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Age Structure and Dispersal of Chesapeake Bay Ospreys

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AGE STRUCTURE AND DISPERSAL OF CHESAPEAKE BAY OSPREYS

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Timothy Patrick Kinkead

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of
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DEDICATION

This paper is dedicated to my wife, Rebecca, whose support, encouragement and enthusiasm guided its completion.

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ABSTRACT

Adult banded ospreys (Pandion haliaetus) were trapped and identified during the summers of 1983 and 1984. The reproductive success of these breeders was monitored also. One hundred and three ospreys of known age, sex and natal location provide the data of this study. Natal dispersal, age-related reproductive success and site and mate fidelity are examined.

Natal dispersal is influenced by numerous factors. The advantage of prior experience and known success in an area draws ospreys back to the natal location. Opposing the advantage of philopatry is the potential for reproductive depression due to inbreeding, which increases in likelihood as offspring breed closer to the natal site. Seventy percent of the ospreys examined in Virginia breed within twenty-five kilometers of their natal nest site. Males breed significantly closer to their natal sites than females.

The breeding ospreys ranged in age from three to fourteen years. Three age classes, four to six, seven to nine, and ten to twelve year old female ospreys, were tested against the mean reproductive performance of each age class. No significant differences were observed between the age classes and clutch size, number of young produced and hatching index. One reproductive parameter was significantly different, however. The youngest breeders hatched their first young, on average, eight days later than the two older classes.

Once a breeding site has been established, ospreys exhibit a strong tendency to use identical sites in following years. Sixty-seven ospreys were color banded in 1983. Seventy-three percent of those birds returned in 1984 to nest at the same site.

Separation of osprey pairs was an uncommon event. Of nineteen pairs banded in 1983, twelve remained together, four were missing and two new pairings were discovered in the following year. Factors influencing pair fidelity are discussed.

AGE STRUCTURE AND DISPERSAL OF CHESAPEAKE BAY OSPREYS

INTRODUCTION

Until this century, identification of specific individuals in a population of birds was difficult. Only general differences among population members, such as dimorphisms associated with gender and maturity, could be discerned. With the initiation of bird banding, utilization of tarsal, petagial and other markers provided the opportunity to gather much verifiable information about the life history of avian species such as their migration patterns, wintering areas and, to a limited extent, survivorship (Lincoln 1936).

Traditional avian studies of banded birds were limited because of the nature of the reports. Information on marked birds usually came from recoveries of deceased birds (Newton 1977, Osterlof 1977). Other reports attempting to characterize individuals have been weakened because of their dependence on unusual markings or behaviors of birds (Osterlof 1977, Janes 1984). Besides lacking verifiability, these reports are based on extremely small and infrequent sample sizes. Very little information on age-related characteristics and natal dispersal historically have been provided by research on banded bird populations. In order to obtain the demographic data of the type lacking in previous banding studies, it is necessary to capture banded birds while they are still alive and, ideally, at the breeding site. Live recapture of breeding and banded birds provides two important characteristics of the breeder: its age and its dispersal distance from natal to breeding site.

In this study, large numbers of banded and breeding ospreys from the Chesapeake Bay area of Virginia have been identified and reproductive measurements for each bird taken in 1983 and 1984. Virginia ospreys are particulary well suited for a study of this type. Ospreys number approximately 800 pairs in Virginia alone (Byrd 1985, unpublished data) at a density greater than anywhere else in the world (Spitzer 1985). Thousands of osprey nestlings have been banded in Maryland since 1964 (Reese 1977) and Virginia since 1970 (Seek 1977). Ospreys generally reach sexual maturity at three years of age (Zarn 1974); therefore, the majority of the banded population is of breeding age now. Adult ospreys are sexually dimorphic (Kennedy 1971); thus in addition to determining ages of banded adults, gender also can be determined. Ospreys build conspicuous nests, frequently on artificial structures over water which are easily reached and examined by boat (Reese 1977). Virginia's osprey population has been extensively studied for years (Kennedy 1971, Via 1975, Stinson 1976, Seek 1977) so that the locations of traditional nest sites and population trends of the last fifteen years are well documented. Further useful characteristics of Virginia ospreys to demographic studies are that these birds tolerate a high level of human disturbance compared with other raptors (Postupalsky 1977, Stinson 1978, Spitzer 1985). Because of this, research identifying banded breeders and collecting reproductive data can be performed with minimal impact on the behavior of the birds. Finally, public interest in ospreys has been kindled since reports of their population decrease in the 1960's (Ames and Mersereau 1964, Peterson 1969). Various attempts to determine the specific causes of their decline (Wiemeyer et al. 1975, Green 1976, Spitzer 1977) as well as use of management techniques to increase osprey numbers (Seek 1977, Spitzer and Poole 1980) have stimulated further public interest in the behavior and protection of these raptors.

By identifying individual ospreys and following their site selection and mate choice in following years, the degree to which these birds display site and/or mate fidelity can be characterized. Fidelity to sites, as well as to mates, is influenced by a number of factors. Prior experience with an area may provide loyal breeders the benefit of familiarity with spatial and temporal variation in resource availability (Greenwood and Harvey 1976). However, familiarity with an area, or a mate, may be of no advantage if the area, or mate, are incompatible with successful production of offspring (Howard 1949). In this case, dispersal to other areas with new and unknown resources may be a reasonable alternative attempt for increasing reproductive output (Hamilton and May 1977).

Accumulation of data on the ages of breeders and their reproductive success permits an examination of osprey age-related fecundity. The significance of age to reproductive performance is a controversial one. Parental age has been shown to correlate positively with increased clutch size and earlier nesting in the great tit (Perrins and Moss 1975), black-legged kittiwake (Coulson 1966) and Canada geese (Lessells 1985). Other studies show no effect of female age on reproductive performance (summarized in Finney and Cooke 1978) and, in a few instances, clutch size decreases with female age (Klomp 1970, Kear 1973). Thus, age may affect osprey fecundity in any of a number of different ways.

