FACTORS INFLUENCING MORTALITY IN NESTLING OSPREYS (*PANDION HALIAETUS)*: AN ANALYSIS OF BREEDING STRATEGIES

by

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ABSTRACT

JENNIFER ANNE RETTEW. Factors influencing mortality in nestling Ospreys (*Pandion haliaetus*): an analysis of breeding strategies. (Under the direction of DR. R. O. BIERREGAARD)

Breeding strategies are important to the evolution of species because they allow individuals to maximize reproductive output while minimizing investment. One such aspect of breeding strategy is nesting behavior. In Ospreys (*Pandion haliaetus*), the female remains at the nest to guard and brood the nestlings while the male hunts. A hierarchy is established among the nestlings through hatching asynchrony and sibling aggression. Aggression occurs primarily in the presence of food, but can also be triggered by other stress. Ospreys are territorial around the nesting site and chase away other Ospreys, as well as other species that present a threat to the nest.

Brood reduction is an adaptive mechanism by which birds can adjust the optimal brood size in a given season to fluctuations in the environment. In Ospreys, reduced prey delivery is the direct cause of brood reduction, with increased prey delivery causing an increase in survival of the nestlings. Sibling aggression further contributes to the size hierarchy set up by hatching asynchrony in the nest, but does not directly influence mortality itself. Sibling aggression occurs in nests with both high and low prey delivery and may be performed regardless of hunger levels. Female Ospreys may supplement the prey available to the nestlings, leaving the chicks unguarded to hunt. Nests with hunting females have lower mortality rates, indicating that increased parental feeding effort may act as a buffer to seasonal fluctuations in the environment.

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INTRODUCTION

Since 1946, many avian species have been negatively influenced by the widespread use of dichlorodiphenyltrichloroethane (DDT) and other biocides. Because Osprey (*Pandion haliaetus*) nests are so conspicuous, it was very obvious when the species' numbers declined. There have been many studies of the breeding biology of Ospreys. Ospreys tend to be tolerant of moderate human disturbance and nests are easy to access and observe (Poole 1984).

Low rates of reproduction in Ospreys were found in the Great Lakes area and in the north and mid-Atlantic coast in the 1960s and early 1970s. Approximately 90% of pairs nesting between New York City and Boston disappeared between 1950 and 1970 (Poole et al. 2002). Because the Osprey is a top-order predator in the aquatic food chain, it accumulates biocides such as DDT in its tissues. The amount of DDT exposure has been correlated with eggshell thinning and poor reproduction, causing severe population decline. With the reduction of DDT contamination in the environment, population numbers have increased drastically across New England (Spitzer et. al. 1978).

Although Osprey populations have nearly reached their pre-DDT numbers, conservation of the species still remains an important goal (Poole et al. 2002). Much is known about the species because it is one of the most studied birds of prey, but there is still a much that can be learned about its life history. Studies of reproduction are of particular importance to conservation of the Osprey because of the impact productivity has on population growth.

Ospreys exhibit a nesting mechanism known as brood reduction to adjust the number of young in the nest to a level that can be maintained due to environmental factors. Brood reduction is defined as selective elimination of nestlings by starvation during periods of food limitation because of different competitive abilities among nestlings (Lack 1947). This can allow for a variable clutch size such that during periods of good food supply a full brood can be fledged, but not all nestlings are risked during periods of poor food supply and parents can survive for future breeding attempts (Poole 1984). This phenomenon is often caused by hatching asynchrony, which is an interval of time between the hatching of the first and last egg. This occurs when birds initiate incubation before the clutch has been completely laid. A hierarchy among chicks is then established, with the oldest chicks most often becoming dominant to younger chicks (Heg and van der Velde 2001).

Several hypotheses have been proposed to explain why parents lay more eggs than they can typically raise to fledging. The theory of evolution suggests that breeding birds have evolved those traits that convey the greatest lifetime fitness. Parents should raise as many high-quality young as possible, that is, chicks that are better able to survive and reproduce. The "resource-tracking hypothesis" states that producing more offspring than can be fledged allows parents to gain from fluctuations in the environment. If resources are plentiful, more high quality offspring can survive to fledging without increased effort. Secondary chicks, eliminated from the nest when resources are low, would then provide a reproductive bonus for the parents if resources are plentiful. Another hypothesis is the "replacement offspring hypothesis," where secondary young are insurance against loss of primary young. This appears to be primarily the case in species, such as eagles, that lay two eggs but only fledge one chick. The secondary chick is always lost to starvation or siblicide unless the primary chick dies because of disease or predation. A third hypothesis is that of “sibling facilitation” in which secondary offspring may convey thermal benefits to primary siblings or may serve as a meal (Forbes and Mock 2000). Most brood-size hypotheses assume that hatching asynchrony is an adaptive trait that allows for the greatest number of viable offspring to fledge, thus conveying the greatest possible fitness for the parents (Valkama, et.al. 2002)

The purpose of this project was to describe nesting behavior and examine the effects of brood reduction on the breeding biology of Ospreys. Because the Osprey is easy to study, it offers a good opportunity to address several topics of interest, including the evolution of specific reproductive behaviors.

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INTRODUCTION

The Osprey (*Pandion haliaetus*), often known as the fish hawk, has a nearly worldwide distribution. Migrant subspecies breed in northern temperate zones and overwinter south of most resident subspecies. All but the southern-most populations are migratory. Resident subspecies breed and overwinter in southern temperate zones of the northern hemisphere and also in Australia (Poole et al. 2002). In New England, most male Ospreys migrate south in September (females leave in August) and return mid March. Young in their first year remain in the wintering grounds during the breeding season (Poole et al. 2002).

The Osprey breeds in cool temperate to subtropical regions. Nesting areas are dependent on water, as the birds need fresh, brackish, or salt water to catch fish. Ospreys prefer shallow water environments because they can only dive to a depth of one meter or less (Poole et al. 2002). The age of first breeding tends to be three years. In New England, some individuals may delay breeding one to two years (Palmer 1988). Older, more experienced pairs arrive sooner and lay eggs earlier than younger pairs (Poole et al. 2002).

Ospreys begin arriving in southern New England in late March, and males tend to arrive a week or two before females and reclaim previous breeding areas. A pair bond between male and female is often continued yearly for each breeding season, provided both members survive. Mate fidelity approximates 60 to 70% per year (Poole et al. 2002). Pairs have strong attachment to the nesting site, which may contribute to the high level of faithfulness between mates (Poole et al. 2002). Courtship feeding by the male seems to secure the pair bond. Poorly fed females are less willing to copulate and less likely to remain faithful to their partner. The high site fidelity and long term monogamy of Ospreys may allow breeding pairs to eliminate the early phases of the reproductive cycle (Poole 1985). This advantage could allow for earlier egg laying and less energy expended on nest defense and finding of a mate.

Early breeding is one advantage to long-term monogamy. Pairs that lay eggs later in the breeding season have lower clutch size, brood size, and number of fledglings. Pairs that lay eggs earlier fledge young that survive longer (Poole 1984). However, quality of young (as indicated by growth rate and number of fault bars in feathers) does not differ between pairs that lay early versus late (Steeger and Ydenberg 1993). There is no seasonal decline in food availability during the breeding season: thus, optimal clutch size is determined by a trade-off between the decrease in fitness of later hatched young and the delay accrued by the egg laying process. Ospreys reduce their clutch size when initiation of egg laying is naturally delayed. Timing of clutch initiation can be due to occupation of the nest by other species (i.e. Canada Geese) or condition of the female after courtship feeding by the male (Steeger and Ydenberg 1993). In addition, broods of three chicks grow more slowly than chicks with one or no siblings (Poole 1984), although Steidl and Griffin found no statistical significance to this difference (1991).

Nests can be built in trees or manmade structures. They can be of almost any height, on flat ground, and can be built on the shore or in the water. Poole et al. (2002)

listed four necessities for nest sites. They must be close to water for access to good feeding areas, have openness for ease of access to nest, be safe from ground predators, and have a wide stable base to support the large nest. Nests consist mainly of large sticks, although various other nesting materials are brought in throughout the breeding season. A new layer is added annually to a previously occupied nest, and a new nest takes approximately three weeks to build before egg laying (Palmer 1988). Ospreys often bring fishing line, beach toys, and plastic such as grocery bags to the nest for material that may cause mortality of nestlings. Studies in Westport, Massachusetts found that 2-4% of nestlings per year die or lose wings because of entanglement (Poole et al. 2002).

Productivity tends to be higher on artificial platforms than in live trees or snags. Pairs nesting on artificial sites have on average twice as many young than pairs nesting on natural sites (Poole et al. 2002). Palmer (1988) suggests four reasons as to why these platforms improve breeding success. They enable pairs to move to places farther from human disturbance, they reduce loss to some predators (particularly raccoons, *Procyon lotor*), they replace defective nest sites that may be blown down, and they increase the number of available nest sites.

Human disturbance has been found to sometimes decrease productivity of Osprey pairs but distance to water or other Osprey nests does not appear to affect productivity. Ospreys are easily adapted to humans and can successfully nest under many circumstances, such as nests on channel markers around constant boat traffic and nests near houses and highways. Pairs with nests near humans eventually become tolerant of human activity, whereas pairs nesting farther from humans are more sensitive to disturbance. Poole (1984) found that careful short-term visits to nests by researchers have negligible effects on the Ospreys.

Eggs are laid in southern New England from early April to early June, peaking mid to late April. There is a 2-3 day interval between the laying of each egg. The average clutch size is three, with a range of two to four eggs (Poole et al. 2002). Egg volume decreases from the first egg produced to the last, causing a substantial difference in egg size. The fourth egg is 8.2% smaller than the first and the third egg is 5.6% smaller than the first. The second egg is on average closer to the size of the first egg, differing by only 2.1% (Poole 1984). Incubation lasts an average of 39 days and starts with the laying of the first egg, although consistent incubation does not begin until the laying of the second egg. This causes the chicks to hatch asynchronously and there is a significant size and age disadvantage to the third chick over the second (Poole et al. 2002).

After the eggs hatch, the female remains at the nest constantly for approximately 30 days. The female shades the young and keeps them dry on rainy days for the first 5-6 weeks. The female distributes food to nestlings, feeding those that beg the closest and the most vigorously. Around 42 days, the young are very active, jumping up and down and exercising their wings (Palmer 1988). Large young will often take a fish delivered by the male and feed themselves. It takes approximately 50 to 60 days from hatching to fledging, but this depends on location, weather, and number of siblings (Poole et al. 2002).

Studies on growth show that Osprey nestlings fit a logistic curve for growth. There is no difference in growth rates between males and females, years of study, brood sizes, or in broods with or without nestling loss (Steidl and Griffin 1991). The average time for a chick to grow from 10% to 90% of the final weight is 36.7 days. An inverse relationship exists between brood size and weight of young at first flight, which occurs when the nestlings are 50 to 55 days old. Young remain dependant on adults until they are 93-103 days old (Palmer 1988). After fledging, some young will fly to nearby nests and be fed by adults that are not their parents. Parents do not seem to discriminate between their young and intruding fledglings, and do not attempt to drive away young that land on nests that are not their own. With the high natal site fidelity of Ospreys, this feeding of neighboring young could be an argument for kin selection because there is a high level of relatedness among closely nesting Ospreys (Poole 1982). Siblings tend to remain together after fledging. Young with siblings show greater initial success rates during hunting sessions than single young. Siblings will hunt together after fledging and tend to become efficient at prey capture more quickly than singles, suggesting that information transfer is important for hunting behaviors of related young. By the end of the post-fledging period, however, hunting success rates do not differ between single young and young with siblings, indicating that single young eventually catch up (Edwards 1989).

