

PRODUCTIVITY OF OSPREYS IN THE GULF OF CALIFORNIA

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The decrease in numbers of Ospreys (*Pandion haliaetus*) that coincided with the use of chlorinated hydrocarbon pesticides aroused interest in determining their population sizes and productivity in North America (e.g., Henny and Wight 1969, Henny and Ogden 1970, Henny 1975, Henny and Noltemeier 1975, Wiemeyer et al. 1975, Roberts and Lind 1977). Many populations along the east coast of the United States have been monitored for the past 15 years (Henny and Ogden 1970). These populations consist of migratory Ospreys that spend the winter in Central and South America (Henny and Van Velzen 1972).

Within North America, non-migratory populations of Ospreys are currently found in southern Florida (Ogden 1975, 1977) and in Baja California, along the coast of Sonora, and throughout the Gulf of California islands, Mexico (Friedman et al. 1950). Prior to 1930, the Baja California population extended into southern California (Kenyon 1947, Jones and Diamond 1976). A recent aerial survey of the Baja California and Gulf of California regions resulted in an estimated population of 810 ± 55 pairs of Ospreys (Henny and Anderson 1979). This paper reports the results of an investigation of the phenology of reproduction and productivity of a portion of this population during 1977 and 1978.

STUDY AREA AND METHODS

The study area encompassed a cluster of 16 small islands in the Bahía de los Angeles ($28^{\circ}57'N$, $113^{\circ}33'W$) on the eastern coastline of Baja California Norte, Mexico. In 1977 and 1978, Ospreys nested on 11 of these islands at the tops of razorback cliffs and rock pinnacles or on rock out-crops that characterized the shorelines. Plant life comprised sparse Sonoran Desert vegetation (Shreve and Wiggins 1964, Coyle and Roberts 1975) and was physiognomically dominated by Cactaceae.

Fieldwork was conducted between 19 January and 7 June and 20 August-16 September 1977, and between 13 January and 6 June 1978. Censuses of Ospreys and their nests were undertaken at approximately 4-5-week intervals. Censuses were conducted by boat along shorelines on clear and calm days when conditions were optimal for locating Ospreys and climbing to their nests. Five breeding season censuses were made in 1977 and four in 1978. Each census took approximately 2 days. Census visits comprised the minimal number of times that any nest was visited; approximately 40% of occupied nests were visited at least once in 10 days in the course of intensive behavioral observations.

Occupancy of nest and stage of the breeding cycle were determined by observations of nest contents and the behavior of adult Ospreys in attendance. During each census, sizes of clutches and/or broods, nest defense by adults, nest construction and size, and the presence and type of food remains were recorded for each accessible nest. Hatching success,

mortality of nestlings, and fledging success were calculated from data obtained during all visits. In some cases, hatching dates could be back-dated for nestlings that were less than 1 week of age by comparison of developmental characteristics with known age nestlings.

Some adult Ospreys could be individually recognized by distinctive head plumage patterns, United States Fish and Wildlife Service bands placed on them as nestlings prior to this study by D. W. Anderson (N = 3), by colored polyvinyl chloride, wrap-around leg bands applied during this study (N = 3), or by combinations thereof. The sex of each adult Osprey was determined by size, breast coloration (Macnamara 1977), and behavior. Young Ospreys were initially identified by ink-marking their tarsi and subsequently by individual colored leg band combinations.

Standard Chi-square analyses of a 2×2 contingency table (uncorrected χ^2 , see Remington and Schork 1970:271) were used to compare proportions except in cases of small sample sizes wherein I used Fisher's Exact Probability test (Sokal and Rohlf 1969:595). A series of "t-tests for the approximate equality of means assuming unequal variances" (Sokal and Rohlf 1969:374) were used to compare mean clutch-sizes of Ospreys for geographical regions of North America.

RESULTS AND DISCUSSION

Nest structures.—Sixty-five and 68 nests were located in 1977 and 1978, respectively. Structural elements of nests included driftwood, woody parts of cardon cactus (*Pachycereus pringlei*), ocotillo (*Fouquieria* sp.), and skulls and long-bones of Brown Pelicans (*Pelecanus occidentalis*). Aquatic vegetation, terrestrial vines, and beach-cast debris were used in both construction and lining of nests.