A theoretical framework on which to rationalize the role age has on reproductive performance in birds was first clearly presented by Lack (1948). Lack proposed that characteristics of breeding in birds have evolved so as to permit the birds to produce, on average, the greatest numbers of surviving young (Lack 1948, 1966).These breeding characteristics include clutch size, laying date, and age at first breeding all of which are examined in this study of Virginia ospreys. Drent and Daan (1980) modified Lack's proposal by incorporating the fact that numerous risks are associated with each breeding attempt. Birds that limit their reproductive effort during any one year may be more likely to breed again the next (Pianka and Parker 1975, Bryant 1979, Poole 1984). Thus, reduced reproductive output among younger breeding ospreys may be expected as they minimize risks and preserve themselves for future output of young. Older ospreys, however, with few breeding seasons left, may maximize their fitness by producing as many young as possible despite the risks associated with producing and maintaining large numbers of young (Curio 1983).

Dispersal of offspring from natal sites has important consequences for maintenance of genetic diversity in a population. The importance of dispersal even in uniform and predictable habitats as a means for maintaining genetic contrast between population members is described by Hamilton and May (1977). Two types of dispersal may be characterized for Virginia ospreys. "Natal dispersal" refers to permanent movements from natal to breeding sites; "breeding dispersal" describes annual movements from one breeding site to a new, perhaps different, location (Greenwood 1980).

Various stimuli would appear to draw offspring back to natal locations to breed. Potential advantages to homing ospreys are previous experience with an area and any genetic adaptations migratory ospreys may have for their local breeding environment (Newton 1977, Lessells 1985). Many studies of migratory avian species describe a general return of offspring to their natal sites. Seventy six percent of all breeding season recoveries of European sparrowhawks are within twenty kilometers of their birthplace (Newton 1979). Natal dispersal of long-billed marsh wrens greater than ten kilometers is a rare event (Verner 1971). Bulmer's data (1973) indicate low natal dispersal in great tits.

Offsetting the advantages of philopatry is the potential for inbreeding depression. Inbreeding increases in likelihood the closer offspring breed to their natal site (Greenwood and Harvey 1978). Close inbreeding has been reported for two percent of all matings in a population of great tits. (Bulmer 1973). The potential for inbreeding may be a selective force promoting dispersal in Virginia ospreys.

Markedly different natal dispersal tendencies between genders of birds have been reported. Most species studied to date, including the great tit (Dhondt and Huble 1968), manx shearwater (Brooke 1978), herring gull (Chabrzyk and Coulson 1976), kittiwake gull (Wooler and Coulson 1977), song thrush (Davies and Snow 1965), and song sparrow (Nice 1937) display female-biased dispersal. In some cases, however, natal dispersal is distinctly male-biased (Sowls 1955, Cooke et al. 1975, Lessells 1985). This study describes differences observed in natal dispersal of Virginia ospreys associated with gender.

The information provided in this study elucidates the relative contribution of offspring by each osprey age class. Because Chesapeake Bay osprey populations historically have been large and stable ones (Kennedy 1971, Spitzer 1977, Spitzer and Poole 1980) it may be expected that members of each age class produce better than average numbers of young for their chronological age. Availability of nest sites will influence dispersal distances of ospreys and habitat quality varies across their breeding range. Natal dispersal observed in Virginia in 1983 and 1984 may, therefore, be different from the corresponding value found in other parts of osprey's breeding range.

METHODS AND MATERIALS

Over four-hundred active osprey nests in Virginia were examined for the presence of banded breeders each year in 1983 and 1984 (Table 1). The study region was divided into five areas according to the major river or bay system which characterized the region (Figure 1). The estuarine systems of this region of Virginia divide the land into multitudes of interwoven marshes, streams and rivers which afford large numbers of potential osprey nest sites (Seek 1977).

Each nest was visited at least twice, and more commonly three times, between April and July of each year. Standard 7 x 35 binoculars were used to examine osprey breeders at their nests from an eighteen-foot outboard motor boat. Each leg of the bird was inspected for the presence of a United States Fish and Wildlife Service or other band. Attempts to trap the breeder were carried out whenever a bird was found carrying such markers at sites which appeared safe for trapping. Aeries located in trees, some duck blinds and some docks with obstructive and potentially dangerous branches and pilings were not used in an effort to avoid injuring any breeders.

Opsreys were captured by positioning a trap on top of the nest, separating the breeder from his or her eggs. The trap was a dome-shaped apparatus made from medium-gauge chicken wire fencing. The base diameter of the trap was

Table 1. Numbers of active nests in each study area

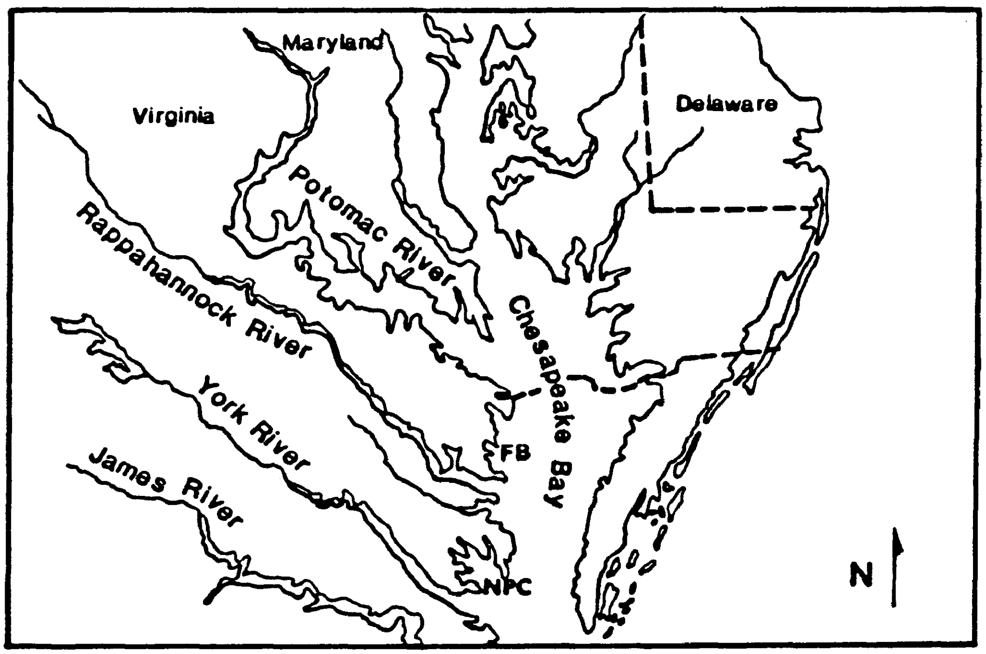
1983	
Rappahannock River	130
York River	53
Fleets Bay	49
New Point Comfort-Mobjack Bay	102
Potomac River	98
	432
1984	
Rappahannock River	140
York River	61
Fleets Bay	49
New Point Comfort-Mobjack Bay	109
Potomac River	119
	478