Weather is a significant influence on breeding success. There are fewer young in years of heavy rainfall. Even when brooded, if the nest becomes wet, mortality of eggs and chicks increases. Younger chicks are vulnerable to becoming too cold. Direct sun can also cause significant mortality among nestlings. This is especially true for younger chicks. Small young are susceptible to overheating on hot summer days (Poole et al. 2002). Severe storms can also cause nestling mortality. Storm killed young are most often older young because they are too large to be effectively brooded by adults. Poole (1984) found that severe storms caused a substantial number of deaths in a third of study sites. However, chicks were also emaciated, indicating that both starvation and exposure during the storms led to mortality. Weather can also cause a decrease in parental provisioning, which in turn can decrease nestling viability. Cloud cover or sun does not have a significant effect on hunting ability but wind speed and water surface conditions do. Precipitation increases the length of hunt duration such that prey delivery rates to the nest decrease in rain. Hunting is no longer profitable for adults in terms of energetic costs when wind speeds are greater than seven meters per second (Machmer and Ydenberg 1990).

Sibling aggression occurs mostly in broods containing three young. The intensity of aggression is inversely proportional to the daily food delivery rates. This can cause a differential growth rate among the nestlings (Palmer 1988). Dominance is established once the chicks are 7-10 days old. Older and thus larger young are strongly aggressive towards younger siblings especially at feedings. The difference in competitive abilities appears to be because of asynchronous hatching, differences in egg sizes, or differences in growth rates (Poole 1984). Nestlings of the same age, however, can vary greatly in size so differences in mass are often more of a determining factor than age in the formation of a dominance hierarchy (Machmer and Ydenberg 1998).

Dominance is established by aggressive pecking on the head and back of younger siblings, forcing submission. After dominance has been established, typically a simple threat of the dominant chick raising its head is enough to elicit submission from the weaker chick (Poole 1984). Sibling aggression and siblicide are believed to be an adaptation to ensure that the maximum portion of the brood can be successfully reared during periods of food scarcity. Dominant chicks are fed first and most during feedings, and younger chicks often starve if food is limited (Machmer and Ydenberg 1998). During times of regular and abundant food deliveries, there is typically no aggression or dominance established and the young feed equally. Parents never intervene in sibling aggression. Loss of nestlings is higher in nests with low rates of food delivery (Poole et al. 2002).

In general, nest predation is not a major factor in nesting mortality compared to starvation because of inaccessibility of many nests and vigorous nest defense by the adults (Poole 1984). Nevertheless, nest predation may come from a variety of sources. Land predators, such as raccoons, are a problem for nests on platforms not surrounded by water. Crows (*Corvus* spp.) have been known to take eggs from Osprey nests. Adult Ospreys will dive at Red-tailed Hawks (*Buteo jamaicensis*) that are close to the nest, but chase crows more during the nestling stage than during incubation (Palmer 1988). Bald Eagles have been known to take nestlings; however the Great-horned Owl is a more significant predator. It will prey on nestlings and will occasionally kill adults. In a southeastern Massachusetts study, over 20% of nestlings lost were probably due to Great-horned Owls (Poole et al. 2002).

Poole (1984) studied Ospreys that nested in loose colonies. He found that mortality of hatchlings was significantly affected by difference in the number of fish brought in to the nest, not the size of each individual fish. However, in his study the adults brought in mainly one of two species: alewife or winter flounder. The distance to foraging sites can affect the delivery rates brought to the nest by the male. In his study, Poole found nestling loss ranged 10-20%, with 75% of the deaths being caused by starvation. Partial loss of broods was therefore a normal circumstance. In cases where there were whole brood losses, half involved successive deaths of nestlings, indicating that disease, predation, or adult abandonment were not factors in chick mortality. Submissive chicks were often found with their heads and backs pecked clear of feathers and occasionally blood was found. However, chicks were never hurt bad enough to limit begging or ability to move. Submissive chicks were pushed to the outer edges of the nest during dominance displays and could have been forced off the nest. Aggression was found to be inversely related to rates of prey delivery (Poole 1984). Size differences among nestlings allowed for dominance and sibling aggression to be established. However, only 5.6% of weight differences could be attributed to differences in egg size where as 20-30% was due to hatching asynchrony, indicating that age differences are more important in determining the hierarchy of dominance than egg weights (Poole 1984). Steeger et.al. (1992) mentioned that it was difficult to determine whether breeding success depended on food availability or whether prey delivery rates depended on brood size, which could have been determined by a variety of other factors in Poole's study.

The purpose of the first part of my study was to examine and describe nesting behavior of Ospreys. Through intense observation of 27 nesting attempts on the island of Martha's Vineyard, my goal was to further increase the knowledge of general behavior of nesting Ospreys such as sibling aggression and parent-offspring feeding behaviors, as well as inter- and intra-specific interactions. In addition, it was the intention of this study to document several rare behaviors previously unrecorded. Because of the large number of hours dedicated to observations, this study was able to record a more detailed picture on Osprey nesting behavior in a non-colonial population.

METHODS

Study Site

Martha's Vineyard is an island seven miles off the coast of southeastern Massachusetts. As a result of glaciations, the northwestern side of the island is a hilly moraine composed of boulders and clay deposits, with deep water of the Vineyard Sound to the east (Fig 1). South and east of this moraine, extends a low, level glacial outwash plain consisting of sandy plains. Several so-called "Great Ponds" exist on the southern shore, created by glacial runoff and sand deposits. These ponds fill with fresh water from rain until they are drained into the Atlantic Ocean. Historically, the great ponds opened when rain runoff had filled them beyond capacity and a pressure differential from the great pond and sea level reached a point such that the water from the pond would break though the land bridge separating the two bodies of water. The pond level would then drop and salinity increase. Currently, the opening of most of the ponds to the ocean is controlled by humans in part for commercial fishing and to protect houses built along the shores of the ponds from flooding.

Although some Ospreys nest in loosely defined colonies, nests on Martha's Vineyard are fairly dispersed. Ospreys on the island hunt in the deep waters of the ocean and Vineyard Sound, saltwater lagoons on the north and east shores, and the great ponds along the south shore. Because the great ponds fill with rain until they are drained into the ocean, their salinity varies throughout the year. When some are opened in the spring, herring (*Alosa* spp.) spawn in them and are often landlocked when the ponds close behind them, providing abundant food for the local Ospreys.

In 1968, there were only two breeding pairs on the island, both in tree nests. Both pairs were fledging large broods, but the local population was not increasing. It was discovered that the local power companies had, for some time, been destroying Osprey nests built on telephone and power poles.

Although the island interior is heavily forested, due to salt spray, trees towards the coast (especially in the southern part of the island) tend to become stunted and shorter than power poles serving beach-front homes. Because Ospreys build nests on the highest and most conspicuous platforms available, many attempted to nest on these power poles. Due to the salt accumulation on the nest and other factors, nests on power poles are susceptible to electrocution and subsequent power outages for surrounding developments. The Felix Neck Wildlife Sanctuary began erecting nesting platforms taller than the telephone poles around areas where Ospreys were attempting to build nests. From 1969 until around 1985, the population on the island grew exponentially, indicating that the population was limited by the availability of nest sites (R. Bierregaard, pers. comm.). In the mid 1990s, reproductive success was low, with substantial numbers of young starving and nests failing (G. Ben David, pers. comm.). This observation, along with the 40 or so available nesting poles that are not used, suggests the population now is limited by prey availability. However, relatively high reproduction rates from 1998 through 2004 (R. Bierregaard, unpubl. data) paradoxically suggest that prey availability should not be limiting the population.

Since 1998, data has been collected on the number of breeding pairs and reproductive output on Martha's Vineyard. The number of breeding pairs has remained relatively constant at around 65 pairs, which nest almost entirely on man-made nest poles. Reproductive rates (0.64 to 1.57 fledglings/active nest; R. Bierregaard, unpubl. data) have been above the estimated "break even" level of 0.8 young per active nest (Sptizer et al. 1983) in all but one year. There are approximately 115 nest poles on the island.

It has been noted that the abundance of winter flounder, typically a staple prey item for New England Ospreys after migrating herring have left the area midway through the breeding season, has decreased in this area. Since the 1990s, when Osprey reproductive success on Martha's Vineyard was significantly reduced (G. Ben David, unpubl. data), flounder have been conspicuously absent from their diet, probably because of over fishing, as evidenced by a decrease in the harvest of the species by the local fishing fleet (R. Bierregaard, pers. comm.).

Observations and Data Collection

Observations of nesting behavior were recorded from the last week of May to the first week in August in 2004 and 2005 field seasons. Observations consisted of four-hour blocks conducted during the period from hatching to the fledgling of chicks at approximately 8 weeks of age. Nests were selected randomly from all areas of the island: 11 in 2004 and 16 in 2005. Observations were conducted using a 20-60 power spotting scope and 8 x 42 power binoculars. Observations were taken during three time increments: AM, NOON, and PM. The AM time period started between 0520 and 0600 hours, the NOON time period started between 0930 and 1030 hours, and the PM time period started between 1430 and 1530 hours. Observations were made in fair weather (sun), moderate weather (cloudy), and poor weather (rain). Both weather and time differences were spread randomly among the 27 nests such that each was observed for approximately equal proportions of each situation.

Sibling aggression within the nest was defined as follows. The weakest act of sibling aggression is threat behavior. This involves a head raised with outstretched neck and beak open, and pushing with the chest and body with open wings is often included. Pecking is the next strongest form of aggressive behavior. In this case, one chick pecks down on another with its beak, usually hitting the head or upper back of the other chick. The final form of aggression is biting and twisting. This usually follows a peck and is where one chick bites loose skin on the neck, face, back, or wing of another chick and twists. Sometimes chicks lock beaks and twist if there is no definite submissive or dominant chick. Submissive behavior is characterized by a hunched over body posture, wings spread slightly and head ducked. Often, a submissive chick is chased to the edge of the nest, where it faces outwards, leaning away to avoid contact from pecking.

The male and female Ospreys that bred at the nest were termed parents or breeders. Ospreys that hatched at the nest were termed chicks or nestlings before the fledged, and fledglings after they had taken their first flight. Ospreys that did not belong to the nest (e.g. were not a breeder, chick, or fledgling) were termed intruders.

RESULTS

Sibling Aggression

The majority of aggressive behaviors within the nest were among nestlings. Aggression began when the chicks were approximately one week of age and continued throughout the nestling period until fledging. In the 27 nests, 374 acts of aggression were observed among siblings. There were 137 observations of threat behavior or pushing and chasing of one chick by another, 168 observations of pecking behavior, and 69 observations of biting and twisting of the skin of one chick by another. There were 14 nests that contained three chicks at some point during the nesting period, and they averaged 1.799 acts of aggression per hour. There were 21 nests that contained two chicks at some point during the nesting period, and they averaged 0.753 acts of aggression per hour. There was only one nest that contained four chicks during the nesting period, and it averaged 0.5 acts of aggression per hour. Nests with only one chick (either hatched only one chick or the other siblings died) did not have any sibling aggression.

Acts of aggression were usually elicited by the presence of a fish in the nest and fighting over access to the feeding parent. Aggression was also caused by the presence of intruder Ospreys not belonging to the nest or disturbance of the nestlings and parents by humans. In several instances, aggression from a dominant caused significant damage to a submissive chick. Downy fuzz was seen pulled out after pecks and bites, and there were several cases where bald spots and blood could be seen on submissive chicks. At one nest, two chicks caused such severe aggression on the smallest chick that it did not get up after several hours of observation and it is suspected that siblicide may have occurred. Once a chick has died, the body usually remains in the nest. Several dead bodies were observed left in the nest throughout the study period. In one case, a body was found on the ground below the nest, and the chick may have been pushed out. Even under the most severe aggression, however, no chicks were ever observed falling out of nests.