Nest use and persistence.—Most nests within the study area were known from previous censuses to be at least 7 years old at the onset of this study (D. W. Anderson, pers. comm.). Nests may be used for many consecutive years or may be abandoned for 1 or more years (D. W. Anderson, unpubl.). Nests are durable and survive high winds and occasional storms characteristic of the Gulf of California; thus, large numbers of unoccupied nests do not necessarily indicate recent, overall declines in the size of the breeding population in this area.

There were nine nest-site changes between 1977 and 1978. Three of the nine changes involved newly constructed nest structures, the remaining six were present but unused in 1977. All nest changes were associated with the abandonment of a nearby nest. Each of the changes (N = 3 pairs) wherein the adult Ospreys were recognizable involved a new pair member in 1978 (at one there was a new male and at each of the other two there was a new female). Seven recognizable pairs used the same nests in each of the 2 years. This suggests that nest-site tenacity and pair-bond maintenance are in some way positively related. Fernandez and Fernandez (1977) concluded that Ospreys they observed were faithful to territory, nest, and mate, in that order.

Forty-eight (1977, N = 65)–51% (1978, N = 68) of the nests were either

unused or were used as "alternate nests" (Postupalsky 1977) for feeding and as perches by pairs of Osprey that laid their eggs in, or spent most of their time at, another nest. Alternate nests were used throughout the breeding season by both successful and unsuccessful breeders.

Residency and nest use in the non-breeding season.—Censuses during the post-breeding season in late August and early September 1977 revealed approximately 12 Ospreys. These Ospreys perched and fed solitarily (not as members of pairs), were not closely associated with nest structures, and exhibited only sporadic alarm vocalizations when I visited nests. Intraspecific social interactions among Ospreys that were initiated during the breeding season by vocal responses to my nest visits facilitated observation; thus, the 12 Ospreys I counted can be assumed to be the minimum number in residence.

Breeding chronology.—Breeding chronology of Ospreys in the Gulf of California was characterized by a high degree of asynchrony. The onset of egg-laying ranged approximately 9–10 weeks from early January to early March during both years (Table 1). The mean incubation period (first-egg date to first-hatch date) for six clutches was 38.3 ± 3.2 days. Minimum lengths of incubation for 10 additional clutches ranged from 32–42 days ($\bar{x} = 37.9 \pm 3.1$). Kenyon (1947) and Jehl (1977) reported that all stages of the breeding chronology could be found concurrently in Ospreys nesting on the west coast of Baja California during April and March, respectively. Resident Ospreys in southern Florida exhibit a similarly protracted breeding season (Ogden 1977). In more northern, migratory populations all eggs are usually laid within a 3-week period (Ames 1964, Garber 1972, Kennedy 1977, Parnell and Walton 1977, Prevost et al. 1978).

Hatching began in early February in 1977 and in late February in 1978, and extended through late April in both years (8–9 weeks) (Table 1). Mean nestling period (hatch to first sustained flight) was 62.5 ± 4.9 days for 10 broods. Minimum nestling periods for six additional broods ranged from 52–76 days. The variation in incubation and in nestling periods is responsible, in part, for the changing distribution of numbers of nests with young hatching and fledging over the season in Table 1. Fledging first occurred during early April in 1977 and in late April in 1978. In both years all nestlings fledged by the second week in June (7–9 weeks).

Breeding success.—Pairs occupied 52% of the nest structures in 1977 and 49% in 1978 as primary nest-sites (nests in which pairs spent most of their time and/or laid eggs) (Table 2). Solitary Ospreys with the dark dorsal plumage characteristic of all but first-year birds (Bent 1937:365) attended at least three additional nests during both years. In 1977, females in 94% of the pairs laid eggs, 75% of these clutches subsequently resulted in at least one nestling, and 66% of these pairs successfully fledged at least one

TABLE 1
BREEDING CHRONOLOGY OF OSPREYS IN BAHIA DE LOS ANGELES: NUMBER OF NESTS (%)
IN WHICH LAYING (L), HATCHING (H), AND FLEDGING (F) BEGAN DURING EACH 2-WEEK
PERIOD

Date	1977			1978		
	L N = 30	H N = 23	F N = 19	L N = 27	H N = 18	F N = 14
1-15 Jan.	8 (27)			5 (19)		
16-31 Jan.	7 (23)			9 (33)		
1-14 Feb.	8 (27)	2 (07)		7 (26)		
15-28 Feb.	4 (13)	7 (23)		5 (19)	2 (07)	
1-15 Mar.	3 (10)	7 (23)		1 (04)	7 (26)	
16-31 Mar.		5 (17)			3 (11)	
1-15 Apr.		1 (03)	2 (07)		5 (19)	
16-30 Apr.		1 (03)	4 (13)		1 (04)	2 (07)
1-15 May			5 (17)			5 (19)
16-31 May			6 (20)			3 (11)
1-7 Jun.			2 (07)			4 (15)

young (Table 2). In 1978, females in 85% of the pairs occupying nests laid eggs, 71% of these yielded at least one nestling, and 50% of these active pairs fledged at least one young (Table 2).