Figure 1. Osprey study area.

Legend

F.B. = Fleets Bay

N.P.C. = New Point Comfort


Maryland
Virginia
Delaware
Potomac River
Rappahannock River
York River
James River
Chesapeake Bay
FB
NPC
N

approximately eighty-five centimeters, surrounding the upper rim and lined area of osprey nests. The height of the dome from base to apex was approximately twenty-five centimeters. Tied to the wire fencing were numerous forty and sixty-pound test monofilament nylon snares. Rubber tubing was attached to the periphery of the trap to decrease the chances of the snare carpet becoming entangled in the sticks and driftwood comprising the nest. A float was attached to the snare carpet to protect the captured osprey once in the water.

While ospreys are incubating, the birds display a strong attachment to the nest and will land to gain access to their eggs even when a foreign snare carpet is positioned. Once the breeders land on the carpet, however, their long talons soon become entangled in numerous snares. When the breeder appeared to be well ensnared, the nest was approached stimulating the breeder to fly off of the nest. The weight of the snare carpet would cause the bird to land in nearby waters, where it was immediately picked up. The raptor's unique band number and gender were recorded and two new color bands were positioned on the unbanded leg of the osprey. These were cemented into a static diameter, thus avoiding slippage of the bands later. The color combination given to each captured bird was unique and allowed later visual identification of the bird from distances up to twenty-five meters.

The number recorded from U.S. Fish and Wildlife Service bands was used to identify the date and location of original banding. All of the ospreys on which dispersal and age data were based were banded as nestlings between four and seven weeks of age. Records used to identify the majority of breeders originally banded in Virginia were maintained at the College of William and Mary. All other records were provided by the Patuxent Wildlife and Research Center in Laurel, Maryland.

Each nest at which breeders were captured was visited at least two more times during the breeding season. At the first of these additional visits record was again made of nest contents, behavior of the adults and the condition of the nest and bands carried by the breeders. When young were found in the nest, their ages were determined and recorded. Nestlings can be aged with accuracy during the first ten days of life by noting such characteristics as down to feather proportions, primary feather length and development, and feather color patterns on the dorsal surfaces of the nestlings (Seek 1977). During the final visit to the nest site, from late June to the middle of July, attempts were made to determine the number of fledglings produced by the breeders.

The distance dispersed from original hatch site to breeding site ("natal dispersal") was measured as the shortest distance between the two nest sites on 1:24000 scale United States Geological Survey topographical maps. Students t test pooled and separate variance estimates were applied to the natal dispersal data (after Sokal and Rohlf 1981) to identify any differences in mean natal dispersal between male and female ospreys.

The ages of the breeders were compared with their reproductive success in an effort to detect age-related differences in breeding performance. The data were pooled into three age categories (four to six, seven to nine and ten to twelve year old females) so that each class had enough representatives to make meaningful analyses of the data.

Numbers of eggs and young produced and the hatching index (number of young hatched/number of eggs in clutch) were examined against age classes with a three-by-two test of independence using chi-square (Sokal and Rohlf 1981).

The date of first egg hatch for each breeder was measured by extrapolating back from the age of the oldest nestling recorded during visits to the nest. For example, if two chicks were discovered on May 4 and the oldest chick was three days old then the date of first hatch was deemed May 1. These dates were converted to their respective absolute day of year value, which is the sum of all days of the year from January 1 to the hatch date. These data were also pooled into the three age classes. Oneway analysis of variance, the Duncan procedure and Student-Newman-Keuls multiple range tests (Sokal and Rohlf 1981) were used to identify differences in hatch date among the three groups.

Data on fledging success were not used as measurements of osprey breeding performance in 1983 and 1984 because of potential inaccuracies in determining these values. The only accurate method for determining the number of fledglings per breeding pair is by seeing the fledglings at the site or perched nearby. However, this determination may be subject to error because many successful fledglings perch in areas out of view of the observer.

RESULTS

One hundred and three banded and breeding ospreys were identified in 1983 and 1984. Significantly (P<0.001) more females (N=79) than males (N=24) were captured due to differences in breeding behavior related to gender (see discussion). Representatives of each age class from three to fourteen years were found (Figure 2).

Banding of Virginia ospreys began in 1970 (Seek 1977). Since nearly all of the sampled birds originally hatched in Virginia (82 percent), the opportunity to capture birds older than fourteen years of age was limited. Ospreys have been banded for years prior to 1970 in coastal ares between New York city and Boston (Spitzer and Poole 1980) as well as parts of Maryland (Reese 1977); however, none of these potentially older banded birds were found in Virginia. Only eighteen percent of the sample was represented by ospreys hatched outside of Virginia (Table 2).