Aggressive behavior was not exclusive to the chicks. In four nests, there was aggression of the chicks directed to one of the parents. Most of the behavior was threatening and pushing, with some pecking. In one instance, the chick grabbed and pulled on the wing of the female (see detailed accounts). The behavior was elicited by the presence of prey in most cases, but adjustment of nesting material by the parents also caused threatening and other aggressive acts.

There were two instances of aggression between the nesting pair. One occurred shortly after nest failure. The second instance involved intruder Ospreys near the nest and aggressive behavior from the male directed to the female. The chicks were one week old and may have been killed in the encounter (see detailed accounts).

Fledgling Behavior

Chicks practiced flying before they fledged. First, they held on to the nest very tightly with their feet and flapped their wings. Next they would step or hop while flapping their wings. Finally, they would jump and hover over the nest for a few seconds at a time. Usually, the chicks were not observed on their first flight, but one chick in a nest of three accidentally fledged when it hovered and a sibling moved underneath it and it could not land (see detailed accounts). One chick was also observed practicing hunting near the nest (see detailed accounts).

Feeding Behavior

The female parent was the one that fed the chicks in nearly all cases. When a fish was brought to a nest, the female usually took it from the male forcefully. In some instances, the male would not immediately give up the fish, and the female would pull on it with her talons and beak while the male held on with his talons. A male, however, never left the nest with the fish after he had brought it unless the female appeared uninterested in it (e.g. did not try to take the fish from the male). Thus gender could be determined from behavior. If an Osprey brought a fish to the nest and left it, in general this was the male. If an Osprey brought a fish to the nest and began immediately feeding the chicks, this was the female. Although rare, males were observed feeding offspring in 4 of the 27 nests. If both the male and female brought fish to the nest, or the male had recently brought two fish, and there were multiple chicks in the nest begging, sometimes the male would feed a second or third chick from the other fish. If the female was gone, the male would generally wait and look around, but if the chick begged, he would sometimes feed it.

The female's tendency to feed the chicks is strong. Females were often observed chasing the chicks around the nest, peeping in order to promote feeding. After chicks fed, they would often lie down and face away from the female. In one case, a full chick yawned, and seeing an open beak, the female placed food into the chick's mouth.

Intraspecific Interactions

The breeding pair responded to intruders with calls and shaking of the wings. In some cases, if an intruder ventured too close or tried to land on the nest, the breeding Ospreys would jump up and bat them off the nest and/or chase them around the nest area. In many cases, this resembled airplane dog-fighting, where the breeder would hit the intruder mid air with its talons or wings, and the intruder would attempt to evade the breeder with tight turns. In some cases, the 'dog fight' would take both the breeder and intruder to the ground, or nearly so.

There were two observed cases of intruders landing on the nest with chicks when no parent was guarding. In neither case were the chicks harmed, but in both the chicks begged at the intruder as if it were a parent. In the first, the intruder left when a begging chick moved too close to it. In the second, the female parent returned, alarm calling, and chased the intruder off the nest and around the area in a 'dog fight' manner. In both cases, the intruder seemed uneasy, feathers laid close to the skin and looking around in a wary manner.

One case of kleptoparasitism was observed, where the female had recently brought in a fish and an intruder Osprey landed on the nest and stole the fish from the female (see detailed accounts). There was another case of attempted kleptoparasitism, but both male and female were at the nest and the male was able to pass the fish to the female before it was stolen, and then defend the nest area from the intruders (see detailed accounts).

There were some cases in which the 'intruder' was a breeding Osprey at a nearby nest. In one case, the female was hunting over a sandbar and was chased back to her nest area by another Osprey. Once the retreating female Osprey had moved into her own territory, the chasing Osprey became an intruder and the female went from being chased to chasing the intruder. In the other cases, two males chased each other over a territory that encompassed both their nests (see detailed accounts). There were also some cases of intruder chicks. The breeding Ospreys seldom differentiated among their own chicks and the intruder chicks, but chicks within the nest differentiated between their siblings and the intruder chicks (see detailed accounts).

Interspecific Interactions

The Osprey poles were often near trees, bushes, and birdhouses. Several smaller birds within the nest territory, such as grackles (*Quiscalus quiscula*), tree swallows (*Tachycineta bicolor*), crows (*Corvus brachyrhynchos*), and kingbirds (*Tyrannus tyrannus*), would mob the Ospreys if they were too close. The crows especially caused complications with nesting (see detailed accounts). In some cases, a crow would attack an Osprey, smaller birds would mob the crow, and the crow would leave. Two species, starlings and house sparrows, were found to live within the sticks underneath the nest on the nest pole. The Ospreys usually ignored these birds, and were ignored in return. In one case, a house sparrow came up onto the nest to look for nesting material, and hopped around near the female. She snapped her beak at it when it got too close, but otherwise ignored it as it took nesting hay.

The breeding pair chased other species when found near the nest. Crows, Canada geese (*Branta canadensis*), Red-tailed Hawks (*Buteo jamaicensis*), Turkey Vultures (*Cathartes aura*), and Great Black-backed Gulls (*Larus marinus*) were all driven away from the nest. Turkey Vultures especially caused issues when a chick died and was left in the nest (see detailed accounts).

Ospreys varied in their reactions to humans. Some pairs reacted very strongly, flushing from the nest and alarm calling, when humans appeared anywhere within visual range of the nest. Others had built up a tolerance such that they did not react unless a human was directly underneath the nest pole. One nest was positioned at the entrance to Oak Bluffs Harbor, and boats would pass within 50 feet of the nest, blowing horns, and the female would not look up from the nest and barely paused if feeding chicks. Another nest was in a backyard of a house under construction and thus constant human disturbance. A third nest was located at a beach access for the Trustees of Reservations. The gate to the beach access was not opened until June 15th. At the beginning of the study, the female was highly sensitive to human presence, but she gradually became accustomed to people as cars, bikes, and joggers passed by the nest as the season progressed.

Nesting Material

Most of the nests were made up of sticks and both the males and females continuously brought in both small and large sticks to the nest. Seaweed to line the nest was another major component, as was rope in many different colors. Clumps of dried grass or other small plants were often substituted for seaweed. In a few cases, the plants had sufficient roots to resprout and grow in the nest. Plastic grocery bags, fishing line, lobster mesh bags (green, yellow, and blue) were also prominent in most nests. Items also seen included several beach toys (shovel, rake, etc), red and blue swim trunks, a dead crab body, a large piece of green rubber/plastic construction material, duct tape, a plastic water bottle, an aluminum soda can, green scum/algae from a nearby pond, a PVC pipe, deflated balloons with ribbon, cellophane wrap, and goose primary flight feathers.

The breeding pair constantly brought in nesting material throughout the entire study. Either the male or the female would bring in a stick, for example, and then work it into the nest. A stick could be moved around several times in the nest before satisfactory placement was achieved. The chicks began mimicking this behavior by two weeks of age, picking up sticks and reworking them into the nest. Both males and females appeared to bring in equal amounts of nesting material.

DISCUSSION

Sibling aggression was more intense in nests with three or four young versus two, but this is because there are more interactions in nests with more than two young. With two chicks, the dominant sibling only has to subdue one submissive sibling. With three or four chicks, there is a more complicated hierarchy. One chick (alpha chick) may be dominant to the other two, while the second (beta chick) is dominant to the third and fourth (gamma chicks). In some cases, there can be co-dominance between the top two chicks, where it is unclear which chick is the alpha and which is the beta. However, if there is a third, gamma, chick, it is usually very markedly submissive to the other two, tends to be much smaller, and if it fledges it does so later than its larger dominant siblings. Steidl and Griffin (1991) also found that aggression was more intense in broods of three versus two young.

Sibling aggression not only prevented smaller chicks from accessing food, but several cases were observed where the smaller chicks were excluded from shelter of the female from both sun and rain. An important aspect of parental care is brooding by the female to keep the chicks warm and shading them from the sun (Poole et al. 2002). Exposure can contribute to the death of chicks, though it is not as important as starvation in determining mortality of the young (Poole 1984).

Aggressive behavior was not restricted to sibling-sibling interactions and can occur when stresses other than hunger are involved, such as threats from intruder Ospreys or because of loss of chicks in the nest. Chicks were observed attacking parents, usually associated with the presence of food or the death of a sibling. In addition, there were some instances when parents attacked each other after stress. This indicates that aggressive behaviors are not exclusive to fights between siblings over food but occurs for a variety of reasons associated with stress between individuals. O'Connor (1978) proposed that aggression should evolve with or without energetic limitations or food supply. Thus, it is not surprising that aggression occurs despite hunger levels or sibling interaction, or that Ospreys are ubiquitously aggressive when threatened.

Osprey intruders were not tolerated at the nest. For each pair there appeared to be a very specific nest territory. Breeders would chase intruders away from the nest up to a point at which they would stop the pursuit and return to the nest or a perch nearby. In one case, a female was chased back to her nest by another nearby breeder. However, once the female and the chaser crossed into the female's nest territory, she began to chase the now intruding bird until it left. Intruder fledglings were also evicted from the nest. Poole (1985) found that colonial Ospreys may feed chicks that are not their own. Parents in my study did not chase fledgling Ospreys; however, chicks appeared to become more aggressive towards intruder fledglings than their own siblings. There may be two explanations for this. First, sibling chicks might be able to recognize each other and would not be aggressive to siblings landing on nests. The other case may be that siblings do not recognize each other and are aggressive to all fledglings that land on the nest; however, chicks that were born at the nest may refuse to be evicted regardless of aggression from their sibling. In effect, there is a general low level of aggression to all fledglings that land on the nest and those that do not belong respond to it by leaving, whereas those that were born at the nest do not respond and remain on the nest. Because this study was completed when the chicks fledged, the exact explanation for this behavior could not be ascertained.

Most small passerine bird species were ignored by the Ospreys. Larger birds, such as Red-tailed Hawks and Turkey Vultures were pursued when they flew close to the nest, presumably because they appeared to be something that might prey on the chicks. Both males and females reacted strongly to the presence of a large bird near the nest by chasing it away.

Ospreys' reactions to humans were varied. Some pairs were very sensitive to human approach or activity, whereas others ignored humans unless they walked directly underneath the nest. The degree of response appears to be due to acclimation by the Ospreys. If there is a lot of human activity when the Ospreys are nesting, they are less likely to react to approach than those that are not used to seeing humans. However, nesting Ospreys appear to be very adaptive, and those that were previously not used to seeing humans can become adapted to human activity and successfully rear young. They reduce the sensitivity of their response by no longer reacting to activity, such as the approach of cars or bicycles, or humans not directly under the nest.

CHAPTER TWO: BROOD REDUCTION IN OSPREYS

INTRODUCTION

Natural selection favors organisms with high lifetime reproduction. Increased fitness is achieved by maximizing survival and reproductive output. However, if an organism puts too much energy into one year's reproductive effort, the probability of surviving to the next year may be greatly reduced. Since both aspects are important for natural selection, there is thus a tradeoff between effort extended towards producing progeny and that which is necessary for survival. In cases of species with low annual mortality rates, such as large birds, a reduced effort in a given season can maximize lifetime reproduction (Lack 1947, Williams 1966). Even though the effort put forth is lower than that which would maximize reproductive potential for a particular season, the lifetime reproductive potential will be maximized by increasing the chance of reproducing in following years.