Clutch-size comparisons.—There was no statistically significant association between clutch timing and clutch-size in either 1977 or 1978 (Fisher Exact $P = 0.10$ and 0.25 for 1977 and 1978, respectively). Combining the data for the 2 years and comparing early vs late clutches via a χ^2 test for association indicated that more large (three-egg) clutches were laid early in the laying period ($\chi^2 = 4.66$, $df = 1$, $P < 0.05$) (Table 3).

The mean clutch-size for active pairs was not significantly different between 1977 and 1978 ($t = 1.58$, $df = 50$, $P > 0.10$). The 2-year mean clutch-size of active pairs (pairs that laid at least one egg) was 2.8 ± 0.08 .

Historic and geographic comparisons.—There was no significant difference between the mean clutch-size of active pairs during this study and the mean clutch-size of egg sets collected in Baja California and southern California prior to 1947 (the year after which pesticide related egg shell thinning occurred in some species in the United States, Hickey and Anderson 1968) (Table 4). Mean clutch-size of Ospreys from Baja California (pre-1947 and current) were significantly smaller than the means of Osprey clutches taken from as far south as South Carolina on the east coast. The pre-1947 Baja California mean was also significantly smaller than the mean for pre-1947 Georgia and Florida breeding Ospreys; how-

TABLE 2
SUMMARY OF OSPREY PRODUCTIVITY

	1977			1978		
	N	(%)	\bar{x} (\pm SE)	N	(%)	\bar{x} (\pm SE)
Nest structures	65	(100)		68	(100)	
No. nests occupied by single adults	3	(05)		3	(04)	
No. nests attempts ^{a,b}	34	(52)		33	(49)	
No. active pairs ^c	32			28		
Average clutch-size/active pair	30		2.7 \pm 0.1	25		2.9 \pm 0.1
No. of nests with nestlings	24			20		
No. of nests with fledgings	21			14		
No. fledged/nest attempt	34		0.6	33		0.4
No. fledged/active nest	32		1.0	28		0.9
No. fledged/productive nest ^d	21		1.5	14		1.9
Hatching success (#hatched/#laid)	49/76		0.6	41/66		0.6
Fledging success (fledged/nestlings)	32/49		0.7	26/41		0.6
Total young fledged	32			26		

^a Nest attempts are number of pairs occupying nests.

^b Sample sizes for some calculations varied due to differences in accessibility of nests in various stages.

^c Active pairs are those that laid eggs.

^d Productive pairs (nests) are those from which at least one young fledged.

ever, the Bahia de los Angeles mean was not significantly different from the pre-1947 Georgia and Florida mean (Table 4). This minor difference may be due to the variety of data collection methods (museum egg sets vs more accurate field observations). The population in southern Florida is the only other North American population that is non-migratory (Ogden 1977). This may indicate that a relatively low clutch-size is related to ecological and life-history characteristics associated with a non-migratory habit. Temperature regimes, annual patterns of food availability, etc. allow year-round residency in the area of the Gulf of California. This residency could, in turn, result in adults investing energy into young for a longer portion of the year (unpubl.) which, in conjunction with the lack of a long migration in the natal year, might result in increased survivorship of juveniles and subsequently might allow lower clutch-sizes than those selected for in migratory populations with high first year mortality (Henny and Wight 1969).