Natal dispersal is defined as a permanent movement between birth site and first breeding (Greenwood 1980). The natal dispersal of all of the identified ospreys was analyzed to determine if any differences in dispersal tendencies existed between male and females. Mean male dispersal was found to be 12.7 km.; the equivalent value for females was 42.3 km. The student's T test result is highly significant (P<.001) indicating that male dispersal

Figure 2. Ages of ospreys in sample

(Note: the number of males per age class is equal to the value obtained when subtracting the hatched column from the solid column)

1983 and 1984

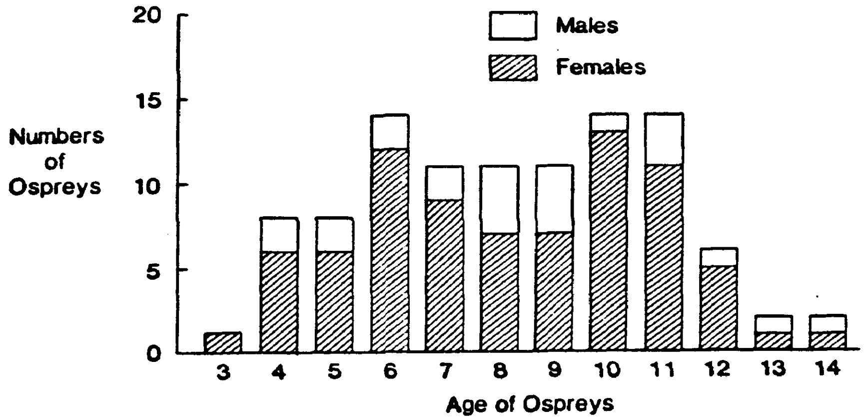


Table 2. Natal origin (by state) of ospreys breeding in Virginia in 1983 and 1984.

Virginia	84
Maryland	17
Delaware	2
	N = 103

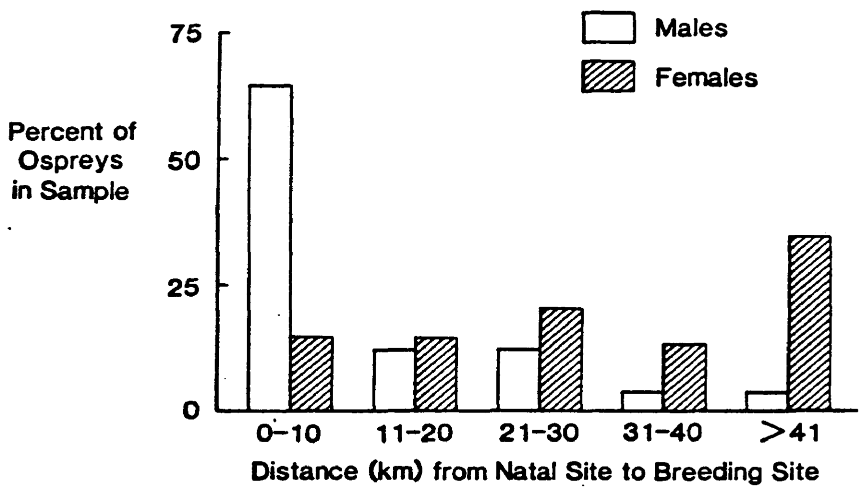
is, on average, of a considerably shorter distance than female dispersal.

The standard deviation of female dispersal is large (40.3 km.). Graphic representation of female natal dispersal (Figure 3) suggests little allegiance to specific natal sites in female ospreys. Conversely, male ospreys tend to breed closer to their natal location.

Nineteen pairs of ospreys were captured in 1983. These birds, in particular, were searched for in 1984 in order to calculate mate fidelity among Virginia ospreys (Table 3). At least sixty-three percent of the pairs were maintained from 1983 to 1984. Four pairs were missing entirely and their fidelity could not be determined. In two cases pairs were found to have separated as new partners were positively identified in 1984.

Ospreys breed frequently on day markers, channel lights, bridges and other man-made structures (Seek 1977) which are readily identifiable and mapped. By knowing the identities of the breeders, the degree to which nest site re-use occurs can be estimated. In 1983, 67 ospreys were color banded. At least seventy-three percent of these birds returned the following year and utilized identical nest sites (Table 4). Site fidelity may have exceeded seventy-three percent. Eleven nest sites, where a total of fifteen individuals had been banded in 1983, were partially or completely destroyed by storms in 1984. While breeders

Figure 3. Natal dispersal of Virginia ospreys



Students' T Test Comparing Male to Female Dispersal, P<0.001.

Table 3. Mate fidelity of ospreys identified in 1983 and 1984.

Pairs	Maintained	Split	Unknown	Deceased member of pair
19	12	2	4	1

were in fact observed at these sites, identification of these individuals was not possible because the breeders would readily vacate the site upon approach of the research boat. In only two cases were ospreys positively identified as breeding at different nests sites.

The reproductive success of known-age ospreys was compared with the ages of these breeders to determine the extent to which age may influence osprey breeding capabilities. Of the seventy-nine females identified, seventy-two were tested for egg productivity by age group. Seven females were not included in this analysis. Three, thirteen and fourteen year old ospreys were not tested because they were lone representatives of their age groups. The remaining four of the seven were ospreys whose ages were known but whose reproductive performance could not be verfied. These four breeders were visually identified from complete color band combinations carried on their legs. However, because they were nesting in the high reaches of trees or atop inacessible buildings a count of their eggs and nestlings was not possible.

The analysis of egg productivity versus female osprey age revealed no significant differences in the clutch size of the three age groups (Table 5). Each group laid numbers of eggs which were roughly similar. The majority of the breeders (69.4 percent), regardless of age, laid either three or four eggs.

Table 4. Site fidelity of Virginia ospreys identified in 1983 and 1984.

Banded	Same site	Different site	*Unknown	Known deceased
67	49	2	15	1

*Birds at these nest sites could not be positively identified as the same birds banded in 1983 (see text)

TABLE 5. OSPREY EGG PRODUCTION BY FEMALE AGE GROUP

TEST OF INDEPENDENCE

AGE (YEARS)	EGGS LAID 1-2	EGGS LAID 3-4	
4-6	4	18	N=22
7-9	9	13	N=22
10-12	9	19	N=28
	N=22 30.6%	N=50 69.4%	

Chi Square = 2.73
Degrees of Freedom = 2
Significance = 0.255

Seventy known-age females were tested for productivity of young and hatching index. Two of the seventy-two females tested for egg productivity were not included in these analyses because their reproductive efforts beyond egg-laying were not ascertained. No significant differences between the age groups were realized for productivity of young or hatching index. Most of the breeders (68.6 percent), regardless of age, hatched from zero to two of the eggs which they laid (Table 6). Also, the majority (65.7 percent) of the breeders successfully hatched greater than fifty percent of their respective clutches (Table 7).

