lake in 3 to 7 m water accompanied by 70 to 200 Double-Crested Cormorants (Phalacrocorax auritus). The

pelicans were distributed throughout the cormorant flocks, and exhibited none of the cohesion of movement and probing behavior seen elsewhere. Closer observation revealed that the pelicans were engaged in a form of kleptoparasitism or piracy. The pelicans would wait for a cormorant to surface with a fish and then one to five pelicans would pounce on the cormorant and endeavor to seize the prey before the cormorant could swallow it. Often the arriving pelicans would actually land on top of the cormorant, forcing it partially beneath the water. In some cases the sheer numbers of would-be parasites would work to the cormorant's advantage, as the pelicans so impeded each other's attack that the cormorant was able to either escape or swallow the fish.

Activity interpretable as piracy was primarily observed between 0445 and 0830 hours, after which the pelicans retired to a sand spit on the east side of the river, where they remained for several hours. In a total of 37 hours of observation, conducted on April 13-15, 22-24, and 26 1985, I recorded 52 instances of attacks by pelicans on cormorants. In 26 of these cases one of the attacking pelicans gave the characteristic "head toss" associated with swallowing at the conclusion of the attack, on two occasions the fish was dropped and lost to all birds, and on two occasions the cormorant definitely managed to escape with its prey.



## NIGHT FISHING

Pelicans were extremely sensitive to the approach of humans or vehicles. During daylight hours pelicans loafing on embankments bordering roads within the Stillwater Management Area or feeding in the adjacent sloughs would usually take off and move away if a vehicle approached to within 300 m. Because many of the roads within the Stillwater region receive a high volume of traffic from sportsmen and campers during daylight hours these areas initially appeared unsuitable for pelican foraging sites.

After dark however the focus of pelican foraging activity may shift to the creeks and sloughs along the roadways. Groups of 20 to 300 pelicans were observed moving upstream, driving fish ahead of them until they reached a weir or road culvert. Additional pelicans would line the banks on each side of the slough, periodically leaping in front of the advancing flock, and taking fish concentrated by the "beaters". Once the swimming flock reached a culvert or some other constriction in the slough, a general free-for-all ensued, with birds at the rear of the "beating" flock flying over the heads of those in front and landing in the area immediately below the slough constriction. At the same time, the birds at the front of the flock and those lining the banks lunged forward, striking at fish struggling to get past the constriction or break back downstream. Although I was



unable to obtain accurate counts of prey capture for entire flocks during night feeding bouts, I recorded 11 captures in 10 minutes by the leading 7 birds of a flock of 150 feeding at the mouth of a culvert in the Stillwater Refuge between 0200 hrs and 0430 hours. In addition to the 11 definite captures other birds could be seen and heard struggling behind the leaders, and these birds may also have obtained fish. Groups of up to 200 birds returned to the same culvert for 5 nights in succession.

#### FLIGHT FLOCK SIZES AND TIMING OF ARRIVAL AND DEPARTURE

Summary statistics on flock sizes arriving and departing at different altitudes observed from April through July of 1985 are presented in Table 4. In each case flocks conformed to Heppner's (1974) definition in that they were coordinated in turning, spacing, velocity, and direction of travel.

A total of 2289 flocks were observed departing from the Anaho colony from April through July, 88% (2017) of these contained 20 or fewer birds. 1124 flocks were observed arriving at the colony, 68.42% (769) of these contained 20 or fewer birds.

Arriving and departing flocks were significantly different in size (Wilcoxon 2-sample test,  $z = 10.74$   $p < 0.001$ ).

Mean flock size among all birds observed departing at any altitude from April through July was 11.14 (23.98 S.D.) with a maximum of 450 birds in a flock. Of these 25506 birds 41% (10537) departed in flocks of 20

Table 4. Summary statistics on flock size for flocks of pelicans seen arriving and departing high and low recorded from April through July 1985. % total refers to the total of all birds that arrived or departed in a given altitude category for a given month.

Month	Arrive		Depart		N	Mean	S.E.	Range	% of Total birds seen or heard
	High	Low	High	Low					
April	118	102	118	102	107	21.76	3.83	1 - 100	50
	409	409	409	409					
May	144	118	144	118	144	19.57	2.29	1 - 476	53
	563	563	563	563					
June	129	263	129	263	731	7.97	0.56	1 - 136	55
	731	731	731	731					
July	58	83	58	83	208	19.59	3.59	1 - 476	68
	208	208	208	208					

Month	N	Mean	S.E.	Range	% of Total birds seen in month	
April	Arrive low	103	20.06	4.63	1 - 297	45
	Arrive high	115	21.76	3.23	1 - 180	55
	Depart low	406	5.3	0.31	1 - 52	52
	Depart High	107	18.72	2.27	1 - 140	48
May	Arrive low	116	21.93	4.40	1 - 475	47
	Arrive high	144	19.67	2.29	1 - 250	53
	Depart low	563	6.30	0.29	1 - 43	90
	Depart high	32	12.88	2.25	1 - 68	10
June	Arrive low	281	21.21	3.13	1 - 470	61
	Arrive high	129	29.35	4.64	1 - 360	39
	Depart low	731	7.97	0.55	1 - 130	53
	Depart high	281	53.6	5.16	1 - 250	47
July	Arrive low	63	59.73	15.23	1 - 69	57
	Arrive high	86	24.92	4.99	1 - 260	43
	Depart low	338	19.53	2.20	1 - 450	99
	Depart high	4	14.00	4.99	1 - 47	1



or less. Mean flock size among all birds observed arriving from April through July at any altitude was 21.75 (44.87 S.D.) with a maximum of 475 birds. Of these 22298 birds 22.96% (5119) arrived in flocks of 20 or less.

Analysis of variance revealed that mean flock size increased for both arrivals and departures between April and July for both altitude groups combined, ( $F = 44.21$  Tukey's HSD test  $p < 0.05$ , 3297 df). Overall flock sizes in May and June did not differ significantly from each other, but both were different from those in April and those in July. Because of the small sample size available I excluded high departures in July from an analysis of flock size and altitude categories. Mean flock sizes in different altitude categories differed significantly in April and June (high vs. low for both arrivals and departures) and in May (departures only) ( $F = 38.2$ ,  $p < .001$  Tukey's HSD test,  $p < 0.05$ ). Low departures in April, May, and June were not significantly different from each other, but all were significantly smaller than those in July. High departures in June were significantly larger than those in April and May. High arrivals differed significantly only between May and June.

The value "% total" in Table 4 represents the proportion of all birds seen arriving or departing during a given month in the given altitude category. Thus the value 52% for birds arriving low during April indicates that 52% of all birds seen arriving during that month did

so below my observation point.

Arrivals and departures to and from the colony followed a similar pattern throughout the season (Fig. 8 a-f). A disproportionately large number of birds arrived and departed between 1100 hours and 1300 hours (chi-square = 40233,  $p < 0.001$  assuming an equal number of departures or arrivals during any given 2 hour period). The total number of birds arriving and departing both overall and during the peak 1100 to 1300 hours period increased markedly between April and July (Table 5).

#### DISCUSSION

White Pelicans rarely dive for fish. Gunter (1958) states that despite extensive observations he never saw a dive, and cites Bent (1924) in asserting that White Pelicans seldom dive. Hall (1925) mentions seeing a pelican executing an aerial plunge on one occasion. Skinner (1917) says that on one occasion he witnessed a White Pelican perform a surface dive leading to complete submergence, and Knopf (pers. comm.) states that he has occasionally seen White Pelicans make shallow dives while feeding. In seven seasons of observing White Pelicans I have yet to see a dive. If, as appears to be the case, diving plays a minor role in White Pelican feeding behavior, the birds are limited to prey that can be reached by maximally extending the neck and bill. Clearly, any activity that would concentrate fish in shallow water or restrict their movement within a given



Fig. 8a-g. Number of birds seen arriving and departing from Anaho Island during half hour periods on given days. Dark bars indicate departures, light bars represent arrivals. The dashed line at the top of each chart indicates the actual observation period. Each pair of bars represents the total number of birds that arrived and departed during the half hour ending at the given time. Note changing scale between Fig. 8a and Fig. 8g.

Fig. 8a. April 22, 1985.

Fig. 8b. April 23, 1985.

Fig. 8c. May 27, 1985.

