

Status and Habitat Use of Breeding Northern Harriers
at Cape Cod National Seashore

Rhys V. Bowen

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Direct correspondence to:

Rhys Bowen

24 Beach St.

Foxboro, MA 02035

Ph: 508-698-3599

Email: rvbowen@worldnet.att.net

SUMMARY

1. This report presents the results of a two year field study of the breeding ecology of Northern Harriers (Circus cyaneus) in the Cape Cod National Seashore (CCNS). Harriers are of interest because their populations have declined markedly throughout the Northeastern United States, and consequently they have been listed as a Threatened species under the Massachusetts Endangered Species Act. This study was designed to gather information on the Northern Harrier's current status and management needs in CCNS, and the major research objectives were: to survey as much of the suitable harrier habitat in the park as possible and determine the number and spatial distribution of harrier nesting territories; to quantify the reproductive success of nesting harriers; and to determine what habitat types harriers utilize for nesting and foraging in CCNS.

2. I resided on Cape Cod and conducted field research full-time during the harrier breeding seasons of 2004 and 2005. I spent a total of 1873 hr afield, with each season being divided into two main phases: from mid-April through the end of June my primary research task was searching for breeding harriers and their nest sites (1390 hr of search time in the two years combined); and from July through early August I made follow-up observations of all nests to measure their productivity and habitat characteristics (483 hr of field time). Observations of foraging behavior were made incidentally in the course of other research tasks.

3. The breeding population of harriers in CCNS in 2004 consisted of 10 nesting pairs, which was probably the largest breeding population anywhere on the Massachusetts mainland and therefore of statewide conservation significance. The population in 2005 was smaller, comprising five nesting pairs plus four other pairs that mated and established a breeding territory early in the season but did not progress to nesting. It is unknown which year, 2004 or 2005, is more representative of the long-term average population size of harriers in CCNS. The harrier population density for the park as a whole was 0.5-1.0 nests per 10 sq. km, which is below the rangewide average population density of 1.8 nests per 10 sq. km. This suggests that CCNS at present provides adequate but not good quality breeding habitat for Northern Harriers.

4. Harrier nesting territories were not uniformly distributed throughout CCNS in 2004. Instead half of all territories (5 of 10) were clustered in the East Harbor area. The other five territories in 2004 and the five nesting territories in 2005 were widely scattered, and large portions of CCNS held no territories in either year. Taking the two years together, there were five core blocks of harrier nesting habitat in CCNS: the brackish marshes at Hatches Harbor; East Harbor wetlands; the eastern half of Pamet River Valley; the marshes north and east of Bound Brook Island; and the Marconi heathlands and shrublands. East Harbor was the most important of these habitat blocks, showing the highest concentration of harrier breeding activity anywhere in the park.

5. Most nesting harriers in CCNS made only a single nesting attempt in a season, but four females whose first nesting attempts failed before May 31 renested and laid replacement clutches. There were a total of 13 nests (including 3 renests) in CCNS in 2004 and six nests (one reneest) in 2005. Seven of the 19 nests, 37%, successfully fledged at least one young. This nest success rate is lower than that found on Massachusetts offshore islands and lower than the rangewide average for mainland North America, and the low proportion of successful nests

meant that overall productivity also was low, at 1.11 fledglings per nest. The primary cause of failure for the 12 nests that fledged no young was nest predation, by unidentified predators. The high rate of nest predation is currently the most important ecological variable limiting the breeding harrier population in CCNS. Those nests that were successful fledged an average of 3.00 young (range = 1-5), which implies that CCNS provides sufficient food resources for harriers to rear average-sized broods if they can avoid nest predation.

6. Harriers nested more frequently in wetlands, which held $10/15 = 67\%$ of nesting territories, than in upland habitats. Harriers placed nests in only four of the 65 vegetation associations present in the park, and the two most commonly used habitat types were cattail marshes and outwash scrub oak barrens. Cattail marshes are the single most important harrier nesting habitat in CCNS, accounting for 50% of all nest sites in 2004-2005. Harriers nest on the ground, and all nest sites in both years were similar in terms of the surrounding vegetation structure, characterized by high stem density and height of 1-2 m, which is typical of the nesting microhabitats selected by harriers throughout their range. At least half of the harrier nest sites at East Harbor in 2004 were located low enough in the marsh that they may be at risk of being altered by restored tidal flows in future years.

7. Harriers utilized a larger proportion of the total park area, and a greater diversity of habitat types, for foraging than they did for nesting. Hunting areas included the cattail marshes and scrub oak barrens favored for nesting but additionally included coastal salt marshes and barrier beach dunes, a wide range of shrublands, and even pitch pine forests. Some foraging trips extended as far as 6.5 km from the home nest, implying that large areas of the park may be needed to provide sufficient prey resources to sustain the breeding harrier population. The rate at which adults delivered prey to their nests was comparable to provisioning rates found in other field studies, and this result, together with a negligible rate of nestling starvation, indicates that overall foraging conditions in CCNS in 2004 and 2005 were adequate for successful rearing of young.

8. Based on the research findings from 2004-2005, I have three main recommendations for managing Cape Cod National Seashore to ensure long-term persistence of the park's breeding harrier population: (a) maintain the current acreages of cattail marsh and scrub oak barrens in the five core blocks of harrier nesting habitat in the park; (b) in the vicinity of nests minimize activities that could disturb harriers, such as vegetation manipulations, during the nesting season April 1 - August 31; and (c) control populations of mid-sized mammalian carnivores in order to lower the high rate of depredation of harrier nests.

INTRODUCTION

The Northern Harrier (*Circus cyaneus*) is a medium-sized, Holarctic hawk that breeds in open wetlands and early successional upland habitats. In the Northeastern United States during the 20th century, large areas of preferred harrier breeding habitat were lost to reforestation, filling of wetlands, and residential and commercial development in coastal regions. These habitat losses, in combination with burgeoning populations of mid-sized mammalian carnivores that depredate harrier nests, caused substantial declines in regional harrier breeding populations. In response, the Northern Harrier was listed as Endangered, Threatened, or Special Concern under the wildlife protection laws of most northeastern states, including Massachusetts, where it is listed as a Threatened species under the Massachusetts Endangered Species Act (321 CMR 10.00). This provides impetus for gathering current data on harrier status and conservation needs, and for taking management steps to halt or reverse ongoing population declines.

In Massachusetts, recent records of Northern Harrier nesting are almost entirely restricted to offshore islands (Martha's Vineyard and Nantucket, in particular) and Cape Cod. There has never been a systematic effort to determine the abundance and distribution of breeding harriers on Cape Cod, but there are scattered records of nesting in marshes on both the Upper Cape and Outer Cape. This includes observations of harriers in suitable nesting habitat during the breeding season in several parts of the Cape Cod National Seashore (CCNS), and more specifically, adult harriers engaged in behaviors strongly suggestive of nesting at Pilgrim Lake (Truro) in 2000 and 2002. Because of the National Park Service's commitment to preserving native biodiversity within CCNS, and because current management programs such as restoration of tidal flow to coastal marshes have the potential to affect harrier nesting habitats in the park, there is a need for up-to-date information on harriers' numbers, distribution, reproductive success, and habitat requirements in CCNS. In order to meet this need I conducted a two-year field study of harrier breeding ecology in CCNS in 2004-2005. This report presents the findings of the study, together with management recommendations to enhance conservation of harriers in CCNS.

RESEARCH OBJECTIVES, SCHEDULE, AND METHODS

This study was restricted to the breeding season ecology of Northern Harriers and did not address any aspects of harrier migration or overwintering. On Cape Cod, the harrier breeding season extends from early April through late August, and in 2004 and 2005 I resided on the Cape for most of this season and conducted fieldwork full-time. The main objectives of the research were: to survey as much of the suitable harrier habitat in CCNS as possible and determine the number and spatial distribution of harrier nesting territories in the park; to quantify the reproductive success of nesting harriers; to determine what habitat types harriers select for nest sites in CCNS; and to make general observations of the behavior and habitat selection of harriers during their foraging.