The date at which the first egg hatched for fifty known-age female ospreys was determined from field studies. Statistical analyses of these data revealed that young ospreys (four to six years of age) hatched their first young, on average, significantly later than either of the older age categories. The delay in hatch date of the youngest breeders is, on average, eight days (Table 8). Of note, there is virtually no difference in the hatch date of the two, separate older groups of breeders (day 145.4 versus day 145.8). The earliest hatch date observed in two years of study was day 131 by a nine year old. The latest hatch date, day 171, was exhibited by a member of the youngest age category.

TABLE 6. OSPREY PRODUCTION OF YOUNG BY FEMALE AGE GROUPS

TEST OF INDEPENDENCE

AGE (YEARS)	YOUNG PRODUCED 0–2	YOUNG PRODUCED 3–4	
4–6	14	8	N=22
7–9	13	8	N=21
10–12	21	6	N=27
	N=48 68.6%	N=22 31.4%	

Chi Square = 1.74
Degrees of Freedom = 2
Significance = 0.418

TABLE 7. OSPREY HATCHING INDEX BY FEMALE AGE GROUPS

TEST OF INDEPENDENCE

AGE (YEARS)	HATCHING INDEX 0.00–0.50	HATCHING INDEX 0.51–1.00	
4–6	7	15	N=22
7–9	6	15	N=21
10–12	11	16	N=27
	N=24 34.3%	N=46 65.7%	

Chi Square=0.86
Degrees of Freedom=2
Significance=0.750

$$\text{Hatching Index} = \frac{\#\text{Young}}{\#\text{Eggs in Clutch}}$$

TABLE 8. HATCH DATE FOR VIRGINIA OSPREYS

FEMALE AGE (YEARS)	N	$\bar{M}$ (ABS. DAY OF YEAR)	S.E.	95% C.I. FOR MEAN
4–6	15	153.6	3.2	146.8 TO 160.4
7–9	16	145.4	2.3	140.4 TO 150.4
10–12	19	145.8	1.2	143.4 TO 148.3

P, Comparing Mean of the Three Groups (from Oneway ANOVA), 0.05. Young Birds' (4–6 years) Eggs Hatch Significantly Later than Older Birds' Eggs. (Duncan and Student Neuman Keuls Procedures at 0.05 Level of Confidence).

DISCUSSION

A goal of this study was to identify as many banded ospreys within the study area as possible and to a reasonable extent this was accomplished. Near the end of the 1984 breeding season few ospreys were discovered which, upon visual inspection, carried Fish and Wildlife Service or other bands. Again in 1985, low numbers of previously unknown banded ospreys were discovered in Virginia (Byrd 1985, pers. comm.). However, because aluminum bands sometimes contrast poorly from the tarsi of ospreys, it is possible that still more banded ospreys are breeding in Virginia which have not yet been identified.

Capturing Banded Ospreys

The method used to trap these ospreys proved to be successful for a number of reasons. While effort was sometimes required to ascertain the status of breeders (banded or unbanded) at their nest site from a rocking boat, the time required to capture incubating females once the trap was positioned on the nest was typically less than eight minutes. Unfortunately, greater time allotments were needed to capture males because of their reduced nest attentiveness compared with females. Exposing eggs to cold temperatures for periods exceeding ten minutes frequently was required in order to capture male ospreys. Rather than risk endangering unhatched young, attempts to capture males were prematurely curtailed in many cases. This resulted in a preponderance of females in the sample.

Because this method of trapping occurs directly at the nest site, there is little question that the birds caught represent the progenitors of the eggs in that nest. While there is always the posssibility that the adults are interlopers, this can be considered improbable. Numerous osprey studies describe a high degree of nest site territoriality among the breeders, particularly the female (Green 1976, Stinson 1976, Levenson 1979). Positve identification of the breeders at the nest site represents a substantial improvement in our knowledge of osprey reproduction. Previous studies of banded ospreys were based on recoveries of deceased birds. It was assumed in these reports that ospreys recovered during the breeding season were breeding near the area where the bird was recovered (Henny and Wight 1969, Osterlof 1977). This assumption may be accurate for mature ospreys which probably are breeding, or attempting to do so (Spitzer 1979). However, it is incorrect to assume that two, three and, sometimes, even four year old ospreys are breeding only because they are discovered within the proper area at the appropriate time. Some of these young ospreys may represent birds which have reached the breeding range but have not yet begun to breed due to physiological and/or behavioral deficiencies (Henny and Ogden 1970, Henny and vanVelzen 1972).

A coincidental benefit of this trapping method derives from its requirement that one must directly approach the nest in order to position the snare carpet correctly. In so doing, it is possible to examine numerous nesting parameters including the number and condition of eggs, quality of nest construction and the presence of any unusual nesting materials. Also, by handling live, breeding ospreys, gross inspection of the bird's health can be measured. In at least three instances during the study period, it was discovered that colored, plastic leg bands attached as supplemantary identifying markers in the early to mid 1970's had become lodged proximally on the leg causing abrasions. These findings made clear the need to adequately cement bands in a stationary diameter in order to avoid slippage. Another breeder was discovered with one broken and one abnormally directed talon. Overall, however, few instances of severe mite infestations, feather loss, eye wounds or abrasions were noted in over one hundred and fifty captured ospreys.

Dispersal of Virginia Ospreys

Virginia ospreys disperse to breed in areas other than their natal location differently depending on gender. Females, on average, breed twenty-nine kilometers farther from their natal sites than male ospreys. Such a substantial difference in dispersal is commonly found among banded populations of birds (Newton 1979). Usually females are the greatest dispersers among the Aves; exactly the opposite pattern is observed in most mammals (Greenwood 1980). The lone avian group in which females are not the extreme dispersers is waterfowl. Canada geese (Lessells 1985), mute swans (Coleman and Minton 1979), lesser snow geese (Cooke et al. 1975) oldsquaws (Alison 1977) and pintail ducks (Sowls 1953) each display male-biased dispersal.