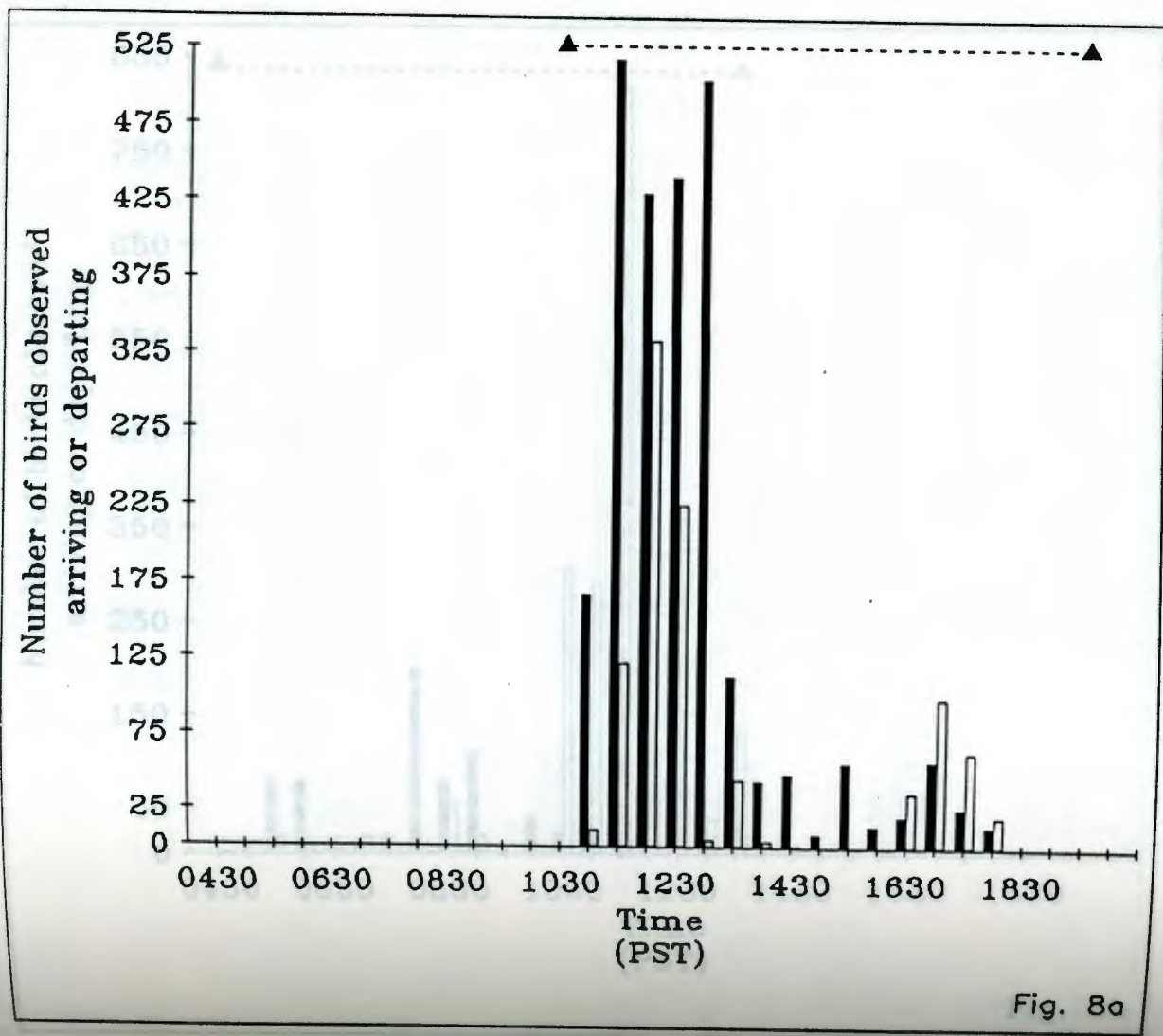
Fig. 8d. June 13, 1985.

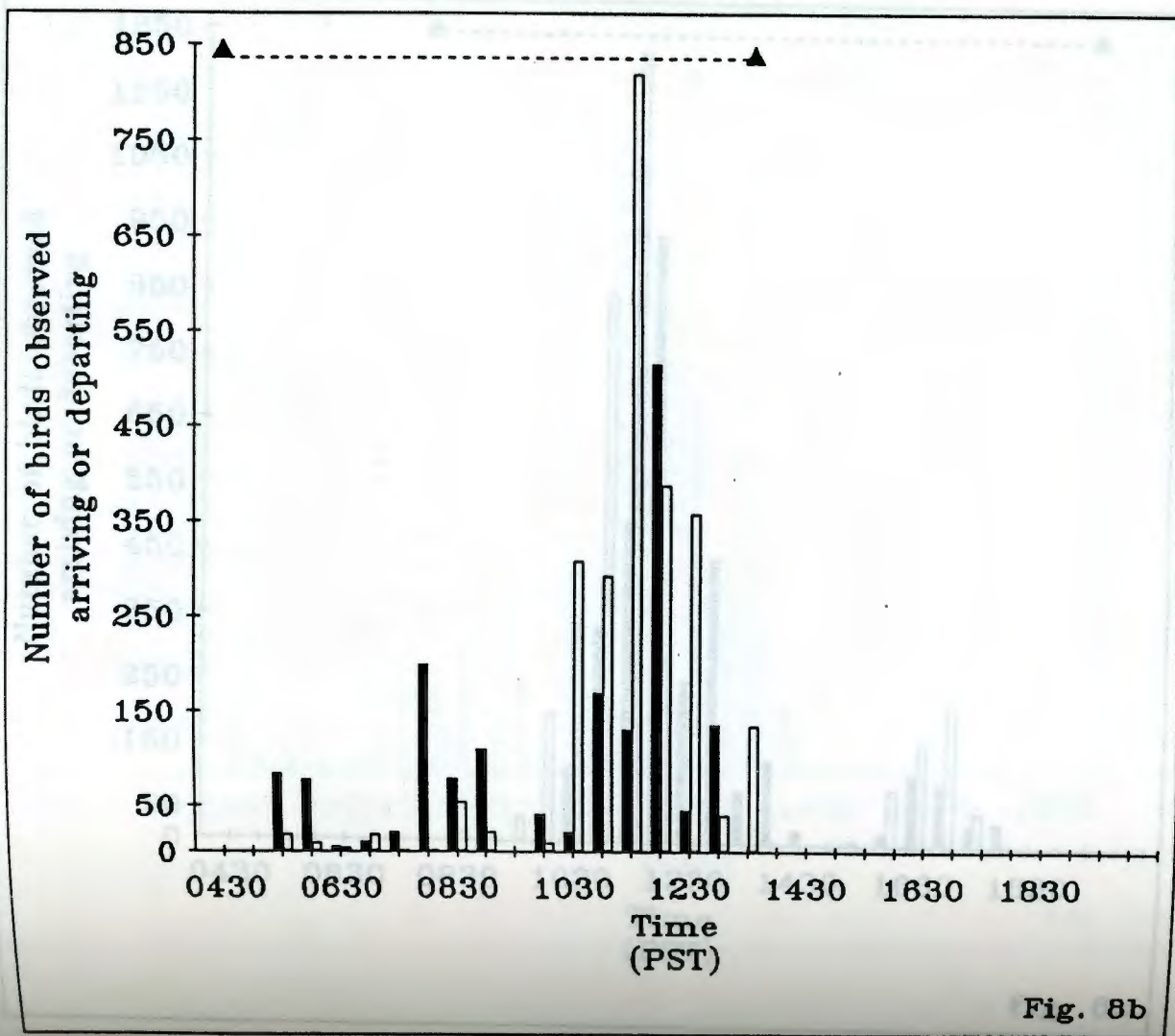
Fig. 8e. June 28, 1985.