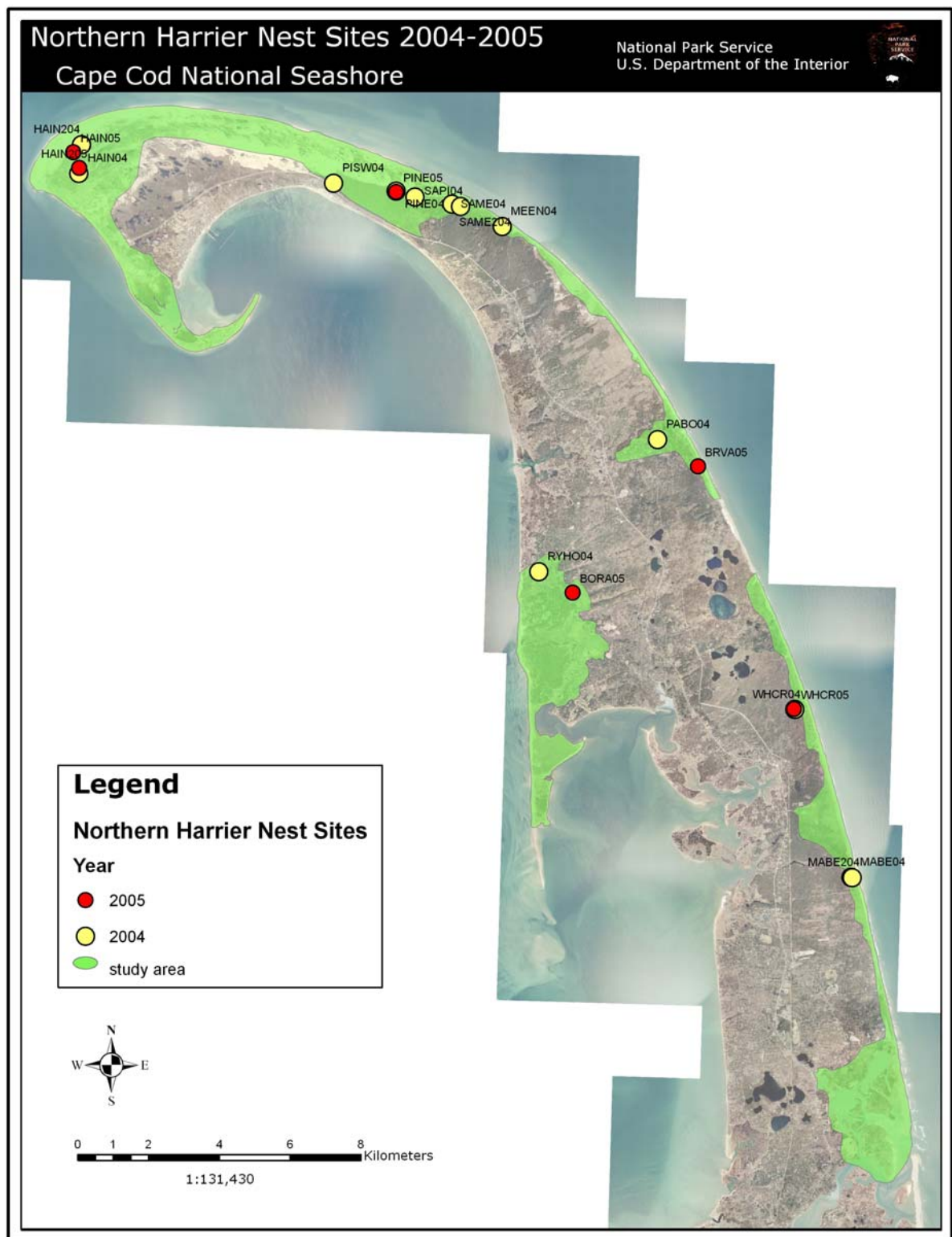
In 2004 I lived on the Cape (in Eastham) April 16 - July 29 and August 8-10 and spent a total of 1007 hr in fieldwork. In 2005 there was less harrier activity in CCNS, so I was resident on the Cape for a shorter period, comprising April 15 - July 3, July 8-21, and August 4; total time afield in 2005 was 866 hr.

In both years the general schedule of research tasks was the same: the early part of the season was devoted primarily to searching for breeding harriers and their nest sites, and in the later part of the season I switched to making intensive observations of already-discovered nests. More specifically, in April and May I worked exclusively on searching for breeding pairs and determining the locations of their territories and nests. June was a transitional period, during which I continued to search for new nests but also began spending part of my time monitoring already-discovered nests (that is, observing them from an unobtrusive distance) and directly visiting known nests after they either fledged or failed. Nest searching was mostly complete by July 4 in 2004 and by June 29 in 2005, so July and August were devoted to follow-up observations at known nests. For the entire season, I spent 687 hr in 2004 and 703 hr in 2005 in which my primary task was searching for territories and nest sites. I attempted to equalize the searching time as nearly as possible between the two years, so as to ensure an equivalent level of search coverage and so that any differences in the number of harriers found could not be attributed to different levels of search effort. Field time in which my main focus was observing already-discovered nests totaled 320 hr in 2004 (when there were more nests) and 163 hr in 2005 (fewer nests).

I did not attempt to cover the entire extent of CCNS in surveying for breeding harriers. Instead I concentrated on areas where harriers had been reported by park personnel in previous breeding seasons (R. Cook, pers. comm.) and areas with open and early successional habitats suitable for harrier nesting (based on my research experience with this species elsewhere in southeastern Massachusetts). I used aerial photos and GIS vegetation maps to identify blocks of potential harrier habitat and to exclude areas predominated by forest cover or extensive development. Due to manpower limitations I also excluded the portion of CCNS south of the Eastham-Orleans town line, from Nauset Heights to Chatham—this area is for the most part a heavily-visited barrier beach, owned largely by the Towns of Orleans and Chatham.

The portions of the park that I did survey for breeding harriers are shown in Figure 1, with a rough catalogue as follows: the northern half of Nauset Marsh, plus adjacent uplands at Fort Hill, Salt Pond, and Coast Guard Beach; a relatively narrow strip of heathland and shrubland habitats along the coastal bluffs between Coast Guard Beach and Newcomb Hollow, including the entire Marconi area; bay side Wellfleet and western portions of the Herring River marshes, from Great Island north to Ryder Beach and extending inland to the lower Herring River, Merrick Island, and Bound Brook; the eastern half of the Pamet River Valley, plus the coastal bluffs to the south around Brush Valley; the coastal bluffs from Bearberry Hill/Pamet Bog northwest to Head of the Meadow, including the Highlands area; East Harbor (Salt Meadow, Pilgrim Lake, Moon Pond); the Province Lands, from High Head to Race Point and Hatches Harbor; Herring Cove Beach, Wood End, and Long Point. Within the overall survey area I made no attempt to distinguish between CCNS property and privately owned inholdings. I also did not ignore areas outside of but adjacent to park boundaries, since any harriers present in these "border areas" were likely to range onto CCNS property and therefore be relevant to the study. This looseness in defining study site boundaries was operative in the case of a harrier territory discovered near Bound Brook Island and Ryder Beach in 2004—the exact nest site was outside CCNS boundaries, but the territory as a whole extended onto CCNS property, and therefore I included it in the data set.

Figure 1. Areas of Cape Cod National Seashore surveyed for Northern Harrier nesting territories in 2004 and 2005, and location of nest sites.



In both 2004 and 2005 I spent a small proportion of my overall search time in areas deemed suitable for harrier nesting but outside CCNS boundaries. These areas included Wellfleet Bay Audubon Sanctuary and Indian Neck in bay side Wellfleet; the large cattail marsh bordering the Mid-Cape Highway at Gull Pond Rd.; and the marshes along the Little Pamet River next to Corn Hill. As it turned out, I did not find any harrier nesting territories in these extralimital areas, but I did make some observations there of breeding harriers, which are included in this report where relevant.

I divided the total survey area into convenient "search sectors" defined by roads and topographic features and averaging 1-2 sq. km in size. Each sector was searched for breeding harriers for a period of 3-10 hr on at least two different dates, once in the early part of the season April 15-May 28, and once during the mid-season May 29-July 4. Most sectors were searched on three or more dates, and I returned to some sectors more than a dozen times (up to a maximum of 32 search visits, for the Marconi area in 2004) until I was confident that if breeding harriers were present in the sector I would have detected them.

Northern Harriers court and form pair bonds at the beginning of each breeding season, and each mated pair establishes a territory that is jointly defended against other harriers. Breeding females build a single nest on the ground somewhere within the territory, with some of the nesting materials being provided by the male, and if this first nest fails due to depredation or disturbance, some females will renest nearby in the same territory. Females do not make more than two nesting efforts per season. The exact point location of a nest is termed the Nest Site; the more-or-less homogeneous area of a single vegetation association within which the Nest Site is located is termed the Nest Patch; and the Nesting Territory is defined as the defended area extending out several hundred meters from the Nest Site.

I surveyed for nesting territories by ranging widely through the search sectors and noting the locations of any adult harriers showing courtship or nesting behaviors, including Sky Dancing displays, persistent Food Calling by females, and carrying of nest materials in the bill or talons. Each location where I observed one or more of these breeding behaviors was termed an Incipient Territory, and the harriers there were termed Incipient Breeders. Incipient Territories, even those in which I never confirmed an actual nesting attempt, were considered suitable nesting habitat, as indicated by harriers having chosen to court there; it is possible that Incipient Territories that did not have confirmed nests in 2004-2005 might be used for bona fide nesting in other years.

Following initial identification, I made repeated search visits to each Incipient Territory to chart the progress of breeding behavior: if I observed a pair courtship feeding (the male transferring prey items to his mate) or copulating, I regarded them as having established a pair bond and they were termed a Breeding Pair. Breeding Pairs were subsequently categorized as Nesting or Non-Nesting Pairs, based on whether or not I observed nest building by the female. It is possible that some Non-Nesting Pairs did begin building a nest, but their nesting effort failed quickly and I never detected it; this would result in my undercounting the number of Nesting Pairs. However, based upon the frequency of my nest searching observations, I believe the likelihood of missed nests was low and that all (or almost all) Non-Nesting Pairs terminated their breeding behavior without ever attempting to nest.