Hatching success.—Hatching success (number of nestlings/number of eggs) was approximately equal for the 2 years of this study (Table 2). In 1977, a lower percentage of eggs in clutches of two eggs hatched (38%) than in clutches of three (68%) ($\chi^2 = 5.16$, $df = 1$, $P < 0.025$; Table 5). Percents of eggs hatching were approximately equal for clutches of two

TABLE 3
CLUTCH-SIZES OF OSPREYS IN RELATION TO TIME OF CLUTCH INITIATION

	Timing ^a	N	No. of clutches with	
			2 eggs (%)	3 eggs (%)
1977	Early	22	4 (18)	18 (82)
	Late	8	4 (50)	4 (50)
	Total	30	8 (27)	22 (73)
1978	Early	18	2 (11)	16 (89)
	Late	6	2 (33)	4 (67)
	Total	24	4 (17)	20 (83)
Both years	Early	40	6 (15)	34 (85)
	Late	14	6 (43)	8 (57)
	Total	54	12 (22)	42 (78)

^a Early and late denotes first or second half of laying period.

and three in 1978 (62% and 57%, respectively) ($\chi^2 = 0.098$, $df = 1$, NS; Table 5). Comparison of the hatching success (hatched vs not-hatched) of early vs late clutches of three revealed a significantly higher success in early 1977 clutches ($\chi^2 = 4.88$, $df = 1$, $P < 0.05$), but no difference in early vs late 1978 clutches of three ($\chi^2 = 1.78$, $df = 1$, NS; Table 6).

Fledging success.—The number of young fledged per egg was the same for the 2 years (Table 2); however, relationships between the time of clutch initiation and success for three-egg clutches to fledging differed (Table 6). During the 1977 season, clutches of three initiated early in the season yielded more fledglings than did those initiated later in the season ($\chi^2 = 6.06$, $df = 1$, $P < 0.05$). In 1978, there was no significant difference in the success of production associated with timing ($\chi^2 = 0.23$, $df = 1$, NS). Combining data from both years showed a significant, overall association of fledging success with early initiation of laying ($\chi^2 = 4.1$, $df = 1$, $P < 0.05$). Fledging success does not appear to be associated with initial clutch-size ($\chi^2 = 0.62$, $df = 1$, NS). In this study, the number of young fledged per active nest is similar to mean numbers of young reported fledging per occupied nest in many prior studies in North America (see Henny 1975 for review). The reason for this is not clear; however, it may be explained if sexually mature, non-migratory Ospreys are more likely to remain in a breeding area without attempting to reproduce than are more northern-breeding, migratory, adult Ospreys.

In neither of the 2 years was there a significant difference in the success of raising nestlings to fledging age among broods from early vs late breed-

TABLE 4
GEOGRAPHIC COMPARISON OF MEAN CLUTCH-SIZES AS DETERMINED FROM PRE-1947 EGG SETS OF MUSEUMS IN NORTH AMERICA AND FOR RECENT STUDIES IN THE WESTERN UNITED STATES^a

Region	N	$\bar{x} \pm SE$	Differences ^b
N.E. North America (ME, NH, VT, NB, NS) ^c	43	3.02 ± 0.04	A
E. North America (CT, MA, NY) ^d	685	3.09 ± 0.02	A
Atlantic Seaboard (DE, MD, NC, SC, VA) ^e	299	3.23 ± 0.03	B
S.E. North America (GA, FL) ^f	57	2.84 ± 0.07	C
S.W. North America (S. CA, BC) ^g	76	2.67 ± 0.07	D
Bahia de los Angeles (1977, 1978)	51	2.78 ± 0.07	C D
N. California (Garber 1972)	80	2.77 ± 0.08	C D

^a Museum data provided by D. W. Anderson.

^b Means for geographical regions that are not significantly different ($P > 0.05$) share the same letter(s) and those that are significantly different have different letters.

^c ME = Maine, NH = New Hampshire, VT = Vermont; NB = New Brunswick, NS = Nova Scotia, Canada.

^d CT = Connecticut, MA = Massachusetts, NY = New York.

^e DE = Delaware, MD = Maryland, NC = North Carolina, SC = South Carolina, VA = Virginia.

^f GA = Georgia, FL = Florida.

^g S. CA = Southern California; BC = Baja California, Mexico.

ers (fledged vs not fledged 1977, $\chi^2 = 2.3$, $df = 1$, NS and 1978 Fisher Exact $P = 0.38$) (Table 6). Combining data from both years and testing for differences in the proportion of nestlings that fledged also revealed no significant difference ($\chi^2 = 0.57$, $df = 1$, NS). Thus, during this 2-year study, the advantage of laying early in the season occurred prior to hatching rather than being related to the chronological period in which nestlings were present.