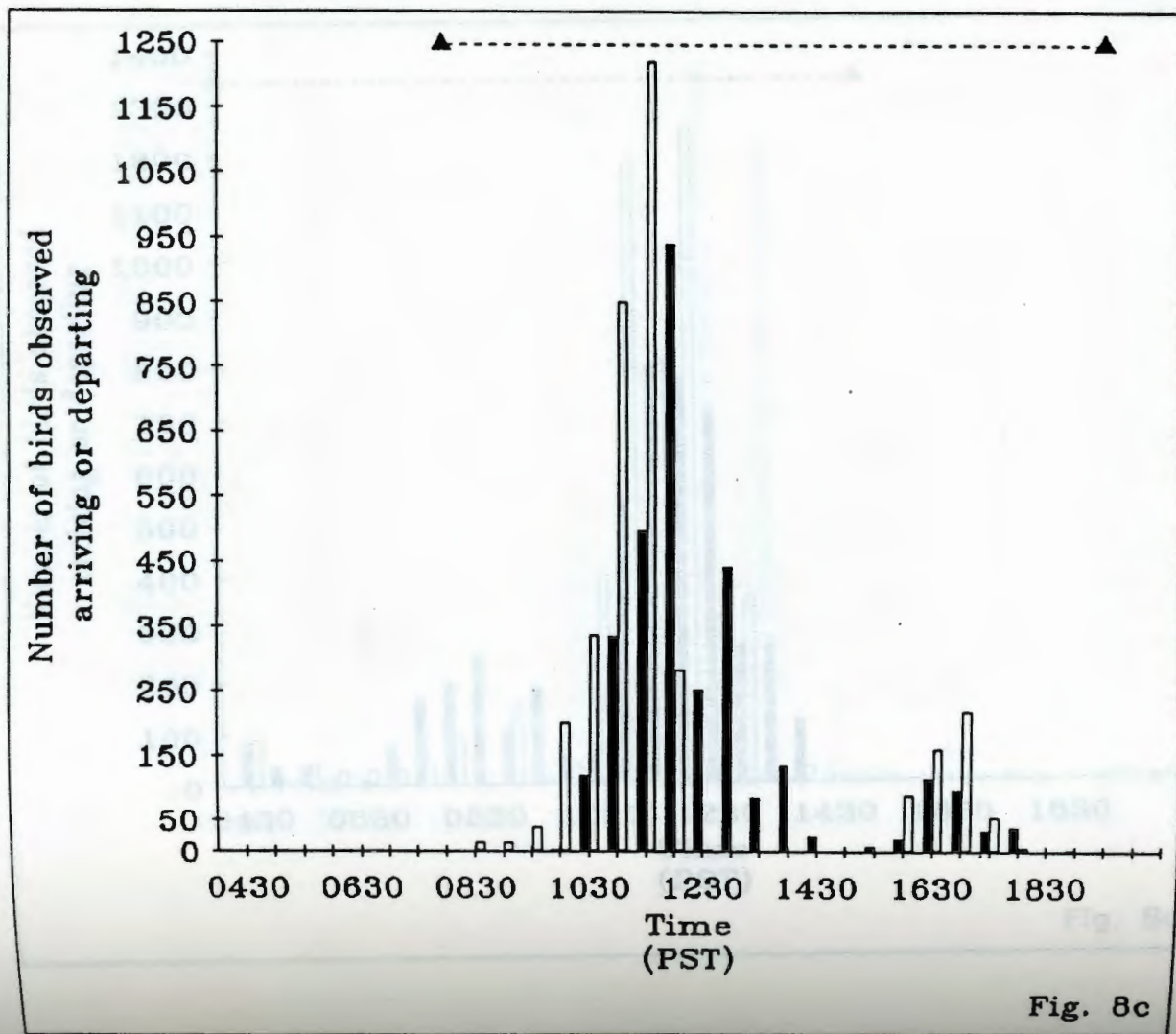
Fig. 8f. June 29, 1985.

Fig. 8g. July 12, 1985.











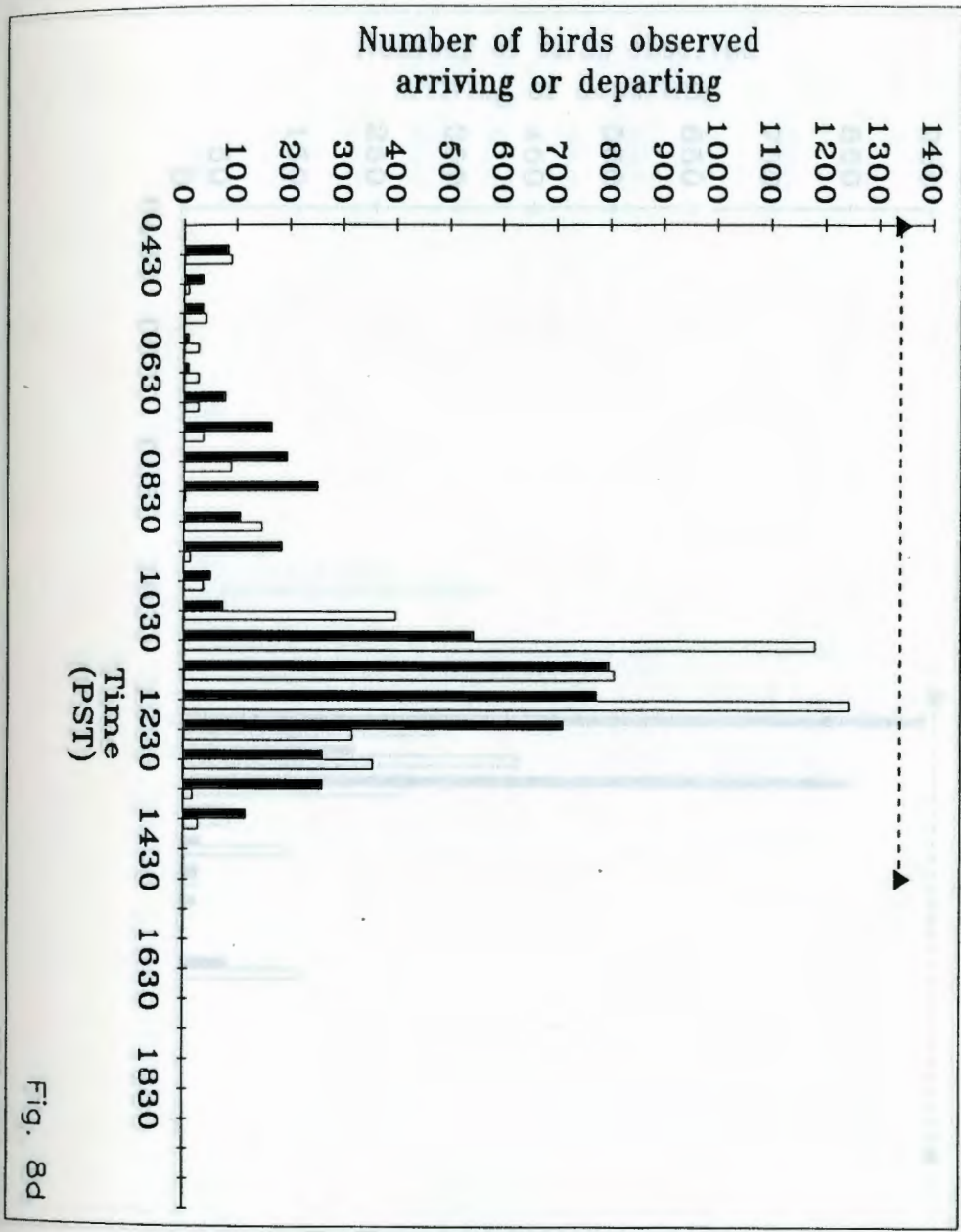
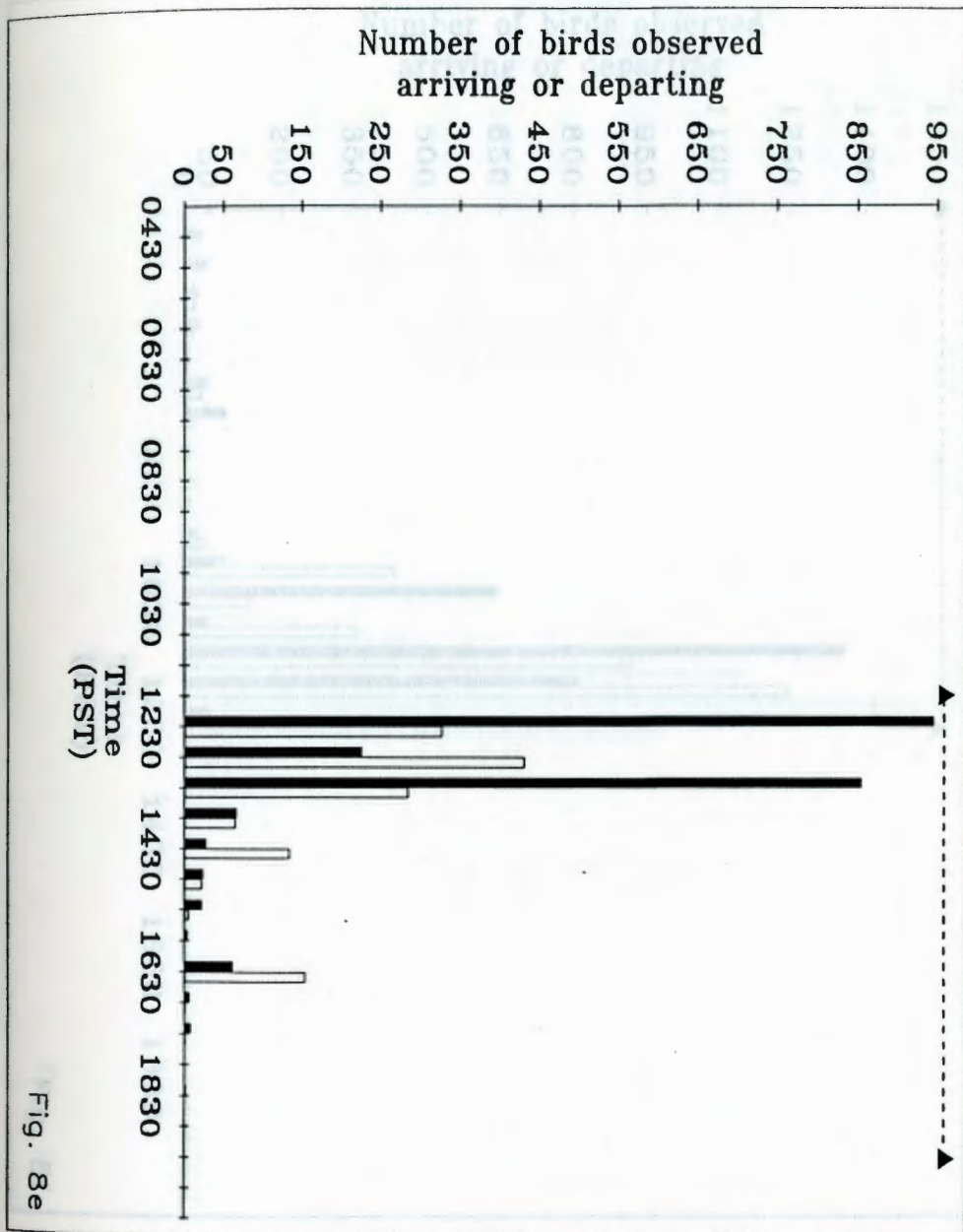