The results of a census of harrier pairs can be expressed either as population abundance (raw numbers) or population density. To convert the counts of nesting pairs into an index of population density, I used two different measures of the area encompassed. First, I computed density for CCNS as a whole—or, at least, all parts of the park from Eastham northwards, since I

did no surveying for harriers in Orleans and Chatham—including areas of suitable harrier habitat and also areas that are ostensibly unsuitable for harrier nesting. This is the most appropriate density measure for comparison with other field studies of harriers, including my own research on Massachusetts islands, which typically have not made any adjustment to total study site area to exclude the habitats deemed unsuitable for harriers. The total land area, not tidally submerged, within CCNS boundaries in the four towns of Eastham, Wellfleet, Truro, and Provincetown is 103.00 sq. km. Population density was calculated with the equation: (number of nesting pairs/103.00)(10) = number of nests per 10 sq. km. A second, more generous estimate of population density was computed by excluding the portions of CCNS that I did not survey for harriers due to difficulty of access or my a priori judgment that the area was unsuitable (e.g., the vicinity of Horseleeche Pond). The total area within CCNS boundaries that I am confident I searched thoroughly was 48.60 sq. km (GIS calculation, M. Adams pers. comm.; see shaded area in Figure 1). Therefore, the second density index was calculated with the equation: (number of nesting pairs/48.60)(10). This index could be more accurate than the first if there were undetected nesting harriers in the areas I judged not worth searching, mainly forested habitats, but I believe the probability of this is slight.

After I discovered a harrier nest, I made follow-up observations using two protocols: in Nest Monitoring I observed the nest for periods of 3-10 hr from a distance of several hundred meters, far enough away to ensure that I did not disturb the adult harriers or disrupt their nest attendance; in Nest Checking, which was not done until after a nest had either failed or completed fledging, I walked to the nest site and examined it directly. During nest monitoring sessions I recorded behavioral data that allowed me to infer the phenological schedule of the nest, and I scrutinized the appearance and ranging patterns of the attending adults in order to determine whether each bird was associated with only one nest or more than one nest for the season (dual nesting efforts comprised renesting by females and bigamous mating by males). I recorded all prey deliveries to the nest by both parents, which allowed me to calculate a food provisioning rate for each nest (averaged across monitoring sessions). If a nest succeeded in fledging young I continued monitoring sessions until I obtained an accurate count of all the fledglings.

During nest checks I recorded the precise location of the nest site using a handheld Global Positioning System receiver (Magellan GPS 315), and I visually examined the surrounding habitat type. GPS locations are not included in this report because of their sensitive nature, but they have been provided separately to CCNS personnel. Each nest patch was categorized as either wetland or upland, based on soil and vegetation characteristics, and its vegetation association was classified using the keys and descriptions of Sneddon and Zaremba (2004). Because I was not confident I could distinguish between two different cattail marsh associations (eastern cattail marsh, and cattail brackish tidal marsh), I lumped the two together into a single habitat type designated "cattail marsh." One nest site, Meadow End (see Table 1 for nest names), was in a transitional zone between adjacent wetland and upland patches and was tallied as one-half of each.

I used line-intercept sampling to measure the vegetation structure in a circular plot, radius = 5 m, centered on each nest. The percent cover of each of four vegetation classes was measured along four transect lines radiating out from the nest: low herbaceous vegetation <0.5 m high; tall herbaceous ≥0.5 m high; low shrubs <0.5 m high; tall shrubs ≥0.5 m high. The height of the shortest and tallest vegetation along each transect was measured, and average minimum height and average maximum height were calculated for the four transects combined. No quantitative measurements were made for the Pamet Bottom nest (2004) because I could not find the exact

nest site, although I was confident that I correctly identified the nest patch and took a GPS reading within 50 m of the true nest site.

In 2004 I made a second check, with the assistance of R. Cook and M. Adams, of six wetland nest sites at East Harbor in order to measure their vertical elevation within the marsh. Elevations were collected with Trimble 5700 Real Time Kinematic GPS equipment. A Trimble GPS base station and radio transmitter provided real time differential correction. Positions were further corrected using the NOAA Online Positioning User Service (OPUS) that references regional Continuously Operating Reference Stations (CORS). The system compares locally georeferenced coordinates and elevations to precise regional benchmarks. Points were measured relative to the GPS ellipsoid and converted to the North American Vertical Datum 1988 (NAVD88).

During nest checks I noted any evidence relevant to the success and productivity of the nest, such as unhatched eggs, remains of nestling carcasses, etc. The presence of eggshell fragments implied that a nest had failed during the egg phase of the nesting cycle, since the shells of successfully hatched eggs are removed immediately by the parents. Conversely, the absence of shell fragments and the presence of guano deposits or runways in the vegetation surrounding a failed nest implied that it failed during the nestling phase of the nesting cycle.

This study gave relatively low priority to observations of the behavior and habitat selection of harriers while they were foraging. Such observations were made incidentally during nest finding and nest monitoring, not as a separate research task, and for the most part consisted merely of noting the habitat types and areas in the park used by foraging harriers. Data on foraging ecology are therefore limited and mostly qualitative (there is no quantitative estimate of proportional usage of different habitat types, for instance). The one exception was the data I collected on nest provisioning rates, which provide an indirect index of foraging conditions and which are presented in the section on Foraging Ecology (see below).

RESULTS

Breeding Population Abundance

I found 10 breeding pairs of Northern Harriers in CCNS in 2004, each pair resident in its own territory (Table 1). Every breeding pair had a unique adult female, so the parkwide breeding population consisted of 10 females, but because of polygynous mating there were only eight breeding males. Six males were monogamously mated, while two males had two mates apiece in adjacent nesting territories (one male for the PINE04 and SAPI04 territories, and one male for the SAME04 and MEEN04 territories, see Figure 1). All 10 breeding pairs progressed to a first nesting attempt, and in three territories—all those in which the first nest failed before May 31 (HAIN04, SAME04, and MABE04)—the resident nesting pair also made a second nesting attempt. In these territories, following failure of the first nest (see below, under Reproductive Success, for timing and causes of failure) the breeding pair quickly resumed courtship behavior and frequent copulation, temporarily widened their ranging pattern within the territory, and then began building a second nest within two weeks. Including the three renests, I found a total of 13 nests for the 2004 season.

Table 1. Habitat type, chronology, and productivity of Northern Harrier nests in the Cape Cod National Seashore in 2004 (n = 13 nests) and 2005 (n = 6 nests). Nests with the same name were located in the same territory, and nest names ending in "2" were renests. Habitat types follow the vegetation classification of Sneddon and Zaremba (2004), with their eastern cattail marsh and cattail brackish tidal marsh lumped together as "cattail marsh." Date of first egg is approximate, and fledging success is the number of young fledged. Dash (—) indicates data value not known with certainty.

Nest Name	Date Discovered	Habitat	Date of First Egg	Fledging Success
<u>2004</u>				
Pilgrim North-East (PINE04)	4/17/4	cattail marsh	4/28/4	5
Salt Meadow (SAME04)	5/1/4	cattail marsh	4/25/4	0
Hatches Inside (HAIN04)	5/4/4	reed-grass marsh	—	0
Pilgrim South-West (PISW04)	5/5/4	cattail marsh	5/2/4	2
White Crest (WHCR04)	5/5/4	outwash scrub oak barrens	5/7/4	1
Salt Pilgrim (SAPI04)	5/7/4	cattail marsh	5/14/4	0
Pamet Bottom (PABO04)	5/11/4	cattail marsh	4/29/4	4
Meadow End (MEEN04)	5/15/4	cattail marsh/ northern bayberry dune shrubland	5/20/4	3
Marconi Beach (MABE04)	5/16/4	outwash scrub oak barrens	—	0
Ryder Hollow (RYHO04)	5/28/4	cattail marsh	5/30/4	0
Marconi Beach 2 (MABE204)	6/12/4	outwash scrub oak barrens	6/9/4	0
Salt Meadow 2 (SAME204)	6/17/4	cattail marsh	6/14/4	0
Hatches Inside 2 (HAIN204)	6/20/4	reed-grass marsh	6/18/4	0
<u>2005</u>				
White Crest (WHCR05)	5/6/5	outwash scrub oak barrens	5/8/5	0
Hatches Inside (HAIN05)	5/11/5	reed-grass marsh	5/14/5	0
Bound Railroad (BORA05)	5/11/5	cattail marsh	5/8/5	2
Pilgrim North-East (PINE05)	5/13/5	cattail marsh	5/12/5	4
Hatches Inside 2 (HAIN205)	6/8/5	reed-grass marsh	6/8/5	0
Brush Valley (BRVA05)	6/13/5	outwash scrub oak barrens	—	0

Breeding harriers were less numerous in CCNS in 2005 than in 2004 (Table 1). In 2005 I found nine breeding pairs, nearly equal to the 10 of the preceding year, but only five of these progressed to confirmed nesting. The other four breeding pairs—which were present at various times April 16 - May 18 at Salt Meadow, Little Pamet River (outside park boundaries), Pamet River, and the Marconi Area—showed advanced courtship behavior, including courtship feeding and copulating, but I never observed them building a nest and therefore they were classified as non-nesting pairs. The five nesting pairs all were monogamous, so that the parkwide nesting population in 2005 consisted of five females and five males. Four of the nesting pairs made only a single nesting attempt, while the HAIN pair renested after their first nest failed in late May; thus, I found a total of six nests in 2005 (Table 1).