There is an optimal balance between the number of offspring parents can produce in a given season and the quality of those offspring. As energy expended on producing a single individual offspring is increased, the fitness of that offspring increases, although the number of additional offspring parents can produce decreases (Smith and Fretwell 1974). In many cases, birds that lay more eggs than the species average will have more difficulty providing food and thus will have reduced number of chicks that survive to fledging (Williams 1966). Those that produce less than the species average, however, may have reduced fitness because of loss of reproductive potential in the form of extra fledglings that the parents could have raised (Smith and Fretwell 1974). Parents may be selected for reproductive flexibility, whereby an individual changes its pattern of production of number and quality of offspring during its lifetime. This would allow for the individual to take advantage of fluctuations in the environment (Howe 1976).

Brood reduction is the selective loss of offspring to adjust brood size to fluctuations in the environment and thus changes in food availability. Species that depend on unpredictable food supplies are expected to show hatching asynchrony as a mechanism for successful brood reduction (Lack 1954). Asynchronous hatching occurs when a female begins incubation of the eggs before the clutch is complete, and it results in a sequential rather than simultaneous hatching of young. Chicks that hatch earlier generally have greater growth and probability of survival that later hatched, marginal offspring (Forbes and Glassey 2000). Parents feed the most active (largest and strongest) chicks in the brood, which are typically the oldest individuals. When those become full, food is then given to the smaller young (Ricklefs 1965). If food decreases abruptly during the nesting period, more food is given preferentially to the larger young and smaller ones starve without endangering the entire brood. If all chicks were fed equally and food decreased, then the entire brood may be lost. This method allows for the greatest number of viable offspring to fledge, conveying the greatest possible fitness for the parents (Valkama et al 2002).

Hatching asynchrony creates a size hierarchy in the nest and insures an initial advantage to those young that hatch first (Howe 1976). In addition, differential growth rates between male and female hatchlings can further contribute to size differences within a brood (Schaadt and Bird 1992). Egg size causes differences in hatching weights as well (Parsons 1975, Howe 1976). The resulting size hierarchy within a nest has been argued to be an adaptation for adjusting brood size to the available food supply (Lack 1947).

Hatching asynchrony results in two levels of offspring: primary and secondary. Loss of secondary (marginal) offspring does not necessarily free up more resources for primary offspring. Primary chicks receive food needed for survival before the secondary chicks are fed. If there is inadequate food for growth for the entire brood, then marginal chicks are lost without harming the primary offspring. Hatching asynchrony creates a buffer by which primary offspring are protected from fluctuations in available food resources (Forbes and Glassey 2000).

The results of hatching asynchrony can be exaggerated through sibling aggression by increasing the effect of the hierarchy. In many raptor species, more eggs are laid than can be successfully fledged in normal years. Chicks are hatched asynchronously and younger birds often starve (Stinson 1979). In some eagle species, the older chick actively causes the death of the younger chick through harassment regardless of food abundance, a fratricidal behavior known as “Cainism.” In other cases, the younger sibling is killed through starvation as well as active attacks from the older chicks (Stinson 1979). Sibling rivalry arises from the differential parental investment received by each offspring. Parents may influence competition among siblings by the degree of their investment (Heg and van der Velde 2001).

Sibling aggression increases with decreased food availability and may contribute to brood reduction. Larger chicks are strongly aggressive towards younger siblings, especially at feedings, and thus are able to receive a greater share of delivered food when hungry because of increased competitive ability. Broods show significantly more aggression at feedings when they are hungry versus satiated. Aggression causes a large feeding advantage to dominant siblings at the expense of submissive siblings and sometimes the mother as well, as she feeds last after the young are satiated (Machmer and Ydenberg 1998).

Birds of prey are known for asynchronous hatching of young and thus are a good model to study brood reduction and sibling aggression (Valkama et al 2002). The Osprey is a good example of a species that exhibits brood reduction in that chicks are hatched asynchronously and greater numbers of young fledge when food supplies are not limited.

Ospreys lay eggs at a 2-3 day interval, and the average clutch size is three. Incubation starts with the laying of the first egg, although consistent incubation does not begin until the laying of the second egg. This causes the chicks to hatch asynchronously. There is a significant size and age disadvantage to the third chick compared to the second. The second chick is approximately 1.4 days younger than the first whereas the third chick hatches about 3.9 days after the first (2.5 days after the second). Survival of a second chick is approximately 88% whereas the third chick has only a 38% chance of surviving to fledging (Poole et al. 2002).

Aggression among sibling Ospreys establishes a dominance hierarchy within the nest. Due to asynchronous hatching, differences in egg sizes, and differences in growth rates, competitive abilities among the chicks differ. Poole (1984) found that 20-30% of weight differences among nestlings were due to hatching asynchrony. Dominance is established once the chicks are a week old by aggressive pecking of younger siblings by older ones, forcing submission. Submissive chicks are often found with their head and backs pecked clear of feathers and occasionally blood is found. After dominance has been established, typically a simple threat of a raised head by the dominant chick is enough to elicit submission from the weaker chick. Parents never intervene in sibling aggression (Poole et al 2002).

Osprey nests with two young need an average of 4.6 fish per day while nests with three young need 5.6 fish per day (Van Daele and Van Daele 1982). Energetic studies indicate that one female with two chicks needs 794 grams of fish per day and a female with three chicks needs 1048 grams of fish per day. However, different fish species have different lipid concentrations and different edible proportions and thus give different energetic values to Ospreys (Poole et al 2002). Water content in fish flesh ranges from 65-85%, while proteins and lipids make up 15-20% and 0-15%, respectively, and net energy available from various fish species depends mainly on its lipid content (Prevost 1982). Thus, the energy delivered to nestlings will vary with the types of fish that are brought to the nest.

The female distributes food to nestlings and preferentially feeds those that are closest and beg the most vigorously. In a study where adults brought in mainly one of two fish species, alewife (*Alosa spp*.) or winter flounder (*Pleuronectes americanus*), mortality of hatchlings was significantly affected by difference in the number of fish brought in to the nest, but not the size of the fish. It was found that nestling mortality ranged from 10-20%, with 75% of the deaths caused by starvation. Partial loss of broods was therefore a normal circumstance (Poole 1984).

Although the intensity of sibling aggression is inversely proportional to the daily food delivery rates, brood reduction occurs even in areas of abundant prey and appears to adjust brood sizes such that surviving chicks can maintain minimum growth rates. Most mortality occurs two to three weeks after hatching when growth reaches the steepest section of the logistic growth curve (Steidl and Griffin 1991). Thus sibling aggression may be an important factor in nestling survival even when food is abundant.

Brood reduction in Ospreys appears to be an adaptive mechanism to increase breeding success such that the maximum number of young survive given the unpredictable availability of resources. It is known that sibling aggression increases with decreased prey delivery rates and that survival decreases with lowered prey availability and increased aggression. However, the extent to which nestling survival is dependent on prey availability and sibling aggression remains unclear. The purpose of this part of my study was to examine the influence of food availability and sibling aggression on the survival of nestlings. The goals of this study were to determine to what extent mortality of young is caused by limitation in food availability to the nest, to describe the degree of sibling aggression as it relates to mortality in the nest independent of prey delivery rates, and to determine to what extent female parental effort relates to the survival of nestlings.

METHODS

Study Site

Martha's Vineyard (see Study Site, Chapter 1) offers a unique opportunity to study brood survivability as it relates to prey delivery rates and aggression in the Osprey. Population dynamics have been studied on the island for the past 35 years (G. Ben David and R. O. Bierregaard, unpubl. data). Introduction of artificial nesting platforms allowed for a drastic increase in population size on the island. Between 1975 and 1990, the number of nesting pairs increased from 2 to 60, approximately doubling every five years

(Poole et al 2002). Since the late 1980s, the population has leveled off (R. O. Bierregaard pers. comm.).

Data Collection

I observed 27 Osprey nests over the field seasons of 2004 and 2005 (see Observations and Data Collection, Chapter 1). Measures of mortality were taken by counting the number of chicks surviving in a nest over several time points during the breeding season. Each time point consisted of four hours of observation approximately once a week for each nest. This study was based on observation from a distance and could not determine mortality of eggs or mortality of hatchlings younger than one week, because the small size of the young chicks made it difficult or impossible to see them above the rim of the nest.

Prey delivery rates were recorded by estimating the total amount of prey delivered to the nest per hour (grams of fish per hour) and the frequency of prey delivered (number of fish per hour). Species of prey were identified using A Field Guide to Atlantic Coast Fishes: North America (Robins and Ray 1986) as a reference.

Grams of fish delivered to the nest per hour was estimated by measuring length of the fish delivered and converting that to grams using a fish length/weight database as follows. The length of each fish delivered was estimated to the nearest centimeter using the body size of the parent bird as a reference. This is an appropriate estimate used in a variety of Osprey prey studies, and can be judged to within 5 cm, about one quarter the length of the Osprey's tail (Poole 1984, Steeger et al 1992). Prey data was transformed from estimated length to weight using the formula $W = aL^b$, where weight (W) is in grams, length (L) is in centimeters, and a and b are parameters particular to the species of fish. Values for parameters a and b were obtained for each species from the FishBase database (Froese and Pauly 2006). Number of fish delivered to the nest per hour was determined by counting the number of fish delivered by the parents during each observation period.

Poole (1984) observed that there are consistent differences existing between observers in the ability to estimate fish length, especially for smaller fish specimens. This could have significant effects on calculations of prey delivery rates. Although this could be a significant source of error in this study, calculations and estimations are internally consistent because there was only one observer.

Intensity of sibling aggression was recorded to determine if sibling aggression has an effect on chick mortality and the degree that sibling aggression is correlated with food delivery. Acts of aggression were weighted based on the strength of the act because stronger acts were more likely to elicit submissive behavior from weaker siblings than threat acts (personal observation). The weakest act of sibling aggression is the threat behavior, which sometimes included pushing with the body, and was given a weight of 1. Pecking is the next strongest form of aggressive behavior and was given a weight of 2. The final form of aggression is biting and twisting of the skin on the neck or back, and was given a weight of 3. Aggression was measured only in the observation periods when there were two or more chicks in the nest.

Statistical Analysis

A logistic regression was used to determine the effect of prey delivery rate and sibling aggression on chick mortality because mortality is a dichotomous variable and thus the logistic regression, rather than a simple linear regression, is the appropriate statistic. The event/trial method of logistic regression using the SAS program was run to remove the effects of nest and brood size by examining mortality of all chicks in the nest. Mortality of the nest consists of two variables: number of chicks hatched and number fledged. The events variable contains the number of positive events and is the number of chicks fledged (survived). The trials variable is the total number of trials and in this case is the total number of chicks hatched in the nest. Prey delivery rate were scored as grams of fish per hour and number of fish delivered to the nest. Degree of sibling aggression was taken as a weighted average in acts of aggression per hour. Correlation analyses were run to determine if there was a correlation between acts of aggression and prey delivery to the nest. In addition, the sequential Bonferroni correction was used to ensure a constant level of significance with the use of multiple tests. All means are reported as $\pm$ one standard error of the mean.

RESULTS

Over one thousand hours of total observations were recorded for 27 active nests in the summers of 2004 and 2005. A total of 67 chicks hatched in the nests during the study period (Fig 2). Of these, 35 fledged and 32 died, which corresponds to a 52.2% fledging rate. The average number of hatchlings per nest was 2.48, and the mean number of fledglings per nest was 1.30. The age of nestling mortality ranged from two to six weeks of age and peaked at 3 to 4 weeks (Fig 3). Mortality increased most from two to four weeks of age (Fig 4).