Fig. 8d



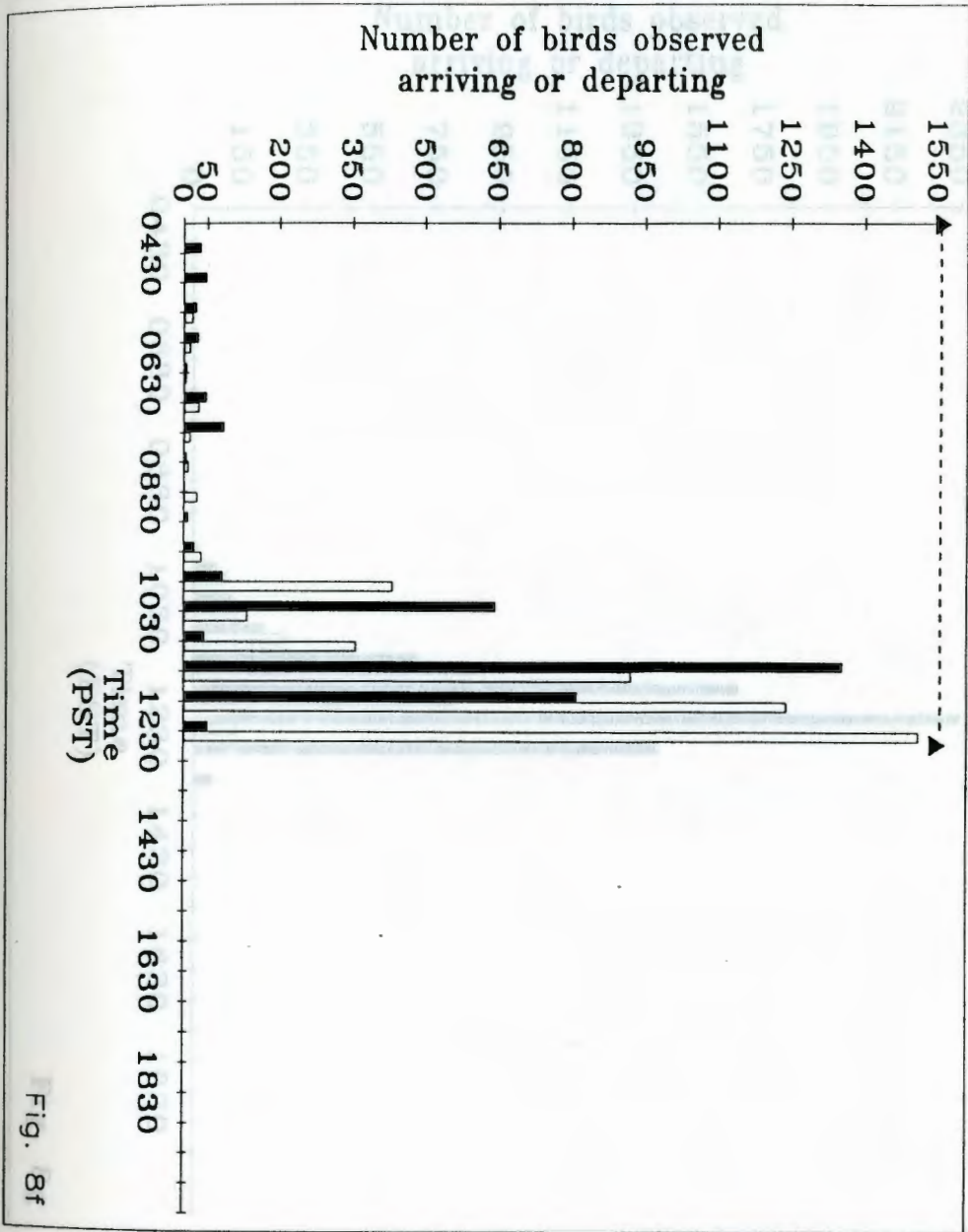


Fig. 8f



Table 8. Summary statistics on the number of pelicans observed arriving at and departing from Anaho Island during both the "peak" 1100-1300 hour period and throughout a given observation period.

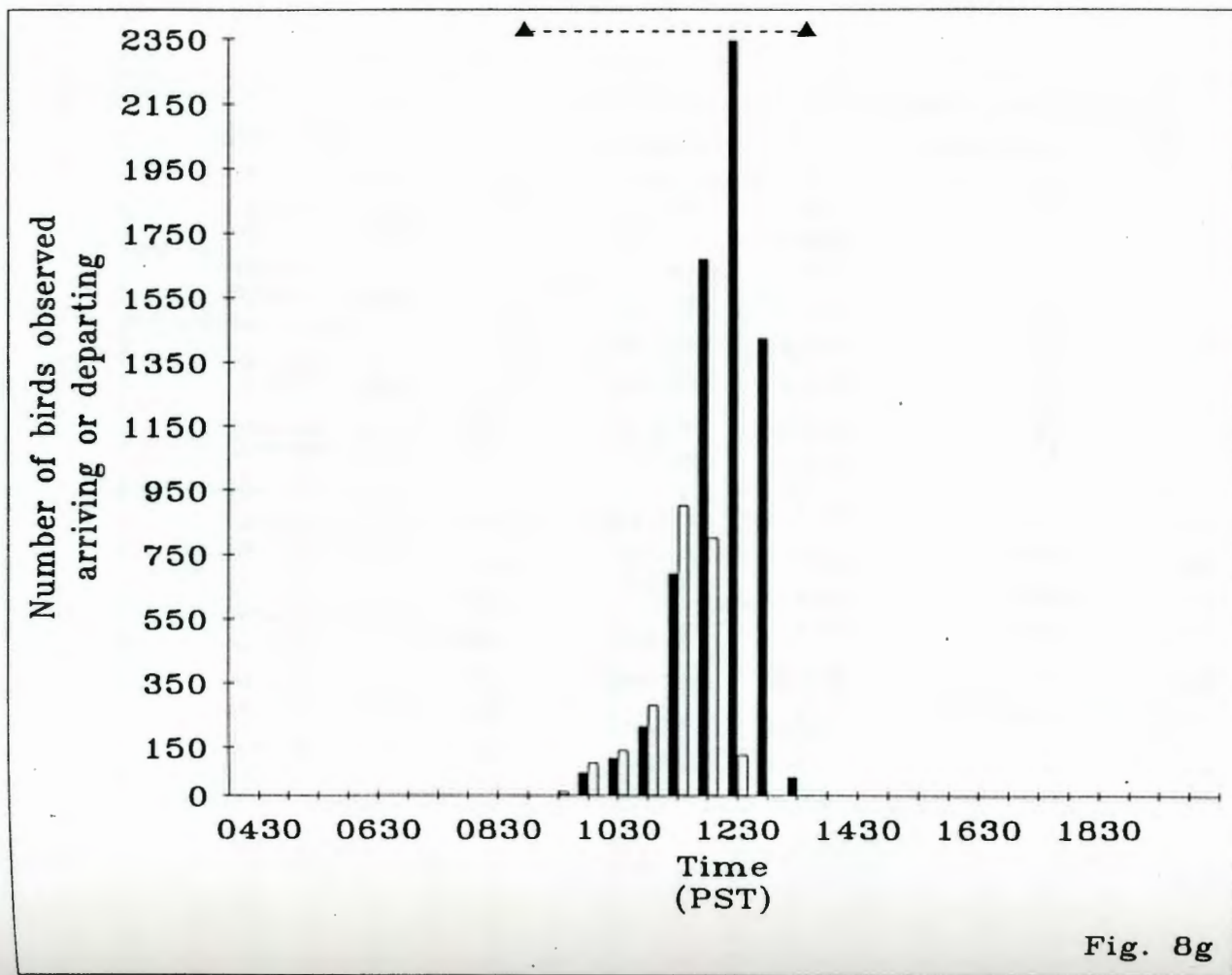


Fig. 8g

Table 5. Summary statistics on the number of pelicans observed arriving at and departing from Anaho Island during both the "peak" 1100-1300 hour period and throughout a given observation period.