The fact that sex-related differences in dispersal are frequently reported in the literature suggests that a system of assymetric dispersal is important to the survival of birds. Various explanations have been forwarded as a rationale for dispersal patterns noted in field studies. Greenwood (1980) argues that the direction of sex bias for a given species is a consequence of the type of mating system utilized by the group. When males defend resources, such as breeding territories, they obtain a large benefit from philopatry because it is easier for them to establish and maintain territories near their hatch site. Females must disperse in order to exercise choice of mate. If, on the other hand, males defend mates instead of resources, it is they who must disperse in order to locate an appropriate mate. Since waterfowl uniquely defend mates and display male-biased dispersal, another uncommon feature among birds, Greenwood offers waterfowl species as examples of birds which follow dispersal patterns described by his theory. However, it is difficult to describe a species as always defending either a mate or a resource exclusive of the other. Within any given breeding cycle both patterns of defense may be observed. Ospreys, for example, are highly territorial of their nest in the beginning of the breeding season but can become, if threatened, extremely defensive of their mates (Green 1976). An additional weakness in this otherwise convenient explanation is that Greenwood's argument largely ignores the benefit which potentially accrues the female from philopatry. It would appear that female ospreys could gain advantage from previous experience with an area just as males apparently do. In this respect, it is unclear what motivates females to disperse based on Greenwood's theory alone.

Howard (1949) reported inbreeding in a population of tagged prairie deermice. Since that time birds have been examined for similar behavioral characteristics. Bulmer (1973) found close inbreeding in seven of three hundred and ninety seven matings in a great tit population. Although the sample was low, he reported significant reproductive depression in the seven consanguineous matings and first suggested that avoidance of inbreeding may be a factor influencing sexual assymetry in avian dispersal. Later data on the same population (Greenwood and Harvey 1978) suggested that the chances of inbreeding vary with dispersal distance. Among close inbreeding pairs abnormal dispersal of one or both pair members was commonly found. No other avian studies report known cases of inbreeding, although few populations are as well marked and researched as Britain's great tits. Inbreeding also was not observed among Virginia ospreys in 1983 and 1984. However, because ospreys can reproduce as old as twenty three years of age (Spitzer 1979) and disperse little, the potential for inbreeding appears to be a strong one. For Virginia ospreys then, inbreeding avoidance may be a stimulus promoting dispersal (Verner 1971) although this factor alone fails to explain why it is that females in particular are the extreme dispersers.

Lessells' (1985) study of Canada geese provides further insight into the question of sexually assymetric dispersal in birds, as geese disperse in an opposite pattern from Virginia ospreys. Lessells agrees with Greeenwood that type of mating system is an important factor determining which sex will disperse. However, Lessells suggests another pressure is involved: female geese may gain more than male geese from philopatry and, therefore, the former disperses less. The proposed reason for female gain relates to geese experiences immediately post-hatching. Young Canada geese are led to separate brood rearing areas soon after hatching; therefore, the most useful information available to the young bird at this time is on the feeding areas. The young are exposed little to the actual nest site. Female geese may gain more benefit than males from prior feeding area experience available immediately post-hatching because female's reserves are at that time far more depleted.

Using similar logic to explain osprey dispersal, it can be argued that male ospreys achieve greater benefit from previous experience with natal nesting, and particularly feeding, areas than females because it is the male osprey's role to feed the female and, later, her young throughout the nesting and brood-rearing periods (Garber and Koplin 1972, Green 1976, Stinson 1978, Levenson 1979). Because female ospreys rarely hunt during the nesting period it seems reasonable that a female's gain from prior experience with feeding areas would be far less critical than a male's gain, assuming that either sex benefits from prior exposure to an area during the first few months of life immediately post-fledging.

At this time, the most rigorous explanation for female biased dispersal observed in Virginia ospreys is a synthesis of Greenwood's and Lessells' theories. In summary, both sexes of ospreys potentially benefit from philopatry because of prior experience or perhaps genetic adaptations for tolerating the environment of the natal area (Greenwood and Harvey 1978). However, one sex or both must disperse in order that inbreeding depression is avoided. It appears that the sex which stands to gain the most from philopatry, due to that gender's role in mating and resource defense, will be the one which maintains the strongest bond to the natal site. In Virginia ospreys, this low disperser is the male.

Mate and Site Fidelity of Virginia Ospreys

The discovery that Virginia osprey pair dissolution may have been as high as thirty seven percent was noteworthy. Lower pair dissolution values, such as eighteen percent reported in the red-billed gull (Mills 1973), were anticipated. Actual pair fidelity may indeed have been higher than stated depending on the fidelity of the four osprey pairs missing in 1984. Severe wind storms in April and May of 1984 destroyed many nest sites and it is conceivable that some of these pairs were maintained at new unknown sites. Separation of only eleven percent of the known pairs was verified visually in 1984.

Coulson (1966) reports that "a change of mate has a direct and depressive effect upon the breeding biology of the pair". His data on the kittiwake gull, as well as Mill's (1973) study of the red-billed gull, identified a general pattern of reproductive depression (measured in terms of eggs laid and young fledged) in pairs with new partners. Coulson (1966) found that pairs taking new mates hatched their young three to seven days later than comparably aged individuals which had maintained the previous year's mate. These data suggest that pair fidelity of Virginia ospreys is one means by which reproductive fitness is maintained or improved.

An important factor, however, influencing pair fidelity is previous reproductive success. In virtually all reported species a high percentage of pairs which split had had poor breeding success the year before (Richdale 1957, Coulson 1966, Mills 1973). Annual monitoring of kitiwake gull pairs (Coulson 1966) indicated that these changes frequently were beneficial; breeding performance in new pairs typically exceeded that of the original pairs eventually. If ospreys behave as other reported avian species do, then pair fidelity of Virginia ospreys may be a dynamic balance which can change depending on previous breeding performance and compatibility of the pair.