Prey Delivery

Of the prey species delivered to the nest, 97% could be identified and included alewife and herring (*Alosa spp.*), striped bass (*Morone saxatilis*), bluefish (*Pomatomus* *saltatrix*), white perch (*Morone americana*), scup (*Stenotomus chrysops*), summer flounder (*Paralichthys dentatus*), tautog (*Tautoga onitis*), brown trout (*Salmo trutta*), Atlantic mackeral (*Scomber scombrus*), yellow perch (*Perca flavescens*), chain pickeral (*Esox niger*), American eel (*Anguilla rostrata*), Atlantic cod (*Gadus morhua*), and Koi/goldfish. Herring and alewife were the most commonly captured fish and comprised 30.3% of the prey delivered to the nest, followed by bluefish (18%), scup (16.9%), white perch (14.6%), summer flounder (6.1%), and striped bass (5.7%). The eight remaining species constituted less than 3% each of the total prey delivered.

Prey delivery rate in grams of fish was significant in determining mortality within the nest. Nests with 100% survival had the greatest amount of food delivered, averaging 169.6 $\pm$ 18.14 grams of fish per hour. Nests with 67% survival averaged 145.2 $\pm$ 37.08 g/hr, with 50% survival averaged 121.1 $\pm$ 16.70 g/hr, with 33% survival averaged 84.2 $\pm$ 11.67 g/hr, and with 0% survival averaged 83.4 $\pm$ 16.42 g/hr (Fig 5). Prey delivered to the nest in grams of fish per hour was highly significant in the logistic regression procedure ($X^2 = 10.4843$, $p = 0.0012$) in determining mortality within the nest.

Prey delivery rate in number of fish was also significant in determining mortality within the nest. Nests with higher numbers of fish delivered to the nest had greater survival than those that had fewer numbers of fish delivered (Fig 6). Nests with 100% survival averaged 0.43 $\pm$ 0.088 fish delivered per hour. Nests with 67% survival averaged 0.29 $\pm$ 0.033 fish/hr, with 50% survival averaged 0.29 $\pm$ 0.042 fish/hr, with 33% survival averaged 0.22 $\pm$ 0.026 fish/hr, and with 0% survival averaged 0.21 $\pm$ 0.042 SE) fish/hr. Number of fish per hour delivered to the nest was highly significant in determining mortality in the logistic regression procedure ($X^2 = 6.7048$, $p = 0.0096$).

Aggression within the nest

A total of 374 acts of aggression were observed across the 27 nests. Of those, 137 were classified as a threat or push (level 1), 168 were classified as a peck (level 2), and 69 were classified as biting or twisting (level 3). Sibling aggression did not show any trend in relation to mortality within the nest (Fig 7). Nests with 100% survival averaged 0.86 ± 0.439 acts of aggression per hour. Nests with 67% survival averaged 0.80 ± 0.203 acts/hr, with 50% survival averaged 0.56 ± 0.166 acts/hr, with 33% survival averaged 2.60 ± 1.098 acts/hr, and with 0% survival averaged 1.11 ± 0.356 acts/hr. Sibling aggression was not significant in the logistic regression procedure ($X^2 = 0.6916$, $p = 0.1574$) in determining mortality within the nest.

Sibling aggression was not found to be significantly correlated with either grams of fish delivered to the nest ($r_{xy} = 0.01883$, $p = 0.9257$, Fig 8) or number of fish delivered to the nest ($r_{xy} = -0.09214$, $p = 0.6476$, Fig 9). Though there was a trend for increased aggression at lower delivery rates, there was no significant effect of feeding rate on aggression because there was tremendous variation among nests. Regardless of feeding rate, dominant siblings fed first, then subordinate siblings. Thus, while feeding triggered aggression in many cases, aggression did not vary with feeding rate in a constant manner.

Female Parental Effort: Hunting Behavior

In 14 of the 27 nests, females brought in at least one fish to the chicks before they fledged. These females contributed from 9.1% to 41% of the total prey delivered to the nest. Females that hunted left the nest to hunt beginning when the chicks were two weeks of age and continued throughout the season fairly constantly until the chicks fledged. Three females were observed hunting near the nest; two on the wing and one from a perch (see detailed accounts). There were many instances where females left for periods of time and returned wet, but it could not be determined if the females had been hunting or bathing. At higher nestling survival rates, more females hunted than did not (Fig 10). Presence of hunting females at the nest was significant in determining mortality in the logistic regression procedure ($X^2 = 7.1404$, $p = 0.0075$).

DISCUSSION

Chick survival was strongly influenced by feeding rate and the participation of the female in hunting, but not by sibling aggression. Mortality increased most from 2 to 4 weeks of age, peaking at 3 and 4 weeks. This corresponds to a one-week delay from the period of most intense growth. This seems logical, because during ideal conditions Ospreys increase in mass the most from 2 to 3 weeks of age (Steidl and Griffin 1991), indicating that this is the peak energy requirement period. In less than ideal conditions, the growth rate for Osprey nestlings would slow down as the food available for growth continued to be inadequate. With continued inadequate prey availability, the chicks would starve to death. This does not happen instantaneously at the time when growth needs are greatest, but is a process that is drawn out over approximately one week.

Fluctuation in prey delivery is the primary cause of brood reduction in Ospreys. During the course of this study, higher rates of prey delivery allowed more offspring to survive to fledging, whereas lower rates of prey delivery were associated with higher mortality rates. Both frequency of delivery (number of fish per hour) and total amount of food delivered (grams of fish per hour) were significant in determining chick survival. These results are consistent with previous findings that food supply is the major factor influencing brood size in Ospreys (Poole 1984).

Sibling aggression was not significant in the logistic regression procedure in determining mortality in the nest. This means that increased aggression between siblings did not necessarily mean that more chicks would die. Aggression appears to occur regardless of hunger level or food supply. Previous studies have found that hatching asynchrony allows brood reduction to occur because some chicks are less able to compete with others, and during seasons of low food availability, the younger siblings starve. Sibling aggression further emphasizes the dominance hierarchy set up with hatching asynchrony by allowing the older, first hatched chicks to feed first and grow faster. Older chicks probably have more experience accepting and handling food and are better suited to gain dominance over younger siblings (Heg and van der Velde 2001). Later hatched chicks suffer from being smaller and having slower growth rates because they are not fed as much as the older chicks (Steidl and Griffin 1991). Thus it appears that sibling aggression may indirectly influence brood reduction by emphasizing the size hierarchy, but it does not affect mortality directly. Several studies have found sibling aggression in Osprey broods in areas with ample prey availability (Jamieson et al. 1983, Steidl and Griffin 1991, Schaadt and Bird 1993).

Machmer and Ydenberg (1998) found that sibling Ospreys were much more aggressive when hungry than when satiated. Sibling aggression exaggerated the feeding advantage of older nestlings in that when hungry, older chicks received a larger portion of the food at the expense of their younger siblings. This is consistent with the results of my study in that sibling aggression emphasizes the size hierarchy, yet does not directly effect survival of chicks. While hunger did affect aggression in Machmer and Ydenberg's study, brood asymmetry was much more significant in determining sibling aggression within a nest. The closer chicks were in size and age, the more strongly they competed and exhibited aggression. Much of the variation in aggression levels among nests was attributed to differences in competitive asymmetry within each brood. The effect of food availability on aggression in Osprey nests appears to be extremely variable (Machmer and Ydenberg 1998). This is no doubt why aggression was not significantly correlated with prey delivery in my study, and why aggression did not effect survival directly.

At least two possible scenarios might explain the apparently paradoxical result that sibling aggression was not significant in determining mortality within the nest. First, zero sibling aggression was hypothesized to indicate that the chicks were all well fed and mortality would be low. However, in the course of the study, several cases were observed to have zero or low instances of sibling aggression and yet the entire nest failed. For example, nests that hatched two chicks and fledged none ranged in intensity of aggression from 2.0 to zero. One possible conclusion to this is that if the chicks were too weak to perform aggression and substantiate the hierarchy set up through hatching asynchrony, inadequate prey delivery would be likely to cause 100% mortality. If there is only enough food for one chick to survive to fledging and there are two chicks in the nest fed equally because neither can afford the energy to attack and exclude the other, then both will die. Second, sibling aggression could be most intense for a short period of time when the hierarchy is becoming established. After establishment, aggression may decrease. Poole (1984) found that after the hierarchy was established, a simple threat behavior was enough to elicit submission from weaker chicks. Since my study only recorded observations approximately once a week, the critical period for aggression, if there is one, may have been missed at some nests.

Parents can increase the rate of food delivery by increasing their hunting effort. It has been noted that females Ospreys hunt extremely rarely before the chicks fledge, spending most of their time at the nest brooding or defending the chicks (Poole 1984, Palmer 1988, Poole et al. 2002). In my study, half of the females delivered prey to the nestlings before they had fledged. Others were also observed exhibiting hunting behavior near the nest, though they failed to bring in a fish. Having a hunting female at the nest influenced survivability. Nests with hunting females fledged more young than those without hunting females. In Barn Owls (*Tyto alba*), females shift from caring for the chicks in the nest to sharing the foraging efforts with the males when the male food provisioning no longer matches the energy needs of the nestlings (Durant et al. 2004).

Poole (1984) studied populations of Ospreys nesting in loose colonies and reported that females rarely hunted before the chicks fledged. My study examined a non-colonial island population where females may have been more willing to leave the nest unguarded to hunt because there were rarely other nests in close proximity. In addition, there are no important predators of Osprey chicks on the island. Most artificial nesting platforms have metal guards to prevent raccoons from climbing the poles and there are very few reported Great-horned Owls (*Bubo virginianus*) and no Bald Eagles (*Haliaeetus leucocephalus*) nesting on Martha's Vineyard. It could be the case that females were able to leave the nest unguarded without major consequences. Female Ospreys in colonial populations may not be able to leave as easily because of the higher frequencies of interactions with intruder Ospreys and thus a greater need for nest defense.

It has been suggested that females are more aware of the nutritional needs of the chicks because they distribute food to the nestlings (Dawson and Bortolotti 2002). If male prey delivery at any particular nest is considered relatively constant, females can then supplement the diet by hunting if they determine the nutritional needs of the chicks are sub-optimal. Indeed, many studies of raptor species have found that male provisioning is fairly fixed and determined by food availability, territory quality, and weather conditions (Dawson and Bortolotti 2002, Durant et al. 2004). Thus, female Ospreys that hunt can act as a buffer against the unpredictability of prey availability and thus brood reduction in a fluctuating environment.

Age of parents may also be a factor in determining optimal brood size. Inexperienced breeders may not be able to provide sufficient food for their young, and brood reduction can limit the number of chicks to a level more easily maintained by them (Parsons 1975). Poole (1984) also found that reproductive success in Ospreys increased with experience and age of the parents, and that older birds delivered more prey than younger birds. While it was beyond the scope of this study to determine age of breeding Ospreys, this factor may explain the extreme variation in survivability among the nests on the island, in that some hatched and fledged three chicks while others completely failed. Steidl and Griffin (1991) found that variation of breeding success within a colony was due to differences in the males' ability, experience, or motivation to provision the nestlings. Additionally, older females paired with younger males may have the experience to hunt for the brood if provisioning rates by the males do not meet energetic demands of the nest. Females in other raptor species commonly adjust their hunting effort to that of the male (Durant et al. 2004).

In conclusion, my data suggests that the rate of prey delivery is the direct cause of brood reduction in Ospreys. Higher levels of available food allow more chicks to fledge, while lower levels of prey cause an increase in mortality. Ospreys hatch asynchronously such that a size hierarchy is established and younger chicks are lost if prey delivery is not adequate to feed all of the nestlings without endangering the entire brood. Sibling aggression further emphasizes the dominance hierarchy so that older chicks feed before younger siblings. Sibling aggression does not directly influence mortality, and occurs in nests with both high and low prey delivery. Female parents can supplement the food availability to the chicks if prey delivery by the males does not meet the energetic needs of the nest. Nests with hunting females have lower mortality rates, indicating that increased parental effort may act as a buffer to seasonal fluctuations in the environment.