The size of the breeding population, censused as a number of nesting pairs or, equivalently, nesting territories, can also be expressed as a population density. In 2004 the harrier density for CCNS as a whole was 0.97 nests per 10 sq. km. In 2005, when there were only half as many nesting pairs as in 2004 (5 pairs vs. 10 pairs), the estimated density was 0.49 nests per 10 sq. km. If portions of the park that I did not search thoroughly are conservatively excluded from the computation, then the population density was 2.06 nests per 10 sq. km in 2004 and 1.03 in 2005. For comparison's sake, the median breeding population density of Northern Harriers in 11 field studies conducted throughout the species range is 1.8 nests per 10 sq. km (MacWhirter and Bildstein 1996).

The absolute numbers and relative densities of harrier nesting pairs that I found in CCNS in 2004 and 2005 could have been underestimates, since it is possible that I missed some nests. In 2004 I made several observations in late July that implied the existence of an eleventh, undiscovered territory somewhere near Wellfleet Harbor. On July 23 I observed an adult female capture prey at Fort Hill and carry it away far out of sight to the north-northwest. On July 26 I twice observed a prey-carrying female at Wellfleet Bay Audubon Sanctuary, traveling along a flight path overlapping the extrapolated path of the July 23 observation, and continuing northward past Lieutenant Island to Indian Neck. These observations are proof of a nesting pair (or conceivably two pairs, although this is unlikely) provisioning young somewhere, perhaps on or near Indian Neck, but almost certainly this undiscovered nest was located outside park boundaries. It is also possible that one or more of the non-nesting pairs in 2005 (see above) did in fact build a nest that I failed to detect. An even lower probability of a missed nest exists for two Incipient Territories in 2004, areas where I observed adults initiating breeding behaviors early in the season but not progressing to pair bonding. A male harrier courted one or more females along the north edge of Bound Brook Island in late April (it is possible that this male subsequently shifted northward and became the nesting male in the RYHO territory), and a single female carried nesting material but did not build a nest in the cattail marshes around Corn Hill and Little Pamet River (outside park boundaries) in mid-May. In all of these cases—the undiscovered Wellfleet Harbor nesting territory in 2004, the breeding pairs classified as non-nesting in 2005, and the two Incipient Territories in 2004—I regard the likelihood of an actual nest undetected within the boundaries of CCNS to be slight.

In both 2004 and 2005 the population of breeding harriers was supplemented by an unknown number of nonbreeding individuals. This could include spring migrants, which would be transient on the outer Cape in April and May, as well as nonterritorial floaters throughout the breeding season and, possibly, wandering post-breeding individuals late in the season. In 2004 I regularly observed migrant or floater individuals, unassociated with any known nesting territory, in many parts of CCNS throughout the spring and as late as June 4. In 2005 I saw individuals I

was confident were nonbreeding even later into the season, up until June 27. Nonbreeders constitute an important auxiliary to the nesting population, since they are capable of replacing breeders that die or disappear part-way through the breeding season (Bowen, unpubl. data).

Breeding Population Distribution

In 2004 the 10 harrier nesting territories in CCNS were neither uniformly spaced nor randomly distributed throughout the portions of the park I surveyed (Figure 1). Instead there was a notable cluster of 5/10 = 50% of all territories at East Harbor, the habitat block comprising Pilgrim Lake, Moon Pond, and Salt Meadow. The other five territories were widely scattered, one each in five different areas: Hatches Harbor; Pamet River; north of Bound Brook in southwest Truro; the scrub oak barrens inland of White Crest Beach on the ocean side of Wellfleet; the coastal bluff above Marconi Beach, also on the ocean side of Wellfleet (Figure 1). Large swaths of CCNS held no nesting territories, including the Province Lands, the ocean side Highlands area (between Head of the Meadow and Pamet River), the bay side of Wellfleet between Bound Brook and Great Island, and Nauset Marsh.

In territories where renesting occurred in 2004, the distance between the first and second nests was variable: 34 m for the MABE territory, 260 m for SAME, and 806 m for HAIN. The MABE figure is typical for harriers, but the internest distances of 260 m and 806 m are somewhat larger than the separation of 200 m or less reported for renesting harriers in New Brunswick (MacWhirter and Bildstein 1996).

Because of the small number of harriers that nested in CCNS in 2005, it is difficult to evaluate whether they were more or less dispersed than would be expected on the basis of chance alone, but at a minimum it can be said that the five nesting territories were widely scattered. They were located one each at Hatches Harbor, Pilgrim Lake, Brush Valley (southeast of Pamet River), Bound Brook, and inland of White Crest Beach (Figure 1). As in 2004, large portions of CCNS were devoid of any harrier nesting territories. In the one case of renesting in 2005, the HAIN territory, the second nest was built 479 m from the failed first nest.

Comparing the spatial distribution of nesting territories in 2004 and 2005, there were both similarities and differences between the two years (Figure 1). The most prominent feature of the distribution in 2004, namely the cluster of nesting territories at East Harbor, did not recur in 2005. However, since one of the four non-nesting territories in 2005 was in Salt Meadow, East Harbor was again the only area in CCNS with more than one concurrently active breeding pair. (There were two breeding pairs in or near the Pamet River valley in 2005, one reoccupying the PABO04 territory in April and a second at Brush Valley, but these two pairs were active at different points in the season, and it is possible that they were only a single pair of individuals.) Three of the 10 territories from 2004 were reused by nesting harriers in 2005: Hatches Inside, Pilgrim North-East, and White Crest (Table 1). Within these territories the precise nest sites were not reused between years: the 2005 nest sites were located approximately 30 m away from the 2004 sites in the PINE and WHCR territories, and approximately 150-300 m away in the HAIN territory (including first and second nests from the two years). It is unknown whether the 2005 harriers that reused 2004 territories were the same individuals. Three other nesting territories from 2004 were occupied by non-nesting pairs early in 2005—Salt Meadow, Pamet (River) Bottom, and Marconi Beach—implying their continued suitability as habitat even though they were not reused for actual nesting. In the general vicinity of the Pamet River valley and the Bound Brook marshes there were nesting territories in both 2004 and 2005 (PABO and BRVA,

RYHO and BORA, see Figure 1), but the between-years internest distances of 1.0-1.5 km in these two areas were large enough to not qualify as territory reuse.

Reproductive Success

In 2004 the harrier nesting season in CCNS extended from early April through the first week of August. At least one breeding female (PINE territory) had already begun nest building when I started fieldwork on April 16, so the precise starting date for the nesting season is unknown, although it is unlikely to have been earlier than the first week of April. Egg-laying, which is coincident with the onset of incubation, began in late April, and females were incubating eggs through most of May (for the earlier nests in the population) and some of June and even July (for later nests). The earliest date of hatching was June 2, and hatching continued throughout June and as late as July 15-18 (SAME2 nest). I observed the first fledgling of the season on July 2 and the first independent juvenile (young of the year traveling outside its natal territory unaccompanied by its parents) on July 23. The latest nests in the population failed sometime between July 28 and August 10, although had they been successful they would have fledged as late as the last week of August.

Variation among nests in their phenology (seasonal timing) can be specified in terms of the date on which the first egg of the clutch is laid (Table 1). At CCNS in 2004 four nests in the population were initiated more or less synchronously at the end of April (April 25-May 2), and four others had first egg dates spread through the month of May (May 7-May 30). Date of first egg (DFE) was unknown for two nests, although it was sometime before the end of May. The three renests, which followed failed first nesting attempts, had DFE of June 9-18; this is a later date of nest initiation than is found in harrier populations on Massachusetts offshore islands (Bowen, unpubl. data). The overall spread of nesting attempts in 2004, that is, the difference between the earliest and latest nests in the population, was approximately eight weeks.

Because of the smaller number of harrier nests in 2005, confidence intervals for phenological parameters were larger, but the nesting season again began in early April, with vigorous courtship already underway when I began fieldwork on April 15, and extended through the first week of August, when the last nest of the season (HAIN2) failed. Benchmark events in the nesting cycle were delayed by approximately two weeks in 2005 relative to 2004. Thus, the date of first egg for first nesting attempts was May 8-14 (Table 1), hatching began June 10, and I observed the first fledglings of the season July 13. The overall spread between earliest and latest nests in the population in 2005 was 4-5 weeks.