Month	N	Mean	S.E.	Range	% of Total	
					Arrive	Depart
April	Arrive Low	100	20.08	4.02	1 - 287	46
	Arrive High	118	21.78	5.83	1 - 180	52
May	Depart Low	408	0.8	0.91	1 - 62	32
	Depart High	107	10.78	2.87	1 - 140	40
June	Arrive Low	116	21.88	4.40	1 - 470	47
	Arrive High	144	19.07	2.08	1 - 290	53
July	Depart Low	283	8.20	0.29	1 - 45	30
	Depart High	52	12.88	2.28	1 - 88	10
Total	Arrive Low	591	21.81	0.12	1 - 470	61
	Arrive High	126	20.25	4.04	1 - 260	39
Total	Depart Low	781	7.97	0.85	1 - 130	53
	Depart High	201	23.6	0.16	1 - 280	47
Total	Arrive Low	73	50.78	15.23	1 - 89	37
	Arrive High	88	24.98	4.99	1 - 260	43
Total	Depart Low	336	10.55	2.20	1 - 450	38
	Depart High	4	14.00	4.88	1 - 47	1

Month		N	Mean	S.E.	Range	% of Total birds seen in month
April	Arrive low	103	20.06	4.63	1 - 297	45
	Arrive high	115	21.76	3.23	1 - 180	55
	Depart low	406	5.3	0.31	1 - 52	52
	Depart High	107	18.72	2.27	1 - 140	48
May	Arrive low	116	21.93	4.40	1 - 475	47
	Arrive high	144	19.67	2.29	1 - 250	53
	Depart low	563	6.30	0.29	1 - 43	90
	Depart high	32	12.88	2.25	1 - 68	10
June	Arrive low	281	21.21	3.13	1 - 470	61
	Arrive high	129	29.35	4.64	1 - 360	39
	Depart low	731	7.97	0.55	1 - 130	53
	Depart high	281	53.6	5.16	1 - 250	47
July	Arrive low	63	59.73	15.23	1 - 69	57
	Arrive high	86	24.92	4.99	1 - 260	43
	Depart low	338	19.53	2.20	1 - 450	99
	Depart high	4	14.00	4.99	1 - 47	1



area would be to the pelicans' advantage.

#### PREY SPECIES AND FOOD REQUIREMENTS

As shown in Table 1 there is good agreement between the results of regurgitate analysis presented in this study and previous work extending over 60 years. My estimate of 1199.9 g of fish/pelican/day is noticeably lower than Hall's (1925) estimate of 1828.5 g./adult or near-fledgling/day. Unfortunately Hall does not include a full account of the method used to arrive at his estimate and I am unable to fully account for the difference. It should be noted however that Hall was on the colony no later than August 3, whereas my collections were done on August 12 after the great majority of the pelicans had departed. Assuming that young birds are fed once a day (Anderson 1982) and that both parents participate in feeding (Hall 1925), and that adult birds require at least as much food as fledglings, an adult pelican must capture somewhere between 9 and 20 138 g fish or the equivalent per day during the last month of the breeding season.

It seemed possible that some birds might attempt to reduce the number of captures required per day by taking a few large rather than many small fish. Although the negative slope of the regression of number of fish fed/weight of individual fish is consistent with a capture minimization strategy, the small r-squared value suggests that the pelicans may be opportunists, taking as many fish as possible during a feeding bout regardless of the size

of prey items. That capture of larger fish may on occasion be in vain is shown by the mummified remains of extremely large (480-500 mm length) carp found abandoned in the breeding colonies after the pelicans have departed. The location of these carcasses makes it extremely unlikely that they were transported by predators other than pelicans. Anaho Island is closed to the general public, thus eliminating human fishermen as a probable source of fish remains.

Applying the lengths of the mummified fish carcasses to a regression curve based on the known weights and lengths of carp captured at the Stillwater Marshes produces estimated weights of 1690 to 2003 g for these fish. While it is hard to imagine even a large adult pelican capturing so monstrous a fish, Koonz (1981) reports that pelicans in Saskatchewan have been known to feed on whole fish and fish scraps left by sportsmen. Bowhunting for carp is a popular sport in the Lahontan Basin and hunters discard all but the largest fish along the edges of sloughs in the Stillwater Marshes. It is possible that a foraging pelican might come across a dead or dying carp and attempt to bring it back to the colony. Although pelicans were frequently seen feeding near piles of abandoned carp scavenging behavior was never observed.

#### FORAGING LOCATIONS

Vigg (1978, 1981) has shown that carp are in low abundance at Pyramid Lake. During the first half of the



pelicans' breeding season (February to June), chub are concentrated in the deep waters of the lake. The fish move to the surface and shallows in numbers only during the summer and Autumn (Kennedy 1978, Kennedy and Kucera 1978, Vigg 1978). Because the pelicans' preferred food source at Pyramid Lake is largely inaccessible for the first half of the breeding season the birds must look elsewhere for their food supply.

Water depths over much of the Stillwater Management Area and Carson/Humboldt Sinks were under 3 meters for the bulk of the study. Flooding of management impoundment areas and the subsequent erosion of levees and shorelines produced a series of large shallow lakes with gently shelving borders suitable for fish herding.

The coincidental increase in the pelican population of Anaho Island in Pyramid Lake (Anderson, in prep.) may be explained in part by this increase in food availability. The importance of food availability in pelican colony establishment and regulation is discussed by Brown and Urban (1969), Tait et al. (1978) and Smith et al. (1984).

As the water levels within the Lahontan Basin declined to pre-flood levels large numbers of fish were trapped and concentrated in isolated pools along the edge of the Humboldt River and Carson Sinks. These fish proved relatively easy to capture, and this concentration of food provides a possible cause of pelican overwintering in the Sinks during 1986-87.



Honey Lake, Lassen County, California has been identified as a historical foraging area for pelicans breeding at Pyramid Lake (Knopf and Kennedy 1980). Few pelicans were observed at this site during a total of 5 visits from April through August. Although this area may serve as a stop-over for birds moving between the Lahontan and Klamath River Basins it appears to be of only minor importance in the pelicans' foraging ecology at present. It should be noted however that the highly variable nature of water levels within the Great Basin region may radically affect available foraging areas. Because the area has supported a pelican colony in the past Honey Lake must be regarded as an important site in any long-term planning for pelican management.

#### FORAGING BEHAVIOR

Both of the behaviors described in Figs. 3 and 4 are consistent with the original reports of cooperative herding. Based on the simulations using moving decoys it is possible that fish are reluctant to break back beneath an oncoming line of predators. Instead of running the risk of a particularly deep-reaching pelican, the fish move away even when this brings them into increasingly shallow water.

Hamilton (1971) has proposed a mechanism whereby individual prey might concentrate as a response to the presence of a predator. Under the "Selfish Herd" hypothesis prey benefit by placing the maximum number of

other prey individuals between themselves and the oncoming predator. Movement away from the predator strike-horizon inevitably exposes new prey who will in turn attempt to interpose other of their fellows between themselves and the predator. The result is a "zero-sum game" in which the prey group as a whole may be more susceptible to the predator than if each individual simply scattered on its own.

More recently Gottmark et al. (1986) have shown that flocks of gulls are more successful at catching fish than single birds apparently because multiple threats serve to confuse the prey and disrupt schooling patterns. Guillet and Crowe (1983) state that fish in turbid water are more likely to panic and do not display coordinated escape responses.

The simulations of pelican foraging behavior conducted with decoys show evidence for an effective form of fish herding, but they do not provide much information on the precise mechanisms used by the fish to detect the oncoming pelicans. Water in the slough was quite turbid, similar to that throughout the Stillwater region. Guillet and Crowe (1983) suggest that turbid water is potentially beneficial to foraging pelicans since it reduces visual cues to the prey and forces greater reliance on their lateral line systems to detect predators. All three trials were run in the late afternoon when the shadows of the decoys fell behind the advancing line. The movement



of shade patterns produced by the decoys may frighten fish behind the advancing flock, and this fear may be communicated to the leaders. In addition the fish may have detected the turbulence patterns of the decoys although the decoys had a considerably shallower draft than real pelicans and create less turbulence when moving than do live birds, especially when the thrust generated by webbed feet is taken into account.

The response of fish to pelicans feeding in the deeper waters of Pyramid Lake is something of a mystery. Water clarity in the lake is much higher than that in the Sinks and it would seem relatively easy for fish to dive below maximal pelican reach as soon as a feeding flock was detected.

Large flocks of pelicans were frequently observed foraging in water over 20 m deep from June through August. The bulk of these birds engaged in variations of the "surround and strike" technique depicted in Fig. 3. The apparent failure of fish to avoid the pelicans by diving may be the result of some form of "Selfish Herd" behavior.

Other groups of pelicans and cormorants were seen herding fish in to shore (Fig. 2) along the south and west sides of Pyramid Lake. Chub use these areas as spawning grounds (Vigg, 1978) so an initial concentration of potential prey occurs coincidental with the pelicans' switch from commuting to Stillwater to foraging at the lake.