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APPENDIX A: DETAILED ACCOUNTS

Aggression of Nestling on Parent

In 2004 at the Chip Chop nest, the female had a scup and was attempting to feed the chick. The chick lunged at the female, trying to take the fish. The female backed away, trying to tear off bites to feed the chick. The chick pecked at the female, head raised in a threat similar to sibling aggression when another chick is feeding. The female threatened back and the chick pecked again, grabbing the female’s wing at the wrist/scapulars and twisted. The female left to feed for 10 minutes and returned with the presence of an intruder Osprey at the nest. The chick repeated biting and twisting the female’s wing after which she left again. After 30 minutes she returned again and the chick allowed her to feed it.

A similar behavior was found in 2005 at the Felix Neck nest. The male delivered a fish and left, and the six to seven week old chick had fed. The male returned to the nest with seaweed for nesting material and the chick threatened it, wings shaking and alarm calling (the same behavior used by the parents against intruder Ospreys). The male left and returned with more nesting material. The chick threatened, wings shaking and alarm calling. The male left and returned a while later with a scup. The female tried to take the fish but the male would not let go. The female pulled and the chick threatened. The male let go of the fish and the chick pecked him on the head twice. The chick threatened again and the male left. One week later, the chick was still responding to the male as if he were an intruder Osprey, even when he delivered fish.

In 2005 at the Hart Haven nest, a three-week-old chick threatened and pecked the female's head once when she adjusted sticks in the nest. The nest had previously contained two chicks and lost the second sometime in the past week.

In 2005 at the Lake Tashmoo nest, both chicks had fledged. Both threatened the male when he returned to the nest, beg/alarm calling and lunging at him. The male left and returned, and the behavior was repeated. The male left and returned with a stick. He worked it into the nest and one chick pecked at him. The male left, returned, and one chick tried to bite him. He left and returned, and the chicks begged but did not act aggressively. The male left and returned with a large stick. As he worked it into the nest, he hit one chick over the head. The other, previously aggressive chick lunged at the male and pecked him twice. The male left.

Aggression between the nesting pair

In 2004 at the Lobster Hatchery nest, there was an instance of aggression between the breeding pair. The nest had recently failed within the past day or two, and the dead body of a chick could be seen on the nest. The male flew to the nest. The female jumped up and batted at the male with her wings. The male guard called and flapped his wings at her, then stood on the nest with his wings apart and hunched over. Both male and female were looking into the nest and moving nesting material around. The male began jumping and batting at the female with his head raised in a threatening pose. The female turned her back to him and flapped her wings to prevent aggression. The female left, circled, and returned. The male repeated the aggressive behavior, causing the female to fall off the nest. Eventually, both male and female left the area.

In 2005 at the Rachel's Way nest, the female had just fed small chicks (0-1 week of age) and left, presumably to bathe because she returned wet. An intruder flew in close to the nest and both male and female guard called and flapped their wings. This is typical nest defense behavior in the presence of an intruder Osprey. After the intruder left, the male began pecking and jumping at the female. The female hunkered down in submissive pose: crouched position, wings drooped, head ducked. The male pecked at her head and neck repeatedly, circling around and attacking the female. The male circled all around the nest and stepped where the chicks were lying down. After 25 minutes of standing on the edge of the nest in submissive pose, the female attempted to brood, head ducked. The male pecked her if she moved (e.g. to fix nesting material). Later, the female stood and the male began pecking at her again. She hunched in submissive pose. This continued for about an hour. It was difficult to determine if the chicks were still alive because they were small and low in the nest; however, the male jumped around the nest, talons extended, where they had been laying. Six days later, the male was standing on the cross arm of the nesting pole and the female had abandoned the nest. There was no activity of any chicks in the nest.

Accidental Fledging

In 2005 at the Big Homer Pond nest, one chick was practicing flying by jumping and hovering in the air above the nest. It was close to the edge and on one of the jumps, its siblings moved underneath it and it could not land. The chick half fell, half flew off the nest. It circled around the nest and the siblings alarm called and shook wings when it hovered over them. It tried to land on a nearby birdhouse but missed grabbing it with its feet because it was flying too high and too fast. It circled around and hovered over the nest again, trying to land. After several passes and 4 minutes later, the chick crash-landed onto the birdhouse. It did not slow down enough and fell forward, but grabbed the edge of the birdhouse firmly and was able to pull itself back upright. It stayed on the birdhouse for the remainder of the observation period (30 minutes).

Chick Practicing Hunting

In 2005 at the Lobsterville nest, a chick left the nest and hovered over the water 100 feet from the nest. It flew low over the water and dropped itself to the surface. It flew up, skimmed the water a couple of times, then shook itself out and returned to the nest. About 45 minutes later, the same chick flew out over the water again, flew down low and flopped back down into the ocean. It floated, rose up, and tried again. It was not diving into the water as an adult Osprey would, but fell into the water and resembled more of a dive from a brown pelican. Two hours later, it repeated this behavior, flying low over the water near the shore and falling in, floating with its wings outstretched for a moment, then flying back up.

Female Perch Hunting

In 2004 at the Scrubby Neck nest, the female was observed hunting from a perch in a pond near the nest. The female left the nest and landed in trees on the edge of Watcha pond, where she would sit and watch the water, dive down, and return to the trees if she had not caught a fish. This behavior was repeated either until she caught a fish, in which case she returned to the nest, or until she began hunting on the wing. She flew down the length of the pond, hovering and diving, repeating until she caught a fish. This female caught 11 of the 27 total observed fish brought into the nest.

Kleptoparasitism

In 2005 at the Big Homer Pond nest, the female left to hunt when the chicks were 3 weeks old and the male had not delivered a fish for at least 3.5 hours. The female had been leaving for 6-10 minutes at a time, and returning wet. She left again to hunt and returned with a large bluefish (approximately 50 cm). The fish was still alive and flopping around in her talons, and almost knocked over the female several times. The female picked at the eyes and mouth some, but the fish continued to flop, making it difficult to begin eating it until it died. Twenty minutes later, the fish had not been eaten very much. An intruder flew in and landed on the corner of the nest. The female alarm called and flapped her wings, but could not fend off the intruder because of the large fish in her talons. The intruder grabbed the fish towards the middle and fell off the nest, using the weight of the fish and gravity to pull it out of the female's talons, then flew off with the fish.

In 2004 at the Lake Tashmoo nest, several intruders were circling around while the female was guard calling and shaking her wings. The male arrived in the midst of the intruders with a relatively small fish (approximately 30 cm). One intruder also tried to land on the nest. The male dropped the fish to the female and left. Several intruders tried to land on the nest and take the fish. The female batted off three attempts and continued with a defensive posture and calls. The male circled around and chased intruders from the air. The female did not begin to feed the chicks for 7 minutes after the encounter because of nest defense.

Intruder versus Breeding Ospreys

At the Mink Meadows nest in 2004, the female had been collecting nesting material from the nearby beach and marsh. She flushed another Osprey from a nearby perch, which happened to be a housekeeper at the Goff Tree nest. The housekeeper returned to its nest, chased by the Mink Meadows female. The housekeeper then chased the female back towards the Mink Meadows nest, and then she chased it. This continued back and forth for 2 to 3 minutes until they flew out of sight. The Mink Meadows female returned to her nest after 10 minutes.

There were several incidences between the Lake Tashmoo nest male and Lake Tashmoo Tree nest male in 2004. In one instance, the two males guard called and chased each other, and then gripped talons for a few seconds before releasing. In another, several intruder Ospreys were circling around both nests, and both males had been chasing them. The Lake Tashmoo nest male left to circle around the nest area. The tree male left his perch to chase the other male. For about 8 minutes, the two males chased each other, landed and called, and chased and batted each other with their wings and talons. The tree male returned to his perch and the other male swooped at him several times, talons outstretched. The tree male jumped up several times to fend off the other male. The other male finally returned to his perch near his nest. The interaction between the males seemed to be set off by stress of other intruders.

There was a sandbar offshore from the Lobsterville nest that contained summer flounder. The sandbar was also close to a nest at the Outermost Inn. The female from the Lobsterville nest was observed hunting over the sandbar. She flew back after a while, chased by another Osprey. Once the two had passed an invisible barrier, the Lobsterville nest female began actively chasing the intruder Osprey. The intruder flew over the nest and the female swooped after it in the 'dog fighting' manner. Both circled around the nest area and two of the three Lobsterville nest chicks hunkered down. The intruder left over trees towards the Outermost Inn nest and the Lobsterville female returned, circling up on air thermals, back towards the nest. The female shook herself out midair and flew back to the sandbar. There, the other Osprey (probably one of the Outermost Inn nest's breeding pair) began chasing her back towards the Lobsterville nest. Once the two had crossed back into the Lobsterville territory, the female reversed and began chasing the intruder Osprey back towards the sandbar. Another intruder flew into the Lobsterville nest area and the female stopped pursuing the Outermost Inn Osprey and returned to the nest.

Intruder Chicks

In 2004 at the Lake Tashmoo and Lake Tashmoo Tree nests, a chick termed 'floater' moved between the two nests. Both nests fledged two young, but at this time only one chick at each nest had fledged. There was one unfledged chick at each nest, and one 'floater' chick that had fledged, but which nest it belonged to could not be accurately determined. The other fledged chick was missing. The floater chick landed first on the Lake Tashmoo Tree nest after a parent brought a fish to the unfledged chick. The unfledged chick picked at the fish, guard called and flapped its wings. It ate the fish, still guard calling, and finished after 30 minutes. Both chicks then preened. The floater chick picked at something in the nest, poked at the sticks. It then left, flew to the Lake Tashmoo nest, and landed with the female and unfledged chick. It guard called and begged, and the unfledged chick and female showed no abnormal behavior towards the floater chick. The floater chick left and circled between the two nests. It was mobbed by a crow and tried to return to the tree nest, but the tree nest chick guard called, jumped at it, and kicked it off the nest. The floater chick landed on a dead tree in between the two nests. After approximately 30 minutes, the floater returned to the Lake Tashmoo nest and began begging intermittently with the unfledged chick, but left the nest again after 3 minutes.