Harrier reproductive success can be measured in terms of Nest Success, which is the percentage of nests that successfully fledge at least one young, and Fledging Success, which is the number of young fledged per nest (Table 2). In 2004, five of 13 nests fledged one or more young, giving a nest success rate of 38%. In 2005, $2/6 = 33\%$ of nests were successful. These figures are lower than comparable results from Martha's Vineyard and Nantucket in recent years; they also are lower than the median nest success rate of 61% for harrier populations elsewhere in mainland North America (Table 2).

Table 2. Measurements of reproductive success for Northern Harriers in Cape Cod National Seashore in 2004 and 2005, compared to previous studies in the Massachusetts coastal islands region and studies conducted rangewide. Successful nests are those which fledged at least one young, and nest success is the percentage of nests that were successful. Sample sizes (number of nests) are given in parentheses. Data for 1998-2005 from RVB; data for 1971-1974 from Bierregaard et al. (in prep.); rangewide data (n = 12 studies) from MacWhirter and Bildstein (1996).

Site and Year	Nest Success	Fledglings/ succ. nest	Fledglings/ nest
Cape Cod, 2005	33(6)	3.00(2)	1.00(6)
Cape Cod, 2004	38(13)	3.00(5)	1.15(13)
Nantucket, 2003	81(53)	2.53(17)	2.15(20)
Nantucket, 2002	77(44)	3.18(17)	2.45(22)
Martha's Vineyard, 2001	50(22)	2.82(11)	1.41(22)
Martha's Vineyard, 1999	63(19)	2.92(12)	1.84(19)
Martha's Vineyard, 1971-1974	59(34)	2.40(20)	1.41(34)
Tuckernuck, 1998	31(13)	2.75(4)	0.85(13)
Rangewide	18-79	2.3-3.8	0.6-2.8

When analyzing the nest success data, it should be kept in mind that treating serial nesting attempts within a single territory as independent, for purposes of statistical inference, is not valid. Furthermore, it may be conceptually useful to consider the success rate of first nests and renests separately. Stratifying by nest attempt number, the success rate for first nests was 5/10 = 50% in 2004 and 2/5 = 40% in 2005, while none (0%) of the renests succeeded in either year. In the two years combined, first nests were more likely to be successful than second nests (47% vs. 0%), but this difference was not statistically significant (Chi-Square test with continuity correction, $p = 0.85$). Nest success also was not significantly influenced by nest site habitat: although there was a trend towards greater success for nest sites in wetlands (5/13 = 38% success) than for nests in upland habitats (1/5 = 20% success), the difference was not statistically significant (Chi-Square test with continuity correction, $p = 0.85$; and the validity of this test is questionable because of violation of the assumption of independence between first and second nests). In the two bigamous harems in the population in 2004 (PINE-SAPI and SAME-MEEN), the nest of the beta female was unsuccessful in both cases, concordant with the species-typical pattern found in other studies (MacWhirter and Bildstein 1996, Simmons 2000). In all of these analyses, interpreting the determinants of nest success is hampered by small sample sizes and low statistical power.

Harrier fledging success in CCNS was similar in the two years (Tables 1, 2). Successful nests fledged between one and five young, with a mean of 3.00 fledglings per successful nest both years. Overall productivity, including both successful and failed nests, was 1.15 fledglings/nest in 2004 and 1.00 fledglings/nest in 2005. The productivity of successful nests was roughly equivalent to that on Martha's Vineyard and Nantucket in recent years and close to the rangewide median of 3.2, indicating that CCNS provided sufficient food resources for harriers to raise average-sized broods to fledging. The overall productivity for CCNS, however, was lower than that on Martha's Vineyard and Nantucket and lower than the rangewide median figure of 2.1, because of the high proportion of nests that failed. Low productivity due to a high nest failure rate is not completely unprecedented in coastal Massachusetts: on Tuckernuck Is. in 1998 only 31% of harrier nests succeeded in fledging young, and the overall productivity was 0.85 fledglings/nest (Table 2).

In both 2004 and 2005 the primary cause of reproductive failure at the nests that fledged no young was nest predation. Eight nests in 2004 and three nests in 2005 fit this pattern: either the entire clutch of eggs was destroyed, leaving only eggshell fragments in the nest (HAIN04, SAME04, RYHO04, and MABE04 nests), or after the eggs had hatched the entire brood died on a single date, with no evidence of partial brood reduction through nestling starvation (SAPI04, HAIN204, SAME204, MABE204, WHCR05, BRVA05, and HAIN205 nests). The identity of the nest predators was not known. The timing of depredation within the nesting cycle was somewhat different from the pattern found in other field studies of Northern Harriers. Although one-third of the CCNS failed nests were depredated during the egg phase of the nesting cycle, depredation during the nestling phase predominated, whereas the typical pattern for harriers is for most depredation to occur during the egg phase (MacWhirter and Bildstein 1996).

Besides nest predation, there were two other minor causes of reproductive failure. At three successful nests, part of the clutch never hatched—two unhatched eggs at PISW04, three at WHCR04, and one at BORA05—and this accounts for the below-average productivity of these nests (Table 1). The other form of nest failure was a single case of abandonment associated with inclement weather. At the HAIN nest in 2005 the female laid her first egg and began incubating on or about May 14 but then deserted the nest sometime between May 18 and May 28. This abandonment was coincident with a series of storms May 21-26, which brought colder than normal temperatures, heavy rains, and strong northeast winds. When I checked the nest on June 3, after the HAIN pair had shifted to another part of their territory and resumed courtship, I found a clutch of four eggs still present in the nest, three of them intact and one broken. The most probable interpretation of this nest failure is that storm surge and/or rainwater runoff inundated the nest site and compelled the female to desert. The entire Hatches Harbor area had higher than normal water levels during this period, and flooding was widespread (R. Bowen and R. Cook, pers. obs.).

Nesting Habitat

Harriers in CCNS selected wetland habitats for nest placement more frequently than upland habitats (Table 1). In 2004, seven nesting territories were located in wetland habitat patches, two were in upland patches, and one territory (MEEN) was in the transitional zone between adjoining wetland and upland patches. In 2005, three nesting territories were in wetlands and two in uplands. Thus, in both years fewer than half of the nesting territories were in upland habitats. This greater utilization of wetlands than of uplands for nest site placement in CCNS differs markedly from the pattern on Nantucket and Martha's Vineyard, where harriers select nest

sites predominantly or exclusively in upland habitats: 62-70% of nest sites are in uplands on Nantucket (varying by year), and 100% of nest sites are in uplands on Martha's Vineyard (Bowen, unpubl. data).

Within the broad habitat classes of wetland and upland, harriers utilized only four specific vegetation associations for nesting, out of a total of 65 associations present in CCNS (Sneddon and Zaremba 2004). Cattail marsh was the most frequently used vegetation association, accounting for 9.5 nest sites in 8.5 territories in the two years combined (Table 1). The other wetland vegetation association used by harriers was reed-grass marsh (two nesting attempts in the HAIN territory each year, for a total of four nest sites). Outwash scrub oak barrens was the predominant nesting association in uplands (five nests in four territories), and northern bayberry dune shrubland accounted for one-half of the intergrade MEEN site. In all territories where renesting occurred (three cases in 2004 and one in 2005), the second nest site was located in the same vegetation association as the first.

In contrast to their floristic variability, all nest sites in CCNS shared the same basic microhabitat structure, namely, a dense stand of vegetation 0.55-2.40 m tall (Table 3). On average, the minimum height of vegetation surrounding nest sites was approximately 1 m, and the maximum height was about 2 m. Vegetation ≥ 0.5 m tall made up 100% of the cover at all nest sites, with herbaceous species predominant in some cases (cattail and reed-grass marshes) and woody species dominating in others (mostly the upland sites). The structural characteristics of the upland nest sites (WHCR, MABE, and BRVA territories) were similar to those measured at upland nest sites on Massachusetts offshore islands (Table 3) and are typical of harriers throughout their range.

Table 3. Composition and height of vegetation at Northern Harrier nest sites in Cape Cod National Seashore and on Massachusetts offshore islands. Vegetation was measured by line intercept sampling within a circular plot, radius = 5 m, centered on the nest. Vegetation cover type was classified into four categories—low herbaceous (height <0.5 m), tall herbaceous (height ≥ 0.5 m), low shrub (height <0.5 m), and tall shrub (height ≥ 0.5 m)—and the value for each vegetation class is mean percent linear coverage, calculated as (Sum length of transects intercepted by a given cover type/Total length of transects) X 100%. Minimum and maximum heights (in meters) were the shortest and tallest vegetation intercepting the line transects. All data collected by RVB except for Nantucket 1985, which are from Holt and Melvin (1986).