## GROUP SIZE AND FORAGING SUCCESS

I hypothesize that the effects of herding behavior are a function of the size of the group doing the herding. With too few birds the fish would be able to escape around the edges of the herding group, with too many herders a combination of mutual interference and greater division of prey items would reduce individual take.

Evidence for this hypothesis is incomplete at best. Members of groups of two through six birds did catch significantly more fish than did birds foraging alone. The small sample size available for larger groups makes it impossible to determine whether there was an eventual point of diminishing returns as group size increased further. It may be that a combination of cooperative herding and social facilitation results in all groups of pelicans doing better than single individuals, but this cannot be stated categorically at this time.

In addition to any increase in foraging success it has been suggested by several authors (Krebs 1974, Caraco et al. 1980, Rubenstein 1982) that group foraging may be a way of minimizing the variance in food intake by individuals. As shown in Fig. 5 there is a marked reduction in variance between single birds and members of flocks. Again however questions of sample size prevent the establishment or rejection of any clear trend within flocks of different sizes.

## STRIKE ACTIVITY

Near simultaneity in striking is a logical outcome of group feeding where position within the flock does not give an individual advantage. A bird striking too soon runs the risk of scaring off prey that may be only partially aware of the pelicans' location. A bird striking too late in a large group may eliminate itself from competition for prey items. In cases where fish are being driven into shallow water, the longer the flock delays striking, the easier it will be to catch the fish. At the same time however, once one bird begins to strike the other flock members have little choice but to join in.

Because a striking pelican is presumably unable to both strike and scan its surroundings for prey or predators, and because striking takes time, there should be an upper limit to the number of strikes performed per bird per unit of time. This limiting function is exhibited in Fig. 6, with the maximum number of strikes per minute falling between 6 and 8.

If the pelicans are taking their cue to strike from each other rather than from some degree of concentration or behavior on the part of the prey, then I expected that the proportion of "early strikers", birds willing to strike before the prey had been driven into an easily accessible location, would increase as group size increased. As a result of this increase in premature striking, I hypothesized that strike efficiency, or the



number of fish caught per strike, would decrease with group size. Single birds that might strike only in response to prey availability would capture the most fish per strike, whereas those foraging in groups might strike to pre-empt other group members or in response to a perceived intent to pre-empt on the part of another group member, and hence would catch fewer fish per strike.

A marked decline in strike efficiency is apparent in Fig. 7 and is consistent with the idea of an increase in the probability of a premature strike with increased flock size. Once again the small sample sizes available for flocks of 7 or more pelicans makes it impossible to assess differences among these larger groups.

#### FORAGING GROUP FORMATION

The results of the decoy experiments showed that pelicans are attracted to an area by the presence of other pelicans. Although it is tempting to suggest further that smaller groups were more attractive than larger ones the small sample of tests conducted makes such a suggestion premature. The failure of the control (goose) decoys to attract any pelicans rules out site characteristics alone as an attractant.

Observed success on the part of an individual or group does not appear to be a major source of attraction. The decoys obviously catch no fish, yet pelicans would land in their immediate vicinity, and often remain near them until approached by an observer.



## PIRACY

Piracy or kleptoparasitism has been reported in a number of bird species (Brockman and Barnard 1979). Generally the kleptoparasite is a smaller, more agile bird (but see Barnard and Thompson 1985) that takes advantage of its victim's slower speed, or inability to swallow a food item rapidly. For example, members of the Pelecaniformes must surface to swallow prey items and are vulnerable to attacks by gulls (Bent 1921, Baldwin 1946 Schnell et al. 1983, Carroll and Cramer 1985).

Large birds rarely use their superior size and strength to obtain prey forcibly from a smaller individual. The only previously published reference to this activity was by Skinner (1917) who mentions instances of kleptoparasitism by White Pelicans on "fish ducks" feeding along the Yellowstone River.

The importance of piracy or kleptoparasitism in either the pelicans' or cormorants' biology is probably minimal. Although the majority of observed attacks by pelicans on cormorants resulted in either a pelican taking the fish or the fish being lost to all birds, the probability of an individual cormorant losing even one fish is very low.

A more interesting question is perhaps that given the small number of fish obtained by the pirates, why does the behavior continue at all? Pelicans at Pyramid Lake that are successful at kleptoparasitism make available a resource relatively close to the nest site (the Truckee

River delta is only 15 km from Anaho Island, whereas the Humboldt and Carson sinks are over 100 km away). At the same time however, kleptoparasites are investing both time and energy that could be spent in foraging for themselves. In addition kleptoparasites run the risk of injury both from their intended victims and from other pelicans.

Throughout the season large numbers of pelicans congregate along the sand bars at the mouth of the Truckee River. Knopf (pers. comm.) has informed me that he has correlated these assemblages with patterns of bad weather over the Carson Sinks. A few pelicans also engage in apparent foraging activity along the lower stretches of the Truckee River as early as the beginning of April. It is likely that the primary reason that the pelicans are in the vicinity of foraging cormorants at the beginning of the season is that the cormorants are feeding near pelican assembly grounds. Kleptoparasitism may thus be an opportunistic response to a given situation rather than a major facet of the pelicans' life history. In any case the impact of the pelicans upon the cormorants is insufficient to make the cormorants change breeding sites or foraging areas.

Hall (1940) has shown that pelicans and cormorants have bred in close proximity within the Lahontan Basin since at least the Pleistocene and cormorants and pelicans overlap in geographic distribution throughout their range.

Kleptoparasitism is not limited to the Pyramid Lake



populations. Hart (pers. comm.) has seen numerous instances of kleptoparasitism by pelicans on cormorants at the American Falls reservoir in Idaho. It is unclear however what effect if any the pelicans in Idaho are having on the cormorant population.

#### NIGHT FISHING

Hall (1925) makes a brief reference to hearing sounds that he assumed were caused by pelicans feeding at Pyramid Lake "into the early hours of the night". Low et al. (1950), working at the Great Salt Lake in Utah, state that "Most feeding activities take place at night or early morning, although there have been notable exceptions to this."

The low levels of prey capture reported here for daylight feeding suggest that the pelicans must be doing a sizable proportion of their feeding at night. Vigg (1981) has shown that chub are found in the upper levels of the water column and hence are available to the pelicans primarily during the hours of darkness. McMahon (pers. comm.) states that she has observed large numbers of pelicans in Manitoba feeding at night. Logistic difficulties prevented me from obtaining accurate estimates of the proportion of birds that actually do feed at night, but clearly this is an area in need of examination.

Because at least for pelicans within the Lahontan Basin night fishing involves a shift in preferred location



of foraging areas, estimates of habitat importance based upon aerial surveys during daylight hours may be seriously in error. Ground-truthing both by day and by night may be the only way to obtain an accurate picture of habitat use.

#### FLIGHT FLOCK SIZE AND TIMING OF ARRIVALS AND DEPARTURES

Determination of adequate criteria that define a flock may be difficult. Bayer (1982) states that "birds departing more than 1 min apart are not a flock". While this statement is intuitively appealing it is important to recognize that the definition of a "flock" is situationally dependent and may vary according to functional properties of the individuals involved. It would be patently foolish to suggest that the members of a "flock" of birds separated by gaps of several kilometers were having an effect on each other's aerodynamic performance. On the other hand individuals might remain in visual contact with each other over extensive distances, thus forming a functional "flock" in the leader-follower sense.

Heppner (1974) defines a "flight flock" as "a group of flying birds, coordinated in one or more of the following parameters of flight: turning, spacing, velocity, and flight direction of individual birds, and time of takeoff and landing." When visibility potentially extends over many kilometers birds acting at a distance may affect one or more of these parameters.

White Pelicans flock in the traditional sense in that

they move from place to place in discrete units of two to several hundred birds. Because pelicans nest in large colonies and typically occupy open habitat (Bent 1924) the possibility for information exchange and following behavior between widely separated groups is high.

Armstrong (1971) has proposed that the evolution of white plumage among many seabirds has been the result of selection on ease of visibility of flock members. More recently O'Malley and Evans (1982a) have suggested that the "flash" created by White Pelicans banking in thermals may aid in attracting additional birds over a wide area. Leaders may thus be affecting followers at distances greater than that supposed by a human observer. Heppner's (1974) definition of a flock when applied to other than aerodynamic characteristics is thus probably quite conservative. The failure of time series analysis to reveal any consistent pattern in arrivals and departures suggests that either no following behavior is occurring or the birds are cueing in on more extended visual flocks.

Previous observations suggested that pelicans flying to foraging areas near the mouth of the Truckee River or along the western shore of the lake flew low, close to the water surface. Pelicans traveling to foraging sites at a distance from the lake often soared in thermals over Anaho Island before departing at high altitudes. Similar behavior was observed at the foraging sites themselves. Because thermal soaring and low flight represent two



discrete forms of behavior I present data for each separately.