Five days later another observation was made of chick interactions. The fledged chick from the Lake Tashmoo nest chased another fledgling (intruder) Osprey away from the nest area for 2 to 3 minutes. Later, another intruder chick flew in and circled around the nest. Both chicks from the Lake Tashmoo nest guard called and shook wings at it. The intruder chick dove at the fledged chick, then flew towards the Lake Tashmoo Tree nest. It landed on a dead tree near the nest and near both the fledged and unfledged chick from this nest. The fledged chick shook wings and guard called at it. Both chicks (fledged and intruder) left and circled. The intruder chick landed on the tree nest and the fledged chick landed on a dead tree near the nest. The intruder chick and the unfledged chick fought over a fish in the tree nest: beg and guard calling with raised heads. The unfledged chick did not give up the fish. The intruder chick left, circled, and tried to land on the tree nest again. The unfledged tree nest chick batted it off three times. The intruder chick circled and landed near the fledged chick and the fledged chick guard called and shook wings. A fourth chick arrived, and both tree nest chicks guard called and shook wings at it. The fourth chick left after 20 minutes and flew towards the Lake Tashmoo nest. The Lake Tashmoo unfledged chick guard called and shook wings. The fourth chick tried to land on the nest, but the adult male hit it in the air near the nest and chased it away. It flew back around the Lake Tashmoo Tree nest (other chicks guard calling), and then flew back to the Lake Tashmoo nest. The unfledged chick guard called, but the fledged chick landed unmolested. It is believed that this chick is the fledged chick from the Lake Tashmoo nest. Meanwhile at the Lake Tashmoo Tree nest, the other intruder chick left the dead tree and landed back on the tree nest. The unfledged tree nest chick guard called and batted it off. The intruder chick circled close a few times, then returned to the dead tree. The fledged chick guard called at it, then left its perch and returned to the nest, where it was allowed to land unmolested by the unfledged chick. The fledged chick took the fish the unfledged chick had been eating. The neighbor chick from the Lake Tashmoo nest (formerly called fourth chick) returned to a perch near the tree nest. Both tree nest chicks beg and guard called at an adult Osprey flying around the nest area. The adult dove at the intruder chick. The intruder chick ducked and flapped its wings. The adult flew over to the water, landed, waded in and bathed. The neighbor chick left and returned to the Lake Tashmoo nest. An adult flew in and chased the intruder chick off the dead tree while the chicks in the nest guard called. The adult landed in the dead tree where the intruder chick had been, then left after a while. The neighbor chick returned to its former perch near the tree nest. A parent brought a fish to the tree nest and the two chicks in the nest fought over it: both lunged for the fish, tugged at it (beak of one, talons of the other), sibling aggression (chick with fish in talons pecked the head of the other). The fledged (dominant) chick got the fish and ate.

In 2005 at the Squibnocket nest, two chicks had survived to fledging. A third chick landed on the cross arm of the nest pole. Both nest chicks alarm called and shook their wings, and one hopped and lunged towards the intruder chick until it left. One nest chick moved to the cross arm and the other nest chick left. The third intruder chick returned to the nest and the cross arm nest chick jumped on its back, alarm calling. The second nest chick returned to the nest, also alarm calling. The intruder chick left and the first jumped at the second and pecked its head until it left. The second nest chick circled around the nest, beg called and landed on the nest again. This time, the first nest chick tolerated it. The third intruder chick flew over the nest, and both nest chicks alarm called and shook wings. The intruder chick landed on the nest and the first chick jumped at it and pecked its head. The intruder chick and second nest chick both left. The second nest chick circled around, beg called, and landed on the nest. The intruder chick circled around, trying to land on the nest, but the nest chicks alarm called and shook their wings. The intruder chick left, then returned after 5 minutes and tried to land on the cross arm. One of the nest chicks jumped across the nest, lunging at the intruder chick. It flew off and circled, tried to land again, then left.

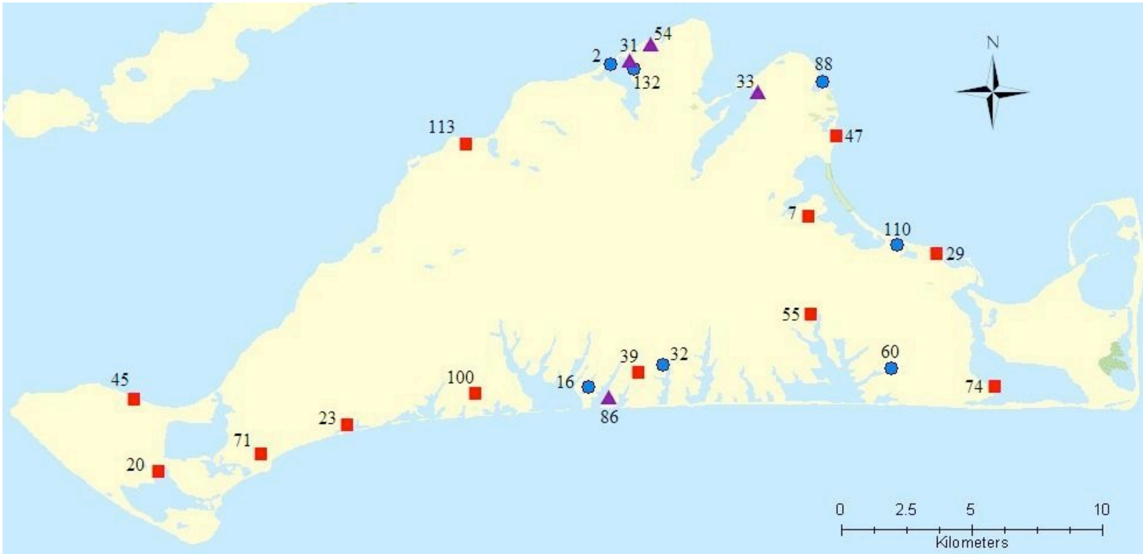
Ospreys and Crows

At the Rachel's Way nest in 2004, the female guard called at crows near the nest. The crows appeared to be nesting in pine trees 50 to 100 feet from the Osprey pole. The female left to chase one crow, swooped at it where it landed in a tree near the nest, then returned to brood. The crow flew away from the female. At a later date, the female stood from incubating, calling in a defensive posture, and chased and attacked a nearby crow. The crows mobbed her in return. The female returned to the nest and the crows returned to the trees. She guard called at the crows flying around the nest area. One crow began repeatedly diving at the female's head. She jumped up to counterattack it once, then hunkered down and guard called. The crows eventually left back to the trees. The female left again to chase a crow, was mobbed by two others in return, and both she and the crows returned to their respective nests. This repeated a second time, with the female constantly guard calling. Another crow dove at the female's head about five times, flying down, pecking at her though not striking, flying back up, hovering, and repeating. The female hunkered down, calling, and sometimes striking back at the crow. She left again to chase a crow about 30 minutes later, another crow flew in and both mobbed her. She returned to the nest, but stood rather than incubated. The crows also mobbed intruder Ospreys that flew into the nest area. The female, guard calling at the intruders, also occasionally left incubating to chase them even if they were not near, perhaps because of increased stress from encounters with the crows. Four days later, the nest had been abandoned.

Ospreys and Turkey Vultures

In 2005 at the Quenames nest, a second chick had recently died within the past week. The male delivered a fish to a living chick (5 to 6 weeks old). Flies were buzzing around the dead body. A Turkey Vulture approached and both the chick and the male alarm called. The vulture swooped around the nest and the living chick hunkered down. A second vulture approached as well. The male alarm called and flew off after the vulture, chasing it through the woods and out of sight. The male returned quickly to the nest and remained alert.

APPENDIX B: FIGURES



Nest Name	Nest Number	Nest Name	Nest Number
Chip Chop	2	Mink Meadows	54
Felix Neck	7	Wintucket Cove	55
Long Point	16	Slough Cove Road	60
Squibnocket	20	Jaws	71
Young Noe Moore	23	Katama Point	74
Eel Pond	29	Big Homer Pond	86
Lake Tashmoo	31	Oak Bluffs Harbor	88
Scrubby Neck	32	Quenames	100
Lobster Hatchery	33	Cow Bay	110
Athearn Road	39	Guiney	113
Lobsterville	45	Lake Tashmoo Tree	132
Hart Haven	47		

Figure 1: Map of Osprey nesting sites on Martha's Vineyard, Massachusetts. Blue circles correspond to nests observed in 2004, red squares correspond to nest observed in 2005, and purple triangles correspond to nests observed in both years.

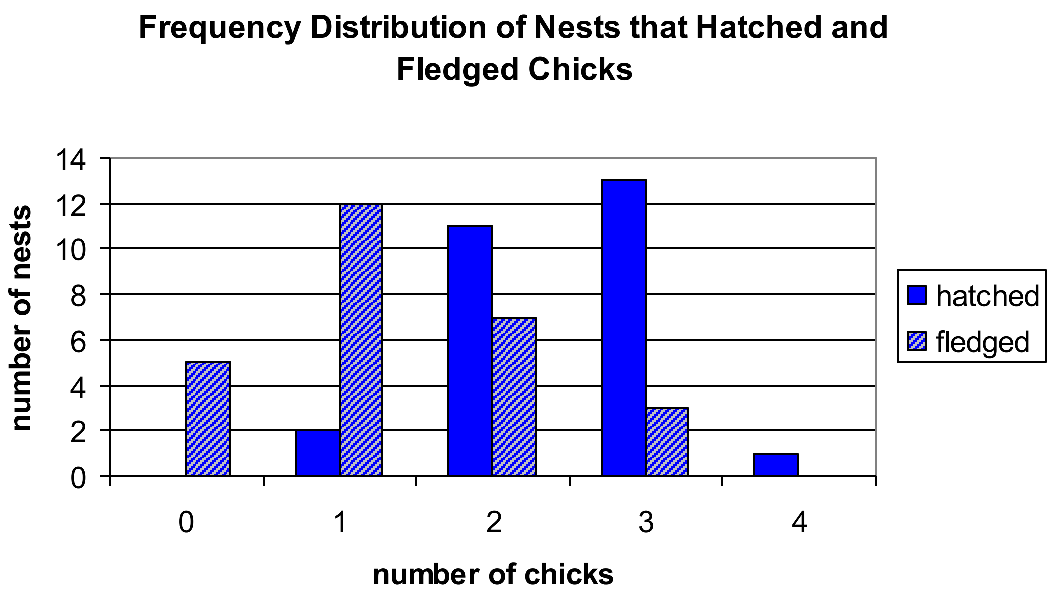


Figure 2: Number of nests that hatched and fledged a set number of chicks.

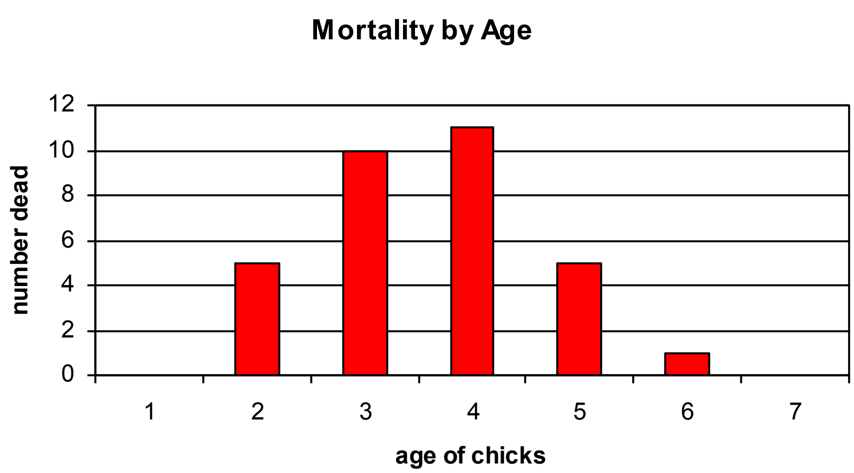


Figure 3: Mortality of chicks by age.

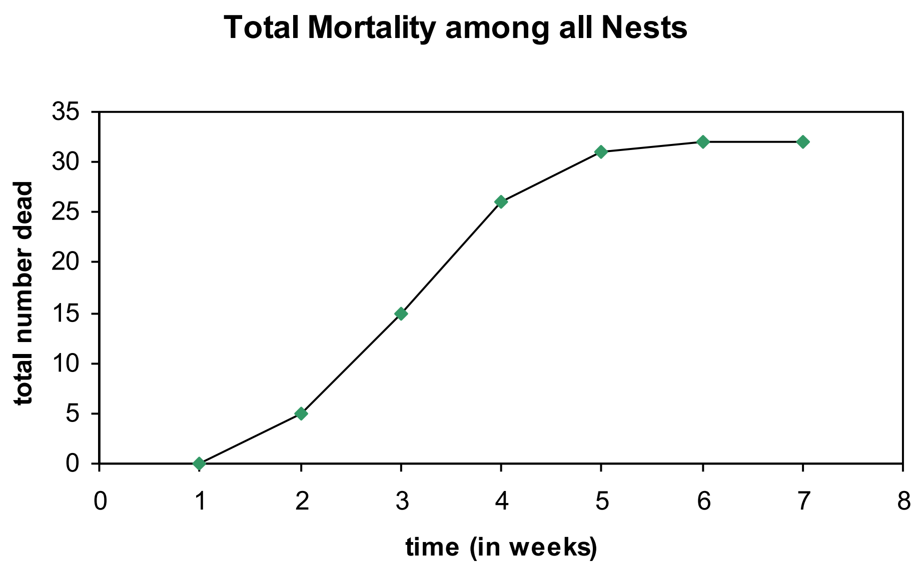


Figure 4: Chick mortality continued over the breeding season. Mortality of chicks increased at the highest rate between two and four weeks of age.