Site, Year	Low Herb	Tall Herb	Low Shrub	Tall Shrub	Min Height	Max Height
Cape Cod National Seashore, 2005						
Wetland territories (n=3)	0.0	54.9	0.0	45.1	1.02	2.00
Upland territories (n=2)	0.0	0.0	0.0	100.0	1.01	1.58
Cape Cod National Seashore, 2004						
Wetland territories (n=6)	0.0	89.5	0.0	10.5	0.76	2.07
Upland territories (n=2)	0.0	0.0	0.0	100.0	0.96	1.72

Many nest sites consisted of a nearly monotypic stand of cattail (*Typha* spp.), reed-grass (*Phragmites australis*), or scrub oak (*Quercus ilicifolia*), but there were exceptions. Three of the four nest sites in the Hatches Inside marsh (2004 and 2005 combined), although dominated by reed-grass, had various admixtures of woody shrubs (*Baccharis halimifolia*, *Rosa* sp., and *Morella pensylvanica*); the fourth was a pure stand of reed-grass. Similarly, two of the sites in cattail marshes had significant amounts of woody vegetation, approximately 50% cover of *Rosa* sp. at PINE05 and almost 90% cover of *Spiraea alba* at BORA05. Besides scrub oak, other woody species present at upland nest sites, in small amounts, included *Ilex glabra*, *Prunus serotina*, and *Rhus copallinum*. Nests in scrub oak thickets were built in small, snug openings in the shrub cover, with a gap diameter of approximately 0.5-1.0 m, just large enough to accommodate adult harriers flying down to or sitting on the nest.

Wetland nest sites had little or no standing water at ground level at the time I visited them, although the substrate was typically moist or even saturated. The PINE05 and HAIN05 sites had 2 cm and 8 cm of standing water, respectively. The six nests at East Harbor in 2004 were located in the marshes around the edges of Pilgrim Lake and in Salt Meadow (the MEEN site was just at the transition between marsh and adjacent upland, at the far east end of Salt Meadow). Nest sites were low enough in these marshes to be subject to tidal influence in the future, depending on how the East Harbor tidal restoration program proceeds (Table 4). Relatively lower sites utilized in 2004 were around the margins of Pilgrim Lake (PISW, PINE, and SAPI), whereas the sites in Salt Meadow were relatively higher (SAME, SAME2, and MEEN).

Table 4. Relative vertical position in the marsh of n = 6 harrier nests at East Harbor in 2004. Marsh Elevation (in meters) is the North American vertical datum reading at ground level at the nest site, and Nest Elevation is the North American vertical datum reading at the top of the nest platform (built up above the surrounding ground).

Nest Name	Marsh Elevation	Nest Elevation
Pilgrim North-East	0.330	0.484
Salt Meadow	0.505	0.554
Pilgrim South-West	0.253	0.502
Salt Pilgrim	0.340	0.496
Meadow End	0.710	0.738
Salt Meadow 2	0.429	0.551

Foraging Ecology

I observed harriers foraging at numerous sites and in diverse habitats in CCNS. In addition to nesting individuals foraging within their territories (see Figure 1 for locations), I observed adult harriers of uncertain identity (breeders or nonbreeders) hunting at: Long Point and Wood End (Provincetown); the dunes and salt marshes near Herring Cove Beach (Provincetown); throughout the Province Lands dunes; several locations in the Highlands (Truro), including Highland Light and the old heliport; along Ocean View Drive and in the Marconi heathlands (ocean side Wellfleet); Great Island (bay side Wellfleet); the coastal bluffs between Marconi Beach and Nauset Light (ocean side Eastham); and Nauset Marsh and Fort Hill (Eastham).

Habitats utilized for foraging included the cattail marshes and scrub oak barrens favored for nesting but additionally included barrier beach dunes, salt marshes, northern tall maritime shrubland (near Highland Light and Pilgrim Lake), old fields, heathlands and northern beach heather dwarf-shrublands, recently burned thickets of Rosa multiflora at Fort Hill, and ruderal roadside shrublands along the Mid-Cape Highway—essentially any open or early successional habitat almost anywhere in the park. Harriers even utilized some forested habitats for foraging in 2004. On several occasions I observed the resident male of the SAME and MEEN territories pouncing at and/or capturing songbird prey in the canopy of the pitch pine forests adjoining the southern edge of Salt Meadow.

Observations of foraging were made incidentally to other research tasks and were not based on a systematic, quantitative sampling protocol. Therefore it is not possible to specify the proportional usage of different habitat types for foraging, but it is clear that harriers foraged in upland habitats in CCNS to a greater extent than they nested there, and overall they made use of a considerably wider range of habitat types for foraging than for nesting.

Breeding harriers foraged both close to and distant from their nest sites. In July 2005 the BORA female often hunted within 50 m of her nest. Similarly, in both 2004 and 2005 the resident adults in the PINE territory frequently hunted in the cattail marshes along the northern and eastern margins of Pilgrim Lake. For example, on July 5 I observed the PINE male make two successive prey captures in a three minute period within 200 m of his nest, both of which he immediately delivered to young at the nest. At other times this male hunted in the parabolic dunes north of Pilgrim Lake or in open areas on Pilgrim Heights, and he and other nesting individuals regularly ranged more than 1 km away from their nest sites. Some foraging trips were even longer, including commutes of 4.0 km (over open water) between Pilgrim Lake and Long Point, ~3.0 km between the Highlands Center and Salt Meadow (presumed destination), ~4.0 km between the BRVA nest and a prey capture site north of Longnook Hollow (20 June 2005), and 6.5 km between Herring Cove Beach and Pilgrim Lake (7 June 2004). These observations, although they suffer from the same unsystematic collection methodology as the observations of habitat type usage, indicate that nesting harriers at CCNS harvest prey resources over large areas, extending well beyond the immediate vicinity of nest sites.

I made only a limited assessment of the relative success and efficiency of harrier foraging. I made no quantitative measurements of prey capture rates, but I did measure the rate at which breeding adults delivered prey to their nests, which can serve as an indirect index of foraging success. In 2004 I spent a total of 183.75 hr monitoring nests with either nestlings or fledglings present, and the mean provisioning rate at these nests was 0.80 prey deliveries/hr (standard error = 0.18, range = 0.32-1.24, n = 5 nests). In 2005, in 72.25 hr of nest monitoring the mean provisioning rate was 0.90 prey deliveries/hr (standard error = 0.22, range = 0.25-1.76, n = 2 nests). The CCNS results are roughly comparable to, or perhaps slightly lower than, the nest provisioning rates of 1.26 deliveries/hr (nestling phase of the nesting cycle) and 0.89 deliveries/hr (fledgling phase) reported for a New Brunswick harrier population (MacWhirter and Bildstein 1996). Although I regard these data as preliminary, due to the small number of nests observed, they suggest that CCNS in 2004-2005 provided foraging conditions—abundance and availability of prey, and spatial distribution of prey in relation to nest locations—adequate to support successful rearing of young.

DISCUSSION

This report presents a description and analysis of Northern Harrier breeding ecology in the Cape Cod National Seashore (CCNS). It is based upon almost 1900 hr of fieldwork over two seasons, which I am confident was sufficient time to find and study in detail all the harriers breeding in the park. However, because this population turned out to be a relatively small one, the sample sizes for many analyses were perforce small as well. This should be kept in mind throughout the discussion that follows, since small sample sizes limit the robustness of inferences and conclusions. Further research, over additional years, would improve the reliability of our understanding of the CCNS harrier population.

Harrier Population Size and Distribution in CCNS

There were 10 breeding pairs of harriers in CCNS in 2004, all of which nested. In 2005 I found nine breeding pairs in the park early in the season, courting and pair bonding, but only five of them went on to make confirmed nesting attempts. Prior to this study, the harrier population had never been systematically censused in any part of Cape Cod, but there is one published estimate of population size: 8-10 breeding pairs for the entire Cape, including the Upper Cape in addition to CCNS and the rest of the Lower Cape (Hill 1965). Given the 2004 count of 10 nesting pairs in CCNS alone, Hill's estimate was probably too low.

The 2004 population count of 10 pairs constitutes what is likely the largest harrier breeding population anywhere in mainland Massachusetts. The CCNS population, however, is significantly smaller than the current populations of 20-30 nesting pairs on Martha's Vineyard and 45-55 pairs on Nantucket (Bowen, unpubl. data). In addition, the ranking of CCNS among mainland populations is less certain for 2005, since it is conceivable that in some years five or more nesting pairs might inhabit Upper Cape Cod, or perhaps even coastal Bristol County (extrapolating from Christianson and Reinert 1990). Nonetheless, under current land use conditions, I am confident that in all years the harriers in CCNS make up a substantial proportion of the total nesting population of harriers on the Massachusetts mainland. The continued viability of the harrier population in CCNS is clearly significant to efforts to conserve the Northern Harrier in Massachusetts statewide; therefore it is desirable that this population be periodically monitored and reassessed.

As a caveat to the CCNS census result of 5-10 nesting pairs of harriers, I should note that it is possible that I missed one or more nests in the park in 2004 or 2005. The total area to be searched was large, and hilly topography made some search sectors difficult to view. Furthermore, it was impossible for a single researcher to survey all sectors simultaneously during the first peak of harrier courting and nest-building early in the season. If there were nesting attempts that failed within a day or two after they were initiated, I may have failed to detect a small number of them.