In 1977, nestlings in broods of two were more successful in fledging (not less than 86%) than nestlings in broods of three (37%) (Fisher Exact $P = 0.0007$, Table 7). In 1978, broods of two and three exhibited fledging successes of 56 and 67%, respectively. Overall, significantly more nestlings in broods of two young fledged (72.5%) than did those in broods of three (51%) ($\chi^2 = 4.08$, $df = 1$, $P < 0.05$). In 1977, an average of 1.5 young fledged per productive nest whereas, in 1978, an average of 1.9 young fledged. Thus, 33% fewer productive nests in 1978 produced only 19% fewer young than were produced in 1977 (Table 2). In the year of lower total population productivity, each pair that was productive fledged (on the average) 0.4 more young than productive pairs in 1977: however, the average number of fledglings per active nest and the average number of fledglings per nest attempt decreased from 1977 to 1978. This indicates that pairs of Ospreys that failed in 1978 did so early in the nesting cycle either by failing to produce clutches or by losing young nestlings.

TABLE 5
FREQUENCIES OF CLUTCH- AND RESULTING INITIAL BROOD-SIZES

Year	Clutch-size	No. clutches	Total no. broods	Resulting number of broods of each initial size					? ^a
				0	1	2	3	4	
1977	2	8	4	4	2	2	—	—	—
	3	22	20	2	3	9	8	—	—
	? ^a	2	—	—	—	—	—	—	2
1978	1 ^b	1	0	1	—	—	—	—	—
	2	4	3	1	1	2	—	—	—
	3	20	15	5	3	5	7	—	—
	4	1	1	—	—	1	—	—	—
	? ^a	2	1	—	—	1	—	—	1 ^c

^a Clutch- and/or initial brood-size unknown but clutch-size not less than one, as determined by adult behavior; at least one nest appeared to have nestlings present as per adult behavior.

^b This egg disappeared within 3 days and no other eggs were laid in the nest subsequently.

^c Nest could not be reached and no fledglings were observed on or near it.

Productivity patterns.—The analyses of productivity patterns over the 2 years showed that, in general, early initiation of reproduction was advantageous to the successful production of fledglings (combined data from both years). Lower population productivity occurred during the year in which there was a greater range of reproductive effort among pairs (from not breeding to the production of three fledged young) and in which early and late reproductive success was more similarly successful. These data might be explained if the earlier failure of pairs with certain characteristics (e.g., inexperience together, youth, etc.) during more stressful years reduced the competition faced by remaining pairs during the latter portion of the nesting chronology. Changing patterns of foraging success indicated that productive Ospreys were able to provide similar amounts of food in 1977 and in 1978, but that a greater time investment in hunting was required in 1978 (Judge 1981; unpubl.). Characteristics of adults that can influence a pair's timing of reproduction and subsequent success include age and/or experience of the members of the pair (Coulson 1966, 1977), incubation behavior and/or its coordination between parents (Lack 1968: 148–151, Skutch 1976, Inglis 1977), and the male's ability to feed the female during egg formation and incubation (during which time female Ospreys in Bahia de los Angeles are dependent upon their mate for food) and his offspring after hatching (see Newton 1979).

A method for comparing patterns of reproductive loss.—The variation between years among several reproductive parameters suggested the need for a method of comparing patterns of reproductive loss between years

TABLE 6
PRODUCTIVITY OF OSPREYS THAT INITIATED CLUTCHES OF THREE EGGS EARLY OR LATE
IN THE BREEDING SEASON

Year	Timing	Eggs (%) ^b	Nestlings (%)	Fledgings (%)
1977	Early ^a	33 (55)	27 (64)	19 (73)
	Late	27 (45)	15 (36)	7 (27)
	Totals	60 (100)	42 (100)	26 (100)
1978	Early	36 (63)	22 (71)	14 (67)
	Late	21 (37)	9 (29)	7 (33)
	Totals	57 (100)	31 (100)	21 (100)
Both years	Early	69 (59)	59 (67)	33 (70)
	Late	48 (41)	24 (33)	14 (30)
	Totals	117 (100)	73 (100)	47 (100)

^a Early and late denote first or second half of laying period.