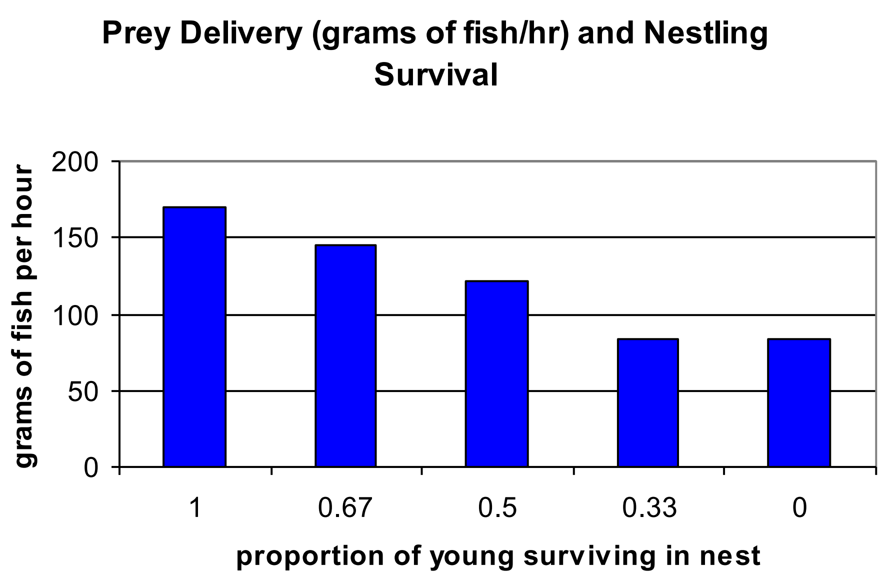


Figure 5: Prey delivery in grams of fish delivered to the nest per hour. Survival decreases as prey delivery decreases.

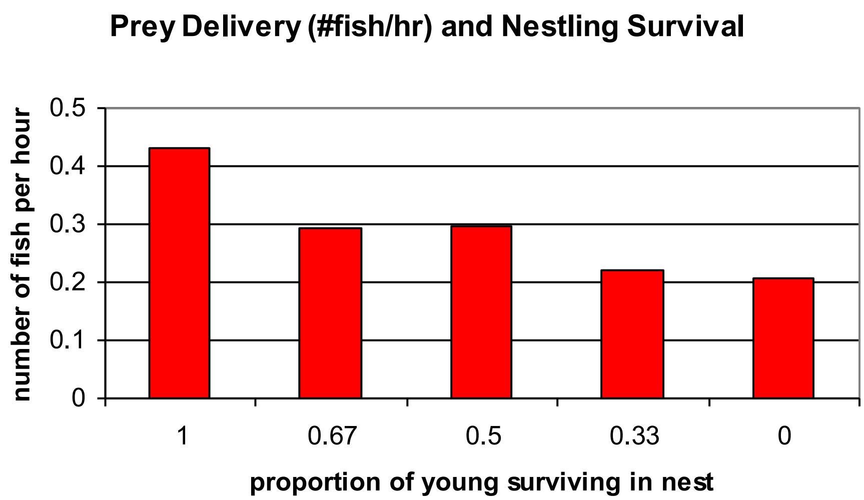


Figure 6: Prey delivery in number of fish delivered to the nest per hour. Survival decreases as prey delivery decreases.

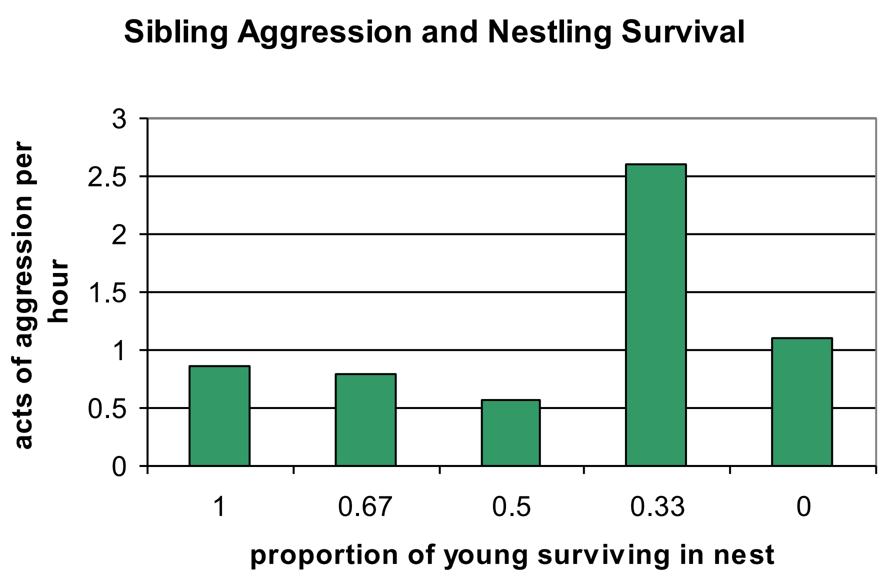


Figure 7: Number of aggressive acts among siblings per hour. Chick survival is not influenced by sibling aggression.

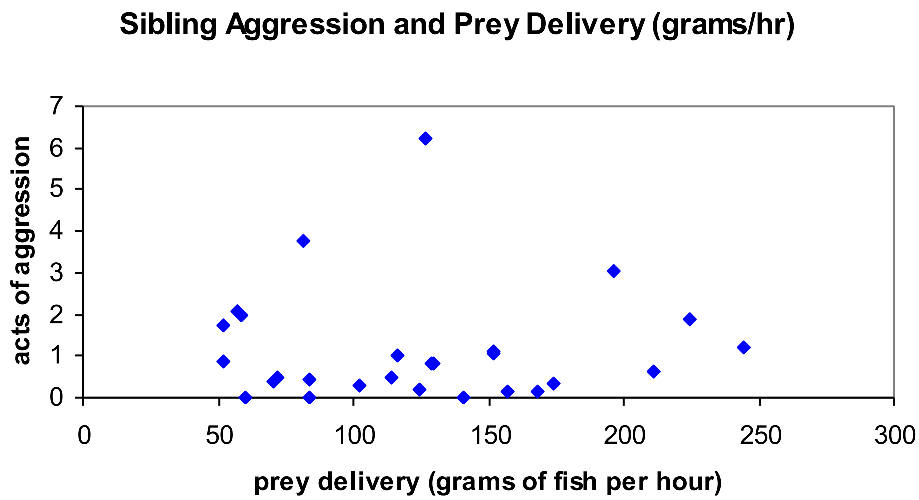


Figure 8: Prey delivery in grams of fish per hour and aggressive acts per hour at 27 nests. Aggression was calculated from interactions of two or more chicks. The two variables are not significantly correlated (p>0.05)

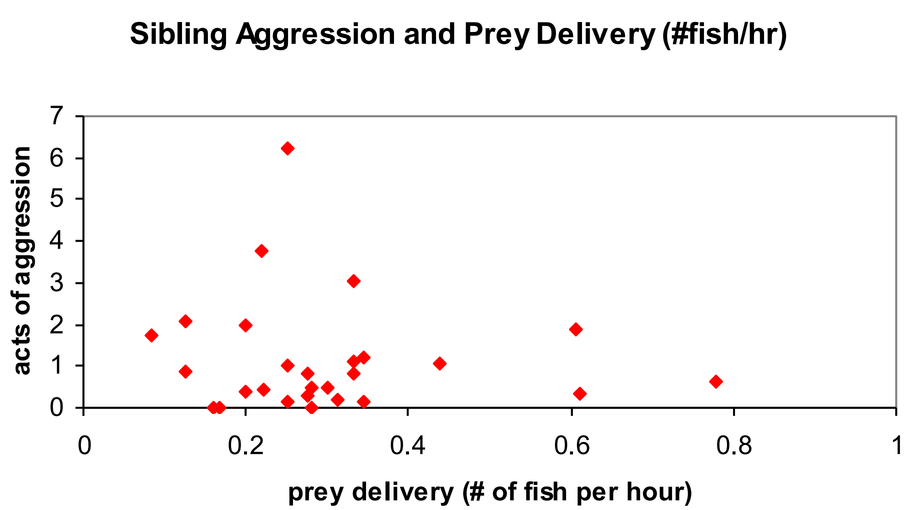


Figure 9: Prey delivery in number of fish per hour and aggressive acts per hour at 27 nests. Aggression was calculated from interactions of two or more chicks. The two variables are not significantly correlated (p>0.05)

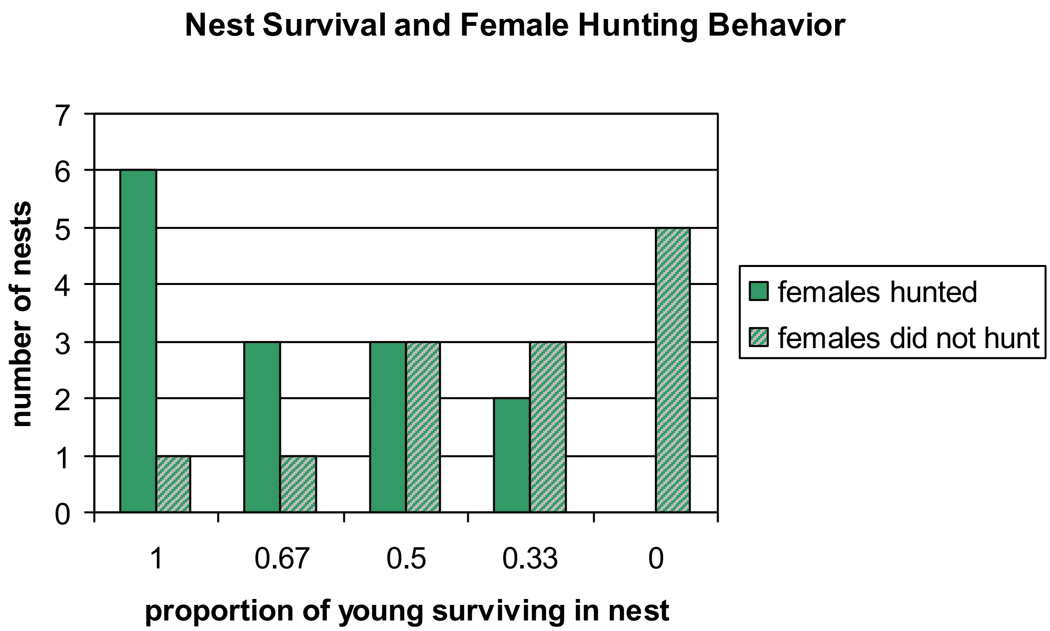


Figure 10: Comparison of survival at nests where females hunted and did not hunt. 14 of the total 27 nests had females that hunted.