Due to temporal constraints on this study, it has been impossible to study known pairs for more than two mating seasons. By following these pairs and their fecundity in years to come researchers will be able to verify any pair dissolution of Virginia ospreys based on breeding histories. The data on red-billed (Mills 1973) and kittiwake (Coulson 1966) gulls as well as the yellow-eyed penguin (Richdale 1957) may be compared as populations whose pair fidelity is significantly influenced by previous reproductive performance.

Nest site fidelity of Virginia ospreys is influenced by characteristics of the birds themselves as well as the quality of the nest site. Between 1983 and 1984 no more than twenty-seven percent of the identified ospreys changed their aeries. The habit of breeding in the same territory year after year is probably advantageous, so long as the territory is complementary to the raptor's reproductive efforts. Where ospreys choose to nest may be an important component of their reproductive performance. Hogstedt (1980) discovered that eighty-one to eighty-six percent of the within year variation in magpie clutch size was linked to differences in territory quality.

Newton and Marquiss' (1976) study of Eurasian sparrowhawks revealed varying degrees of territory fidelity. Females who occupied high quality territories (measured in terms of occupancy rate and previous reproductive success) remained there significantly more frequently than femles occupying poor territories. The possibility that high quality territory holders are simply better territory defenders, hence more loyal, than poor quality territory holders is considered to be only partially responsible for the findings. Similar behavior is reported in the European kestral (Cave 1968). Female red-tailed hawks, however, exhibited high territory fidelity despite wide variance in territory quality within the study area (Janes 1984). The well documented movement of ospreys in Virginia (Seek 1977), Michigan (Postupalsky 1977) and Maryland (Rhodes 1972) from poorly-successful, on-shore nests in trees onto off-shore artificial structures where breeding success generally has been greater, suggests that osprey nest site fidelity is strongly influenced by the quality of the nest site. Although differences in individual dominance presumably also influences who will be able to defend and maintain nest sites annually (Newton 1977), inferior sites will elicit only marginal loyalty from ospreys. Nest site deficiencies may well have contributed to breeding territory movements observed in Virginia's osprey population in 1983 and 1984.

Reproductive Success and Female Breeder Age

Four parameters of Chesapeake Bay osprey breeding success were measured in 1983 and 1984: numbers of eggs laid, young hatched, hatching index and hatch date of first young. Numerous studies recently have shown varying correlations of age with reproductive success. The Eurasian sparrowhawk's breeding performance is highest among birds aged three to five years (Newton et al. 1981). First year mallards started laying later in the season and stopped sooner than more elderly breeders (Batt and Prince

1978). Mean clutch size of lesser snow geese steadily rises from two to nine year age classes (Rockwell et al. 1983). One year old great tits lay on average two days later than two to four year olds (Perrins and Moss 1974). Finney and Cooke (1978) reported that mean clutch size increases and laying date advances with female age in snow geese. An additional report of age-related reproductive success includes Kear's (1973) finding that captive Hawaiian geese increase their average clutch size between two and seven years, and then the average decreases steadily until twelve years of age when only one egg is normally produced. The number of chicks fledged per pair of kittiwakes increases with breeding age of female parent, reaching a peak among birds with two year's breeding experience (Coulson 1966). Ospreys included in this study were found not to differ in egg productivity, young hatched or hatching index. However, an interesting discovery was that the youngest osprey age class hatched their young, on average, eight days later than both of the remaining age classes. The hatch date delay documented in this study is greater than nearly all others reported in the literature (Table 9).

Table 9. Reported hatch date delays among young and/or inexperienced breeders.

Species	Mean hatch date delay	Source
Snow geese	2.6 days	Finney and Cooke 1978
Sparrowhawks	4 days	Newton et al. 1981
Great tits	5.3 days	Perrins and Moss 1974
Osprey	8.2 days	Present study
Kittiwake	10 days	Coulson 1966

Although the breeding performance of Virginia osprey age classes differed in only one parameter it is highly probable that the annual reproductive success of the youngest age group is inferior simply due to the delayed hatch date alone. The rationale for this statement comes fom the likelihood that fewer of the late-fledged young will survive than early young. It was not possible to follow the fate of large numbers of young ospreys once they had fledged, but numerous studies of other avian species and one study of ospreys (Poole 1984) support the notion that late-fledged young have poorer rates of post-fledging survival. Early Manx shearwaters had up to a seven-fold better chance of surviving the first year of life than late young (Perrins et al. 1973). Cape gannets most likely to survive and be seen at the colony in future years were fledged earlier on average than non-survivors (Jarvis 1974). Bierman and Robertson (1981) found decreased probabilities of survival for late nesting red-winged blackbirds. In every season that redbilled gulls have been studied, the survival rate of young fledglings was highest for the earliest broods (Mills 1973).

The lone exception to these studies showing highest survivorship among early young is a recent study of puffins (<u>Fratercula arctica</u>). Harris and Rothery (1985) found that neither fledging date nor chick growth rate had any significant effect on post-fledging success of young puffins and caution against using hatch date and/or weight of young as indicators of parental breeding success. However, during the period of this puffin study conditions were near optimal; the population was growing by an average of twenty-two percent annually. And, as the authors stated, even the lightest or latest young had good chances of survival. In more normal conditions which prevail most of the time, fledge date and chick weight probably would affect survival rates of young puffins.

Further, Poole (1984) reported evidence that ospreys which had hatched earlier in the breeding season were more viable than late young. The author found that Westport, Connecticut osprey fledglings known to have returned to this colony to breed (by band recovery or live recapture) as new breeders came from eggs which were laid considerably earlier than others in the colony (mean = seven days). As the delay in hatch date of four to six year old ospreys found in this study is near the mean delay described by Poole above, evidence supports the premise that the young fledged later by the youngest class of Virginia ospreys will have poorer survival rates. Later young must contend with depleting food supplies and worsening weather at younger ages. Additionally, they may have less post-fledging experience with parents before the adults migrate to their wintering areas. These are the presumed factors which could result in poorer survivorship among late-fledged young reared by four to six year old ospreys in Virginia.