^b Percentages are percent of column total.

from the earliest possible stage of the breeding cycle and relative to some standard potential in the population. I calculated a “hypothetical maximum production of young” (HMP) for the study population that was based upon the maximum number of pairs resident in the study area multiplied by the maximum observed mean annual clutch-size (34 pairs × 2.87 = 97 potential young). The maximum mean clutch-size was used rather than the maximum observed clutch-size of any active pair for purposes of con-

TABLE 7
FREQUENCIES OF BROOD-SIZES AND RESULTING NUMBER OF FLEDGINGS

Year	Initial brood-size	No. broods	No. young	Broods (no. young) fledged					Total young fledged (%) ^a
				0	1	2	3	?	
1977	1	5	5	1	4 (4)	—	—	—	4 (80)
	2	11	22	0	2 (2)	8 (16)	—	1 ^b	19 (86)
	3	8	24	2	3 (3)	3 (6)	—	—	9 (37)
	? ^c	2	—	2	—	—	—	—	—
1978	1	4	4	2	2 (2)	—	—	—	2 (50)
	2	9	18	4	2 (2)	4 (8)	—	—	10 (56)
	3	7	21	1	—	4 (8)	2 (6)	—	14 (67)
	? ^c	1	—	1	—	—	—	—	—

^a Percentage of nestlings from broods of specified size that fledged.

^b At least one young fledged.

^c Nestlings were present in nest but initial brood-size unknown.

TABLE 8
CALCULATIONS AND VALUES OF THE "HYPOTHETICAL MAXIMUM PRODUCTION" (HMP) FOR
THE 1977 AND 1978 BREEDING SEASONS

Reduction in potential young due to	1977		1978	
	No.	(%) ^a	No.	(%)
Reduced number of nesting pairs (34 - N) 2.87 ^b	0	—	3	(03)
Inactive pairs (N - n) 2.87	6	(06)	14	(15)
Reduced mean clutch-size (2.87 - \bar{x} clutch) n	3	(03)	0	—
Hatching failure (no. unhatched eggs)	38	(40)	39	(40)
Nestling mortality (nestlings - fledglings)	16	(17)	15	(16)
Fledged young	32	(33)	26	(27)

^a No. = number of potential young.

^b N = number of pairs occupying nests, n = number of pairs that were active (i.e., laid at least one egg).

trolling for possible age and pair-bond effects on clutch-size (Coulson 1966, Klomp 1970:11). This assumed that the relative proportions of age/experience classes remained similar from year-to-year and was not unreasonable in a long-lived species with deferred maturity.

The "fates" of these potential young were calculated from observed breeding failures, egg mortality, nestling mortality, and disappearance of pairs for each year. Observed rates of loss for each year were converted to proportions of the HMP. Loss of potential reproductive success could thus be classified into distinct and non-overlapping categories (Table 8). Although differences in productivity between 1977 and 1978 were not great, use of the HMP emphasized the stage of the breeding chronology wherein differences did occur. The greatest difference in patterns of loss of potential young between years was the increased loss due to inactivity of resident pairs in 1978. This difference was augmented by a small reduction in the number of pairs that were present in the study area in the second year. Proportional loss due to hatching failure was essentially the same during both years and accounted for the greatest loss of potential young Ospreys. Comparisons of the proportions from different populations would allow analyses of the importance and seasonal timing of those factors influencing their reproductive success under different environmental conditions.

SUMMARY

The 1977 and 1978 breeding seasons of non-migratory Ospreys (*Pandion haliaetus*) in the Gulf of California extended from early January through mid-June with a high degree of asynchrony among pairs that was not caused by reneating. Thirty-two and 28 pairs produced eggs in 1977 and 1978, respectively. Mean clutch-sizes (\pm SE) were 2.7 ± 0.1 in 1977 (N =

28) and 2.9 ± 0.1 ($N = 24$) in 1978. Hatching success (0.6 nestlings per egg) did not differ in the 2 years although the number of young fledged per active nest decreased from 1.0–0.9. Twenty-one pairs in 1977 produced at least one young to fledging ($\bar{x} = 1.5$) and 14 pairs in 1978 averaged 1.9 fledglings. In 1977, pairs that initiated egg-laying during the first half of the laying period were more successful in producing fledglings than were pairs that laid later. Thirty-two fledglings were produced. In 1978, 26 fledglings were produced and there was no significant association of reproductive timing and success.

Success in raising nestlings to fledging was similar in both years, indicating that factors influencing the differential production for the two breeding seasons occurred early in the breeding and/or environmental phenology. A comparison of patterns of reproductive loss indicated that the greatest difference between 1977 and 1978 breeding seasons in patterns of reproduction was an increased loss of reproductive potential due to non-breeding.

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