The spatial distribution of the harrier nesting territories in CCNS in 2004 and 2005 was patchy, with some areas of suitable habitat occupied and other similar areas devoid of nesting harriers. In 2004 territories were neither regularly spaced nor randomly distributed; instead there was a notable cluster of 5/10 = 50% of all territories at East Harbor. The other five territories were widely scattered. In 2005 breeding harriers reoccupied five of the same territories used in 2004 (although only three were used for actual nesting), but the clustering of territories at East Harbor did not recur—only two of the five 2004 territories at East Harbor were reestablished in 2005 (Pilgrim North-East and Salt Meadow), and only one was used for nesting.

Considering the two years together, there were five "core blocks" of harrier nesting habitat in CCNS: the brackish marshes inside the dike at Hatches Harbor; East Harbor (Pilgrim Lake, Moon Pond, and Salt Meadow); eastern Pamet River, including the wetlands in the river bottom plus the adjoining coastal bluffs to the north and south of Ballston Beach; the marshes north and east of Bound Brook Island; and the Marconi heathlands and shrublands. The scrub oak barrens inland of White Crest Beach, north to Cahoon Hollow, are arguably a sixth important nesting area, since there was a nesting territory there both years, but there was less overall harrier activity (including floaters as well as breeders) in this area than in the five core blocks. East Harbor was the most important of the five, since it was the only one that held ≥ 2 breeding pairs in both years (albeit only one nesting pair in 2005).

It is unclear why such a high proportion of breeding pairs settled at East Harbor. There is no obvious structural or floristic difference between the cattail marshes there and the extensive cattail marshes along Bound Brook and elsewhere in the Herring River drainage. Possibly there is some landscape-scale feature of East Harbor that makes it particularly attractive to nesting harriers, such as proximity to extensive and/or high quality foraging areas. But in spite of uncertainty about the causes of the concentration of breeding harriers there, East Harbor should be regarded as essential to the long-term persistence of harriers in CCNS. This makes maintaining the suitability of harrier habitat at East Harbor a high priority (see below, Management Recommendations). It would be prudent to assume that if the current nesting habitats at East Harbor were altered or eliminated—if, for instance, the current tidal restoration project at East Harbor resulted in cattail marshes being replaced by *Spartina* salt marsh—the resident harriers there might not respond by shifting to other locations in the park but instead might be eliminated along with their habitat.

Large areas of open-country habitat in CCNS were devoid of harrier nesting territories, perhaps most notably Long Point - Wood End (Provincetown), the Province Lands dunes and interdunal swales, and Nauset Marsh. This does not necessarily imply, however, that these areas are unimportant in sustaining the park's harrier population. I frequently observed harriers foraging in diverse wetland and upland habitats throughout the park, and several observations documented that nesting harriers made long foraging trips, 5 km or more, outward from their nesting territories. Thus, a much larger proportion of the total park area is utilized by harriers than is apparent from a cursory inspection of the nest map (Figure 1), and it may be that most of the park area is necessary to provide sufficient prey resources for harriers to breed successfully.

Our ability to draw general conclusions about the abundance and distribution of breeding harriers in CCNS is limited by the strong interannual variation found in this study. There were striking differences between 2004 and 2005 in both number of nesting pairs and spatial dispersion of their territories within the park. As reported above, there were only half as many nesting pairs in 2005 (five pairs) as in 2004 (10 pairs). It is important not to overinterpret these admittedly small numbers, but nonetheless there were other indications, besides merely the lower census tally, that 2005 was a less favorable year for harrier breeding. First, although only five pairs of harriers nested in 2005, early in the season I found nine breeding pairs in CCNS, almost equal to the 10 pairs of 2004. It was because four of these pairs broke up or left the area without nesting, an unusually high rate of pair disengagement, that the final census result for 2005 was lower than that of 2004. Second, the phenology of the harrier nesting cycle was about two weeks later in 2005 than in 2004, indicating that harriers delayed their breeding for some reason. It is conceivable that both the high rate of non-nesting among pair-bonded harriers and the delayed nesting phenology in 2005 were attributable to reduced availability of prey resources,

since both of these parameters have been shown to correlate with spring prey density in a New Brunswick harrier study (MacWhirter and Bildstein 1996). I did not collect any data on the population dynamics of prey species in CCNS, so it is not possible to evaluate this hypothesis without further research.

The spatial distribution of harrier nesting territories also differed in important ways between 2004 and 2005. The notable concentration of territories at East Harbor, 50% of all the territories parkwide, did not recur in 2005, although East Harbor was again the only habitat block in the park settled by more than one breeding pair. This discrepancy between the two years makes it impossible to say whether the normative distribution pattern in CCNS is uniformly overdispersed (i.e., all territories widely scattered) or at least partly clustered. Additional years of study are needed to resolve this question.

Harrier Population Limitation and Habitat Quality in CCNS

The population density of nesting harriers in CCNS in 2004 and 2005 was relatively low. Density estimates for the park ranged from 0.49 to 2.06 nesting pairs per 10 sq. km, depending on the year (density was lower in 2005) and the computation method. In comparison, harrier populations on Massachusetts offshore islands have current densities of 0.8-1.3 pairs per 10 sq. km on Martha's Vineyard and 3.5-4.4 pairs per 10 sq. km on Nantucket (Bowen, unpubl. data). The median density estimate for mainland populations of Northern Harriers is 1.8 pairs per 10 sq. km (MacWhirter and Bildstein 1996). Thus, the CCNS harrier population has a considerably lower density than the healthiest island population in the region (Nantucket), and even relative to other mainland populations the CCNS density is at or below average levels.

The relatively low harrier breeding density in CCNS is probably due, at least in part, to the limited proportion of the total study area currently covered by undeveloped, nonforested habitats (marshes and early successional uplands). It is unclear whether the low population density may also indicate unfavorable conditions of some sort within the suitable habitats at CCNS, such as a high density of mammalian nest predators, which harriers may have learned to avoid.

Besides the below-average population density, two other findings support the conclusion that CCNS currently affords only average to poor habitat quality for breeding harriers. One is the high rate of non-nesting among the breeding pairs that established territories in the park in 2005. The cause of this reproductive breakdown is unknown, but it suggests that some aspect of habitat quality in CCNS may have been particularly poor in 2005, creating conditions inadequate to stimulate full development of breeding behavior, nest-building, and egg-laying. As mentioned above, reduced prey availability in early spring is one habitat quality variable that can account for courtship failing to progress to actual nesting. Alternatively, habitat quality may not have been limiting in 2005, but the quality of individual harriers may have been low. For example, yearling harriers are less likely to nest than older individuals (MacWhirter and Bildstein 1996), so it is possible that low breeding experience characterized the CCNS population in 2005.

The other finding that corroborates the general conclusion of low habitat quality for harriers in CCNS is the relatively low reproductive success of the population. Both nest success (7/19 = 37% for the two years combined) and nest productivity (1.11 fledglings/nest) were well below average figures for harrier populations on Massachusetts offshore islands and on the North American mainland (Table 2). Furthermore, if I missed one or more harrier nests in the park, then the true nest success rate was probably even lower than 37% (the Mayfield bias; see Mayfield 1975). The primary cause of this low reproductive success in CCNS was a high rate of nest predation. Other forms of reproductive failure occurred at low rates more typical for

harriers. At nests that fledged at least one young there was little or no evidence of nestling starvation. I found no emaciated nestling carcasses when I checked nests, and the mean productivity of 3.00 fledglings per successful nest was close to the average result reported in other harrier studies (Table 2). At all three of the successful nests that fledged fewer than three young, the low productivity was attributable to hatching failure, which is not unusual in harriers (Simmons 2000). Nest provisioning rates were close to those found in other field studies of harriers, indicating that general foraging conditions in CCNS are adequate to support normal nestling growth and survival. Nest predation is the only obvious limitation on successful breeding by harriers in CCNS, but its frequency is high enough to depress the overall quality of the park as harrier habitat.

Habitat Selection and Usage by Harriers in CCNS

Two main findings characterize the selection of nesting habitats by harriers in CCNS: wetlands are preferred over uplands, and only a small proportion of the diverse vegetation associations found in the park are used for nest site placement.

The most important finding with regard to habitat selection is the predominance of wetland sites among the locations chosen for nesting territories. In the two years combined, 10.5 territories were located in wetlands versus 4.5 in uplands (the MEEN04 territory was intermediate). In contrast, harriers on Nantucket and Martha's Vineyard place their nest sites predominantly or even exclusively in uplands. Within wetland habitat patches, harriers in CCNS select nest sites that are low enough in the marsh to be potentially subject to tidal influence. At East Harbor in particular, tidal influence may begin to affect harrier nest sites as the tidal restoration program there proceeds. Tidal flow will first affect lower sites around the margins of Pilgrim Lake—such as the sites PISW, PINE, and SAPI used in 2004—and only later, if ever, affect relatively higher sites in Salt Meadow, such as SAME04, SAME204, and MEEN04 (Table 4).