Observations of birds foraging at the mouth of the Truckee River and at the South East end of Pyramid Lake suggest that it is unlikely that birds that had initially gained altitude over the island would descend to feed at the river. Thermal soaring, although energy efficient (Pennycuick 1972), is costly in terms of time, and birds commuting to and from the South end of the lake appeared to be taking advantage of a ground-effect similar to that observed in Skimmers (Rhynchops niger) (Withers et al. 1977) rather than soaring to a high altitude only to descend after covering a short linear distance.

On several occasions I saw large flocks of pelicans soaring over the sand dunes at the South East end of the lake. In each case these flocks subsequently departed to the South, in the direction of the Carson Sinks. Thus birds that may have traveled this far near the surface were clearly opting to continue their journey at a higher altitude.

The continued arrival and departure of thermal flocks through July of 1985 (best shown by the values of % total for high and low arrivals in Table 4) suggests that a large number of pelicans continued to feed in the Carson Sinks even after fish became available at Pyramid Lake. Reports from the Stillwater Refuge confirmed that the birds were taking advantage of fish trapped in drying



pools along the Humboldt River and within the Sinks.

The distribution of flock sizes with many more small flocks than large ones is similar to that reported by O'Malley and Evans (1982b) for pelicans breeding in Manitoba. It should be noted however that the majority of birds at Pyramid Lake both arrived and departed in large flocks. Flocks departing at high altitudes were significantly larger than their low counterparts during April, May, and June. This is consistent with predictions that birds traveling some distance to a foraging area would have greater need of leaders than those simply commuting to areas within eyeshot of the colony. Slow spiraling in thermals also increases the amount of time available to would-be members to join the flock.

Mean flock sizes at Pyramid Lake are much larger than those in Manitoba (a mean of 4.7 for O'Malley and Evans' "thermal flocks" versus means of 12.8 to 45.3 for my "high departures") and more varied (O'Malley and Evans report Standard Errors of .06 to .28 compared with my .28 to 15.2). Although differences in identification are certainly possible, pelican flocks are sufficiently discrete units that it is unlikely that this form of sampling error could completely explain the difference. It seems more likely that the overall differences in colony size between the Manitoba colonies (1,257 nests, O'Malley 1980, = < 3000 birds) and Pyramid Lake (approx. 7000 birds) are reflected in flight flock sizes. The

change in flock size at Pyramid Lake between April and July may also be a reflection of the increase in the number of birds commuting to feeding grounds.

O'Malley and Evans state that the Manitoba birds are breeding in "a lake with few fish" and that "Round-trip flight distances between the colonies and these (feeding) sites ranged from 80 to 100 km." Whereas the latter values are equivalent for Nevada pelicans feeding in the Carson Sinks and Stillwater Marshes, birds breeding at Pyramid Lake have the lake itself as a prime feeding area during the last half of the season. Large numbers of birds congregate on sand bars at the mouth of the Truckee River 16 km south of the breeding colony, and may engage in communal feeding near these loafing areas. It is these aggregations that form the basis for many of the flocks returning to the island. Possibly the Manitoba birds lack suitable assembly areas between their feeding sites and colonies and flocks become more diffuse as the birds move over the greater distances.

The increase in total numbers of birds seen arriving and departing to and from Anaho Island as the season progressed is due to both members of a pair of breeding birds being freed from incubation duties by the development of the young. A similar increase in total birds observed has been reported by O'Malley and Evans (1982a).

Somewhat surprisingly the timing of peak arrivals and



departures did not shift with either the advancing season or the increased use of Pyramid Lake as a foraging area. Similar patterns of arrivals and departures are reported for American White Pelicans in Manitoba by O'Malley and Evans (1982a) and in Pelecanus onocrotalus, which also feeds at some distance from breeding colonies, by Brown and Urban (1969). This suggests the possibility that a variety of factors may be influencing the pelicans' behavior.

One possible explanation for the observed distribution of arrivals and departures lies in the interplay between the adults' foraging behavior and the behavior of pre-fledging young. If the greatest part of the pelicans' foraging is done at night or in the early morning, departure times from the feeding areas would begin within the period 0800-1100. Ross (1933) estimated the level flight speed of the White Pelican at 32 mph (51 kph), with an error of 1 mph. The Stillwater Marshes are approximately 100 km from the colony, thus a two to three hour flight time from the feeding grounds puts the returning birds over Anaho within the peak 1100-1300 period.

If young are fed at 1200 hrs there is plenty of time for the adults to return from the island to the feeding areas for afternoon and evening fishing. Guillet and Crowe (1983) report that Carp (Cyprinus carpio) move into shallow water as the water temperature increases during the day. The "evening rise" exhibited by many fish



species has been known to generations of human fishermen and I suggest that the pelicans may be tailoring their commute times to take advantage of this phenomenon.

As the season progresses an increasing number of adult birds can be seen fishing in Pyramid Lake, often within 0.5 km of Anaho Island. Vigg (1978) has demonstrated that chub are most common in the upper portions of the water column from approximately 1600 to 0800 hours. Thus, although pelicans feeding at the lake are not constrained by commute time, there is still an advantage to conducting non-feeding business during the middle portion of the day.

Once the young pelicans develop a cover of protective feathers and are large enough to defend themselves from would-be predators both parents engage in feeding activity away from the colony, returning only to provision their young. The young birds wander around the island either singly or in pods of several birds often congregating near the island's shoreline which is up to 1 km from nesting areas. Feeding of young takes place on the original nest site. Adult birds feed only their own young (Hall 1925). I observed adults that were not greeted by a fledgling at the nest scrape depart from the island following a brief wait.

Young pelicans return to the nesting areas during the middle of the day, gathering in dense clusters in any shaded spot near the nest scrapes. Adult pelicans

arriving high over the island dive on the colonies at steep angles, producing a pronounced whistling tone that can be heard at some distance. As the adults begin to arrive young birds at a distance from the nesting areas hurry back to the colonies to receive nourishment.

If adult arrivals at the colony were randomly distributed young pelicans would be unable to disperse far from their nest sites for fear of missing a day's feed. This daily wandering may be important for both muscle development and water balance. The young pelicans spend several hours a day running along "runways" away from the breeding areas flapping their wings in an apparent prelude to flight. Apart from the moisture in the food brought by the adults the only source of water available to the young is the lake, and dehydration in the intense desert heat is a real possibility. Adults would also benefit from having a set time of return to their offspring. Birds that had to search for chicks over the 300 hectare expanse of Anaho Island would reduce the amount of time that they had available for feeding.

The peak in arrivals between 1100 and 1300 hrs therefore may be a compromise between the need of the young birds for exercise and for water from the lake, and the need of the adults to minimize the amount of time spent at the colony and away from the foraging grounds.

#### THEORETICAL IMPLICATIONS AND CONCLUSIONS

The role of social behavior in foraging by birds has



been the subject of a number of theoretical and experimental studies (Ward and Zahavi 1973, Krebs 1974, Pulliam and Millikan 1982, Caldwell 1981, Barnard and Thompson 1985, Gotmark et al. 1986). A possible evolutionary pathway to cooperation has been proposed by Axelrod and Hamilton (1981) and discussed at some length by Axelrod (1984) and Maynard Smith (1982). Herding by pelicans lends itself to a somewhat modified form of the "Tit for Tat" model of cooperation in that the beneficiary of herding in any one group over the course of a given time interval appears to be randomly selected. While increasing flock sizes dilutes the benefit to the individual, colonial breeding and foraging over a limited area increases the probability that birds will re-encounter each other over the course of the season. Given sufficient iterations of a sequence in which the group herds and the individual captures, all individuals will ultimately benefit. Because the prey may be unavailable for all practical purposes until herding has occurred, the benefits of "defection" may not exist.

It could be argued that a possible alternate strategy to either fishing alone or participating in herding might be to wait outside of a herding group and then snatch prey items once they had been driven into the shallows. It is interesting to note that the only example of this form of "cheating" behavior that I observed was during herding sessions conducted at night, when it was presumably more



difficult to identify individuals.

Although a "cheat by night, cooperate by day" strategy is intuitively appealing from a rather venal perspective, closer examination suggests that it may be dangerously anthropocentric. Herding groups are frequently unsuccessful at maneuvering prey into a location suitable for capture. A would-be "cheater" unless it is circling over the herding group will have a poorer idea of the prey's location and might arrive too early or too late to take advantage of fish concentration. Time spent observing herding groups reduces time available for personal hunting. Given these disadvantages it is perhaps easier to see why cheating appears to be the exception rather than the rule.

In discussing cooperation in relation to pelican foraging behavior it is important to separate the phenomena of social facilitation (Thorpe 1956) in which individuals adapt their behavior to imitate successful foragers, and local enhancement (Hinde 1959) in which individuals obtain positional information on scattered prey patches by interacting with other foragers. Social facilitation may be the driving force behind some aspects of pelican foraging behavior. The synchronicity in striking observed in groups may be regarded as a form of social facilitation, but it should be evident that social facilitation alone cannot be regarded as "cooperative" behavior in the sense of an activity granting mutual

benefit to both parties.