Differences in breeding performance related to age are theorized as being the result of either "reproductive constraint" or "reproductive restraint" (Curio 1983). Four to six year old ospreys either cannot rear their young as early as older ospreys ("constraint") or they will not rear them as early for some reason ("restraint").

The probable causes for reproductive constraint are described as being due to behavioral and/or physiological deficiencies young breeders may bear. Explanations for poorer reproductive performance of young breeders based on behavioral inadequacies have been reported. Rockwell et al. (1983) suggest that inexperienced female lesser snow geese may be less efficient in accumulating food reserves and, for this reason, lay later than older geese. The decreased clutch size and breeding success as well as retarded lay date shown by great tits may indicate that young breeders are not yet efficient enough to be able to collect food both for themselves and for their young (Perrins and Moss 1974). Dunn (1972) verified that immature sandwich terns took significantly longer than adults to collect food that they needed. A recent study of European sparrowhawks described a clear advantage to both adults and yearlings in mating with adults (Newton et al. 1981). The authors argue that differences in reproductive performance noted between adult-adult, adult-yearling and yearling- yearling breeding pairs could have been due to yearlings of both sexes being less proficient than adults at foraging or at acquiring good territories. Finney and Cooke (1978) observed that the efficiency of female snow geese in acquiring adequate resources for egg laying has been postulated to affect both clutch size and timing of lay and hatch date. In light of the preceeding studies, one reasonable explanation for the observed delay in hatch date of young osprey breeders is that these breeders are, in general, slower than older ospreys. Their territory defense, nest construction and breeding behaviors may take longer to initiate and complete. Although these behaviors were not timed in the course of this study, future comparisons of known-age osprey breeding behaviors could verify or refute this postulated cause for young osprey's delay in hatch date.

Some studies suggest that poorer reproduction is due to constraints caused by physiological defiencies in young breeders. While studying the effects of age on captive mallards, Batt and Prince (1978) found that first-year breeders entered the breeding season in suboptimal physical condition compared with older mallards. Lehrman et al. (1961) reported that secretions of gonadotropins in female ring doves was stimulated by the presence of a male and augmented by the presence of nesting materials. Males are stimulated into breeding condition by environmental cues, including daylength (Lehrman et al. 1961). Similar stimuli probably are involved in conditioning ospreys to breed; however, the rapidity of physiological response may be slowest for the youngest class of breeding ospreys. The testes of young red-billed gulls matured more slowly than older birds; thus, females mated with older males were stimulated earlier in the breeding season (Mills 1973). The behavioral inadequacies of young breeding ospreys may be related to slower physiological response to the numerous stimuli conditioning ospreys to breed.

An additional argument presented by some biologists to explain reproductive inferiorities in young breeders is that young breeders are restraining themselves from reproducing maximally. Young breeders do this in an effort to reduce the risks associated with raising large numbers of young and thus preserve themselves for future reproductive attempts (Poole 1984). Such restraint should be most commonly observed in long-lived species with high future breeding prospects (Charnov and Krebs 1974, Curio 1983). This theory, applied to ospreys, assumes that the risk of raising one young is appreciably less than raising three or four ospreys. The theory also suggests that ospreys have a degree of foresight which is difficult to verify. Nonetheless, papers whose authors support the restraint model are found in the literature. Finney and Cooke (1978) opined that the lowered reproductive output of first-time snow geese breeders is an attempt to maximize their lifetime fitness by reducing the risks associated with maximum clutch rearing. The results of a kittiwake gull study did not support the idea that increased age or breeding experience caused annual development of gonads to be slightly more rapid or start slightly earlier in the breeding season leaving open the possibility the reproductive restraint was occurring (Coulson 1966). Charnov and Krebs (1974) stress that the number of surviving young each year is an incomplete measure of fitness. Since many birds reproduce several times, adult survival must also be considered in terms of lifetime fitness. The authors propose that an "optimal clutch size" exists which maximizes the breeder's lifetime fitness. This optimal clutch size varies depending on the maturity of the bird. According to this theory, young ospreys breeding in Virginia will produce fewer young and thereby reduce the risks associated with reproduction. Future prospects for reproduction are high for these young ospreys if they survive until the next year. Poole (1984) remarks in his study of ospreys that "maximizing reproduction over such a long [osprey] lifespan probably involves restraining foraging efforts, among other parental investments, for any particular brood".

In order that the restraint hypothesis be supported by ospreys in this study, young Virginia breeders would have had to exhibit some avoidance of risk associated with reproduction. However, in no noticeable way did the young breeders avoid the risks of reproduction compared to the older groups. Statistically, the young breeders laid clutches equal in size to the older groups. Young breeders also endured equivalent risk in feeding their young since all three age groups produced equal numbers of young. The youngest breeders may have in fact risked more than all others since, by hatching their young late, they were more likely to experience inclement weather and reduced food supplies while rearing their broods. Thus, the data accumulated in this study does not support the restraint hypothesis as an explanation for the retarded lay date of young osprey breeders.

The best explanation for the delayed hatch date of four to six year old ospreys is that these younger breeders are slower at performing the appropriate reproductive behaviors. This is probably associated with physiological inadequacies which disappear with age, as discussed earlier. Further studies of known-age osprey breeding behaviors will elucidate more completely the causes of reproductive delay in young breeding ospreys.

Consideration of prior studies led to anticpation that elderly ospreys might display smaller clutches and fewer young due to senescence. Kear (1973) found a sharp decline in the clutch size of captive Hawaiian geese beyond nine years of age. European sparrowhawk's breeding performance deteriorates after five years of age (Newton et al. 1981). No indications of reproductive inferiority among the oldest ospreys was noted. However, the breeders in this sample were relatively young, with none older than fourteen years. Spitzer (1979) discovered a successful osprey breeder twenty-three years old, suggesting that ospreys have numerous years of fertility beyond fourteen. As the banded population of ospreys in Virginia ages and increasingly older birds are reproducing, it will become possible to determine the extent to which reproductive depression associated with old age occurs.

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