Only four of the total 65 vegetation associations found in CCNS were used by harriers for nest site placement, and half of all nests in the two years combined (9.5/19 nests) were in a single association, cattail marsh (actually a lumping of two closely related associations, eastern cattail marsh and cattail brackish tidal marsh). Cattail marsh is the most important nesting habitat type for harriers in CCNS. It is unclear why harriers were not found nesting in a greater diversity of associations, especially some of the upland shrub communities with apparently suitable structure (namely, high stem density and height ≥ 1 m). One hypothesis is that harriers avoid visibly sandy substrates with low litter cover. Substrates of this sort are more prevalent in CCNS, especially in the Province Lands, than on Martha's Vineyard and Nantucket, where harriers place nests in a greater diversity of vegetation associations (Bowen, pers. obs.).

It is worth noting that the four nest sites (over two years) in the Hatches Inside territory were located in reed-grass marsh. It is conceivable that all four sites were selected by just a single pair of individuals (the within-year nest-reneest selections were definitely by the same individuals), so this may represent an idiosyncratic choice rather than a representative one. Nonetheless these HAIN nest sites prove that at least some Northern Harriers in coastal Massachusetts are willing to nest in wetlands that have been invaded by Phragmites and will place nests in stands of vegetation where P. australis is the dominant species or even a pure monoculture. Northern Harrier nesting in Phragmites has also been documented in New Jersey (Kane 2001), indicating a useful adaptability on the part of harriers and challenging the conventional assumption that alien Phragmites makes marshes unsuitable for native bird

communities. On the other hand, no pair other than HAIN nested in reed-grass marsh, even though there were Phragmites stands available to harriers at scattered locations in the East Harbor and Bound Brook areas. This may indicate that although reed-grass marsh is acceptable to harriers for nesting, it is less preferred than cattail marsh. Further study of harrier nest site selection in CCNS is needed to resolve this question.

Harriers in CCNS are more flexible in their selection of habitats for foraging than for nesting. I observed harriers, including known nesting adults, foraging in a broad range of open-country habitats—salt marshes as well as freshwater wetlands, and diverse grassland, heathland, and shrubland vegetation associations. These observations were categorical, merely whether or not a given habitat type was utilized, and cannot be used to quantify the relative intensity of usage of the different habitat types. However, it is apparent that many vegetation associations not utilized by harriers for nest site placement in 2004 and 2005 are nevertheless important to the viability of harriers in CCNS. The harriers' flexibility in selecting habitats for foraging broadens management options, and it is important not to focus too narrowly on just nesting habitats when considering harriers' needs in the park.

Regional Context for the CCNS Harrier Population

Four main results from this study contrast with my previous field studies of Northern Harriers in southeastern Massachusetts, 1998-2003. Relative to the populations on Martha's Vineyard and Nantucket, the harrier population in CCNS is distinguished by: (1) low population density; (2) high rate of nest predation and consequently low reproductive success; (3) preference for wetlands over uplands for nest sites; (4) high frequency of within-season renesting. The first three of these findings have been discussed above. Renesting occurred in 3 of 5 territories with a failed first nest in 2004 and 1 of 3 such territories in 2005; more strikingly, renesting occurred in every territory where the first nest failed before May 31 (both years). This contrasts with Martha's Vineyard and Nantucket, where only 0-1 cases of renesting occur per year, in populations that have more nesting pairs overall (Bowen, unpubl. data).

It is plausible that the preference for nesting in wetlands and the high rate of renesting that characterize the CCNS harrier population represent an adaptive response to the population's second distinguishing feature, the high rate of nest predation and low reproductive success. Harriers at CCNS may prefer to nest in wetland sites because they are generally more resistant to depredation than upland sites (MacWhirter and Bildstein 1996), and the harriers may regularly make two nesting attempts per season, at least if the first nest fails early enough, to compensate for the low probability of any one attempt succeeding. If these characteristics of the CCNS harrier population have been favored by natural selection, they are only partly successful as adaptive responses. Wetland nest sites were more successful than upland sites in 2004-2005 (38% nest success vs. 20%), but this difference was not statistically significant, and none of the second nesting attempts in either year succeeded in fledging any young.

MANAGEMENT RECOMMENDATIONS

I have three main recommendations for managing the Cape Cod National Seashore to ensure the long-term persistence of the park's breeding harrier population.

(1) Maintain suitable harrier habitat.

The documented nesting habitats, especially the favored cattail marshes and scrub oak barrens, should be preserved in their current acreages for the park as a whole and specifically in the five core blocks of harrier habitat identified in this study (see Discussion, Harrier Population Size and Distribution in CCNS). The primary focus should be on maintaining nesting habitat because harriers in CCNS utilize a sufficiently broad range of habitat types for foraging that it is difficult to envision circumstances under which foraging habitat availability would become limiting. The low diversity of habitat types utilized for nest sites in CCNS, only 4 of 65 total vegetation associations, facilitates management by restricting the number of habitats that need to be considered, at least to maintain the current harrier population size. It would be prudent, however, to provide for potential population increases, and the utilization of additional nesting habitat types that might accompany such an increase, by maintaining at least some of the currently-unutilized shrubland associations, such as sandplain heathland (especially patches with dense, mature stands of Gaylussacia baccata, which are preferred nest sites on Nantucket) and blueberry wetland thicket.

Active habitat management may be necessary to prevent the loss of nesting habitat. For example, colonization of scrub oak barrens by pitch pine (Pinus rigida) should be monitored and counteracted as necessary, by cutting or prescribed burning. The proposed restoration of the cultural heathland landscape in the Marconi area (NPS 2006) is one way to help maintain harrier nesting habitat in the face of secondary succession. Restoration of tidal flow to wetlands such as Hatches Harbor, East Harbor, Pamet River, and Herring River has the potential to eliminate some existing harrier nesting habitat. The extent to which this will occur depends on the degree to which tidal flow is restored, and the concomitant degree to which cattail marshes used by harriers are altered. In light of the demonstrated value of these marshes, particularly those of East Harbor, to Northern Harriers, these management projects should consider ways to balance restoration against maintaining nesting habitat for harriers. For example, restoring tidal flow to the point where water quality is no longer impaired and estuarine benthos is restored, while limiting tidal flow so that the higher elevation cattail marshes are not altered, may be a way to eliminate most of the negative impacts of historic tidal restriction while still minimizing loss of harrier nesting habitat. Planning and implementation of these restoration projects should consider such alternatives, model their likely results, and document the selected alternative in the projects' environmental analysis.

Ideally, from the point of view of harrier preservation, acreage of open-country habitats in CCNS would not only be maintained but increased. Forest clearing and prescribed burning would be appropriate tools to achieve this goal, but I acknowledge that this would involve trade-offs or outright conflicts with other park management objectives.

(2) Avoid disturbance to harrier nests.

In the habitat types known to be utilized by harriers for nesting, especially cattail marshes and scrub oak barrens, National Park Service activities that can significantly alter vegetation structure should be conducted outside of the harrier nesting season (April 1 - August 31). This includes large-scale brush-cutting, mechanical clearing (e.g., plowing), and prescribed burning, all of which have the potential to disturb harrier nests. If such activities cannot be rescheduled

for the September-March nonbreeding season, then potential nesting areas should be carefully checked for the presence of nesting harriers before the areas are cut or burned.

CCNS personnel conducting more limited vegetation manipulations, such as trail maintenance and roadside trimming, or engaged in off-trail interpretive activities, should be reminded of the potential for disturbing harrier breeding activity in suitable habitat. Ideally these personnel would monitor their own actions and the behavior of any harriers seen nearby, and then curtail or modify activities as needed to prevent disturbance to harriers. Independent contractors working on park property should follow the same guidelines. They should be encouraged to consider potential impacts of their activities on harriers and adopt less disruptive alternatives when possible. Mosquito control operators working in cattail marshes might be one target group for consultations.

It is worth noting that ignoring these recommendations could increase the potential for a violation of the "take" provisions of the Massachusetts Endangered Species Act (321 CMR 10.04), which in turn could trigger undesirable restrictions on park management and recreation activities in the future. The likelihood of this scenario is slight, but it is easily avoided.

(3) Control populations of harrier nest predators.

The identity of the animals depredating harrier nests in CCNS is unknown. However, it is reasonable to assume that in many cases they are mid-sized mammalian carnivores, such as coyotes, foxes, raccoons, and skunks. I observed all of these species in harrier habitats in CCNS during my research, and they are confirmed nest predators in other field studies of harriers (MacWhirter and Bildstein 1996). Although lethal control of native animals in national parks is frequently controversial, it is worth considering whether some management decisions in CCNS could be subtly tailored in regard to their effects on harrier nest predators. Perhaps hunting, which has a well-established tradition in CCNS, could be expanded beyond game birds and rabbits to include, for instance, raccoons. Rabies epizootics, which have the potential to significantly reduce wild carnivore populations but which currently are suppressed on Cape Cod, could be allowed to follow a more natural course.

The recommendation to cull predators is admittedly difficult to implement; but since the primary limiting factor for the CCNS harrier population at present is nest predation, ensuring long-term viability of harriers in the park would be considerably easier if some way could be found to reduce predator populations.

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