Eltringham (pers. comm.) has suggested that there is no practical way to differentiate between the often passive "communal" behaviors involved in local enhancement and "cooperative" behavior in which a group of individuals actively perform some pattern of behavior that results in a mutual reduction of some cost and/or a mutual increase in some benefit. August (pers. comm.) has suggested that not resisting a would-be group member may be regarded as an active behavior and indicative of a form of cooperation.

New arrivals to a feeding group are certainly competitors and there is justification in expecting that they would be resisted unless they provided some benefit to group members. Although non-resistance is consistent with a cooperative advantage from increased group size it would also be indicated in cases where the cost of resistance is greater than that of increased competition. Knopf (1975) has pointed out that pelicans have the potential for doing severe damage to each other with their sharp bill edges. Quite apart from immediate physical injury the cost of increased vigilance and the time required for defense will reduce any benefit derived from a reduction in competition. Finally, there appears to be no ready way of distinguishing between the two hypotheses and I have an etymological difficulty in regarding a non-behavior as "active".



Local enhancement in the traditional sense certainly occurs in pelican foraging in that pelicans are drawn to specific sites by the presence of other foraging or apparently foraging pelicans. This point has been demonstrated by the decoy experiments. I suggest however that this behavior is relatively simple, may well be passive on the part of individuals already at the feeding site, and can hardly be regarded as "cooperative" in the sense outlined above.

In contrast to the more traditional forms of local enhancement, the active herding behavior discussed here in White Pelicans and found in some other vertebrates (Cormorants, Bartholomew 1942, Lions, Schaller 1972, (but see Packer, 1986) Mergansers, Emlen and Ambrose 1970, Wild Dogs, Kleiman and Eisenberg 1973, Grebes and Egrets, Leck 1971) is relatively complex, requires active participation by group members, and fulfills the requirements for true cooperation. As such, herding forms a distinct sub-set of local enhancement in which groups of foragers actually create or enhance food patches to the ultimate mutual benefit of all group members. Further examination of this phenomenon may provide useful insights into the development of complex social relationships among unrelated individuals.



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APPENDIX I

Withers, P.C. and P.L. Tinco. 1977. The significance of ground effect to the aerodynamic cost of flight and energetics of the Black Skimmer (*Rhynchops niger*). *J. Exp. Biol.* 70:13-26.

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## APPENDIX I

### Management implications of the study

The management implications of the study are fourfold. First of all the results of the regurgitate analysis (Table 1) demonstrate once again that at least at the height of the season the pelicans are taking an insignificant proportion of game-fish in their diet. The large numbers of Carp (Cyprinus carpio) removed from the Lahontan system by pelicans can only have a beneficial effect on other species of fish who would otherwise encounter increased competition or loss of fry as a result of the carps' feeding behavior.

Because of the high visibility of pelicans and their reputation as voracious fish-feeders I suggest that it is important to ensure that the sports-fishing public be made aware of the importance of pelicans in the Pyramid Lake ecosystem. Many of the fishermen that I spoke to during the course of my study expressed interest in the birds and a seemingly sincere concern for their well-being. The history of the colony has been marked however by periods of deliberate disturbance by individual humans under the mistaken impression that the pelicans were responsible for the decline in the Pyramid Lake fishery. Inclusion of

information on the pelicans' role in the fishery in the tourist literature available at the entrance to the reservation might reduce the possibility of deliberate destruction.

The second point to emerge from this study is the extremely dynamic and yet inherently fragile nature of pelican foraging behavior and habitat requirements. Cooperative foraging appears to be a behavioral adaptation that offsets the White Pelicans' inability or reluctance to fully submerge. Although there are reports (cited in the first portion of this dissertation) that White Pelicans do occasionally dive, diving is a relatively rare phenomenon. Given that the birds are restricted to fish in the upper levels of the water column cooperative fish-herding is one mechanism of ensuring access to food. Pelican flocks observed departing from Anaho Island tend to be much larger than those that eventually engage in fishing (Fig. 4 and Table 4). Much of the birds' time away from the colony is spent on loafing grounds in the immediate vicinity of foraging sites, and it is here that the feeding flocks form. It is critically important that these loafing areas are preserved in any management scheme.

For much of this study increased water levels in the Lahontan drainage system had resulted in widespread flooding. Although this has had a severe impact on many refuge facilities in the Stillwater Wildlife Management

Area it may have been extremely beneficial for the pelicans. Partial submergence of many of the levees near the Carson Sinks created numerous low mud islands that were ideally suited for loafing spots. In addition to providing additional loafing areas the flooding created a number of large shallow lakes whose shelving shorelines were well suited for fish herding.

The constant change in the amount of water entering the Lahontan Basin makes the designation of specific sites "pelican habitat" at best misleading and at worst dangerous. Pelicans appear to prefer areas with water less than 2 m deep containing partially submerged vegetation and a gradual sloping contour to the bottom. Limits on human traffic through foraging and loafing areas is desirable. Pelicans frequently abandoned feeding sessions within the Stillwater Refuge upon the approach of a car or human foot traffic. It should be noted however that I observed pelicans at Eagle Lake, Lassen County California feeding near an active boating dock.

Pelicans are true opportunists. The examples of kleptoparasitism cited in the text show clearly that when prey is unavailable by conventional or cooperative means the pelicans will resort to piracy. It seems unlikely however that the levels of kleptoparasitism that I witnessed are having an adverse effect on the cormorant population as a whole. Cormorants and pelicans breed together at most major colonies, and fossil evidence



indicates that this overlap has been going on since at least the Pleistocene.

Refuge personnel should be encouraged to establish and maintain graded sides to impoundments as post-flood repairs continue. The pelicans' use of sloughs as fish traps can be enhanced by elevating culvert mouths slightly above the stream-bed to slow fish passage upstream.

Because pelican use of the Stillwater region is greatest at the beginning and end of the season it would be advisable to regulate water levels in a number of impoundments such that appropriate water depths for foraging are maintained. The critical period of pelican use extends from mid February to May and mid July through September.

As the flood waters continue to recede there will be a gradual reduction in available foraging habitat. Initially we may expect this to have a positive effect on pelican numbers as schools of fish become concentrated in drying pools. Reports from the Fallon region during the Winter of 1986-1987 indicate that a number of pelicans may have over-wintered in the basin, presumably in part to take advantage of the flush of food.

An inherent danger to this concentration of food is that it will also lead to a concentration of waterfowl, and this in turn may lead to an eventual increase in mortality due to predation and disease. Newspaper accounts of a bird die-off in the Carson Sinks have

suggested that avian cholera and botulism may be taking a toll of the pelican population. Prompt removal of dead and dying fish and bird carcasses when practical may reduce the possibilities of an epidemic.

A further source of concern engendered by the declining water-levels in the Basin is the inevitable concentration of pesticide residues, industrial wastes, and heavy metals that are the inevitable by-products of the use of much of the terminal stage of the Carson/Truckee/Humboldt watersheds as a dumping ground. Continual monitoring of levels of these toxins is vitally important to the health of the entire Lahontan ecosystem. Dead birds should be analyzed for the presence of pesticides, and a program of water-quality monitoring throughout the Basin should be encouraged.

As fish populations decline with the receding water we may expect a corresponding decline in the number of birds breeding at Anaho. Offsetting this assumption however is the fact that the Anaho colony appeared to be increasing in size prior to the increase in foraging habitat. It is likely that a number of factors may be affecting the western population of White Pelicans as a whole. Close monitoring of breeding success at a number of colonies would provide much useful information as to the general trend.

The third point relating directly to management programs is the importance of nocturnal feeding to overall

pelican foraging success. In view of the low capture rates recorded for pelicans feeding during daylight hours it seems certain that a sizable proportion of the birds total catch must come at night. Nocturnally foraging pelicans made extensive use of the creeks and sloughs in the Stillwater region, in some cases feeding near roadways that are in heavy use by humans during daylight hours. Aerial surveys of pelican habitat use or studies based on ground visits during daylight hours would tend to underestimate the importance of these areas as active foraging sites. I cannot emphasize too much the need for frequent nocturnal ground-truthing.

The final point emerging from the study, and one that deals directly with recent developments in the Stillwater region, relates to the significance of pelican flocking behavior on air-traffic throughout the basin. The selection of Dixie Valley for a naval Strike Warfare Center and the increasing use of the Fallon Naval Air Station will inevitably result in an increase in the number of aircraft passing through airspace frequented by pelicans. Peak pelican flight periods are both regular and predictable. A collision between a jet and a flock of pelicans would have serious consequences for all concerned. I strongly advise that flight operations over the Carson Sinks/Pyramid Lake region be curtailed as much as possible and certainly restricted to periods when pelicans are unlikely to be flocking. I observed military



aircraft passing low over the Stillwater Wildlife Refuge on a number of occasions during the course of my studies, and in three separate instances—once along the Humboldt River and twice at Pyramid Lake—was "buzzed" by attack aircraft engaged in simulated strafing runs. Given the large number of pelicans flying through these areas this activity amounts to an accident waiting to happen.