BEHAVIOR OF PEREGRINE FALCONS IN THE NEW YORK CITY REGION

RICHARD A. HERBERT AND KATHLEEN GREEN SKELTON HERBERT

THIS paper summarizes the general behavior of Peregrine Falcons (*Falco peregrinus*) at eight nesting sites in the Hudson River valley, at a New York City eyrie, and at a number of New York City wintering sites, based on observations made over a 30-year period. The more intensive part of our study, involving about 1,200 visits to these eyries, was carried out from 1949 to 1959. The nesting pairs along the Hudson had become nonbreeding by the early 1950's, and by 1961 the entire population was extirpated. The history of these pairs, their productivity, and the factors contributing to their extirpation will be discussed elsewhere.

In this paper the term *eyrie* refers to a cliff or series of cliffs and to nest ledges which are the nesting domain of a single pair of Peregrines and their successors over a period of years. The term *cliff* here includes the face of an abandoned quarry as well as a New York City skyscraper used as a nesting site. Each cliff used by the birds has at least one nest ledge known to have been used in the years of our study. The term *nest ledge* is used in this paper to refer to past as well as to contemporary use.

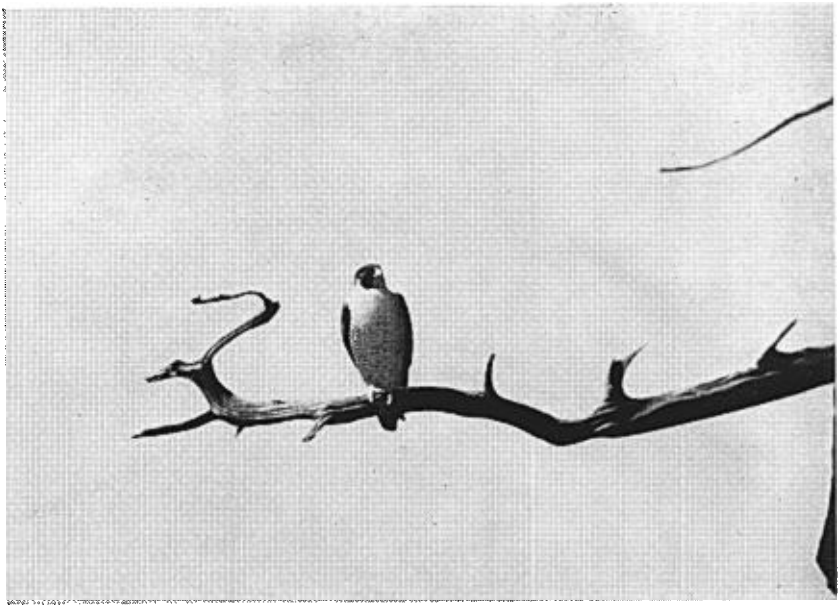
THE STUDY AREA AND ITS POPULATION

The sheer rock walls of the Hudson Palisades, rising to heights of 400 feet and dominating a majestic river, were fitting sites for the eyries of the Peregrine Falcon. The eight Hudson River eyries treated in this paper were distributed along the west shore of the river, extending north from New York City for a distance of 55 miles in New Jersey and New York State, within the jurisdiction of the Palisades Interstate Park. A ninth Hudson River eyrie, about 55 miles north of New York City on the east side of the river and opposite the eyrie referred to hereafter as no. 8, has not been included in this paper, although it produced young in the 1940's and 1950's. It is the only eyrie in this valley on the east side of the Hudson. A tenth, marginal eyrie situated in an abandoned quarry near the no. 6 eyrie has been included in our field observations, although it was usually unoccupied after 1941.

The Hudson eyries are numbered from south to north in this paper, 1–8. Six are situated on steep traprock cliffs with open, exposed ledges

→

Figure 1. Upper: female Peregrine Falcon at eyrie no. 1, May, 1953, when she was at least 13 years old (see pp. 67, 87). Lower: nesting ledge and banded young Peregrines at eyrie no. 6, showing plant growth which the birds appeared to prefer (see pp. 77, 84). Photographs by Richard A. Herbert.



above the talus slope; two are located in abandoned quarries. A primary characteristic of the Peregrine in this region is to dominate the landscape, and height is thus an important factor in the selection of its nest sites and perches. It does not appear, however, that extremely high cliffs are preferred, nor that extreme height is related to nesting success. Indeed, the highest cliff on the Hudson, the no. 8 eyrie, has had less nesting success in our experience than the much-molested no. 1 eyrie with its long, sheer cliffs. More important factors in nesting success would appear to be: (1) suitable ledges for nesting, feeding, and perching; (2) absence of large trees that would impede visibility and flight; (3) length of cliff, a long cliff with several ledges being preferable to a narrow one; and (4) inaccessibility to disturbance from above. Attachment to a traditional site is marked; if a better territory becomes vacant, a pair of Peregrines does not leave its traditional territory.

Although only four, or possibly five, of the Hudson eyries are first-class eyrie sites in the definition of Hickey (1942)—the poorest of the eight is located in a quarry having the dual disadvantage of only one nest ledge and easy access from above—they have compensatory advantages that have made them consistently sought by the Peregrine population for as long as its history is recorded. They might be compared to a Park Avenue address with a waiting list; in our first two decades of observation any vacancy in the eyries was immediately filled, a fact that led to a false impression of stability in the population.

Hickey (1942) and Cade (1960) have pointed out the attraction of rivers for the Peregrine. Like the seabird islands of the Pacific Northwest described by Beebe (1960), one magnetic attraction of the Hudson River cliffs is a bountiful food supply. Not only do the cliffs command a migration flight line with a prodigious supply of flickers (*Colaptes auratus*) and Blue Jays (*Cyanocitta cristata*) for several months of the year; they are also situated on a year-round route of homing pigeons speeding up the river. Cade (1960) also mentions, in relation to rivers, the Peregrine's fondness for bathing. However, we have never seen wild Peregrines bathe.

Another factor that has made these cliffs attractive is the protection originally extended to them. Protected for many years by the no-trespass regulations of the large estates along the Hudson, and then less effectively by the sanctuary status of the Palisades Interstate Park that swallowed up these estates in the 1930's, the Hudson eyries enjoyed more security than many inland eyries. Although the Peregrine has been officially protected throughout New York and New Jersey since 1934, protection was not enforced, even in the Palisades Interstate Park.

Peregrines wintered regularly on some 20 different New York sky-

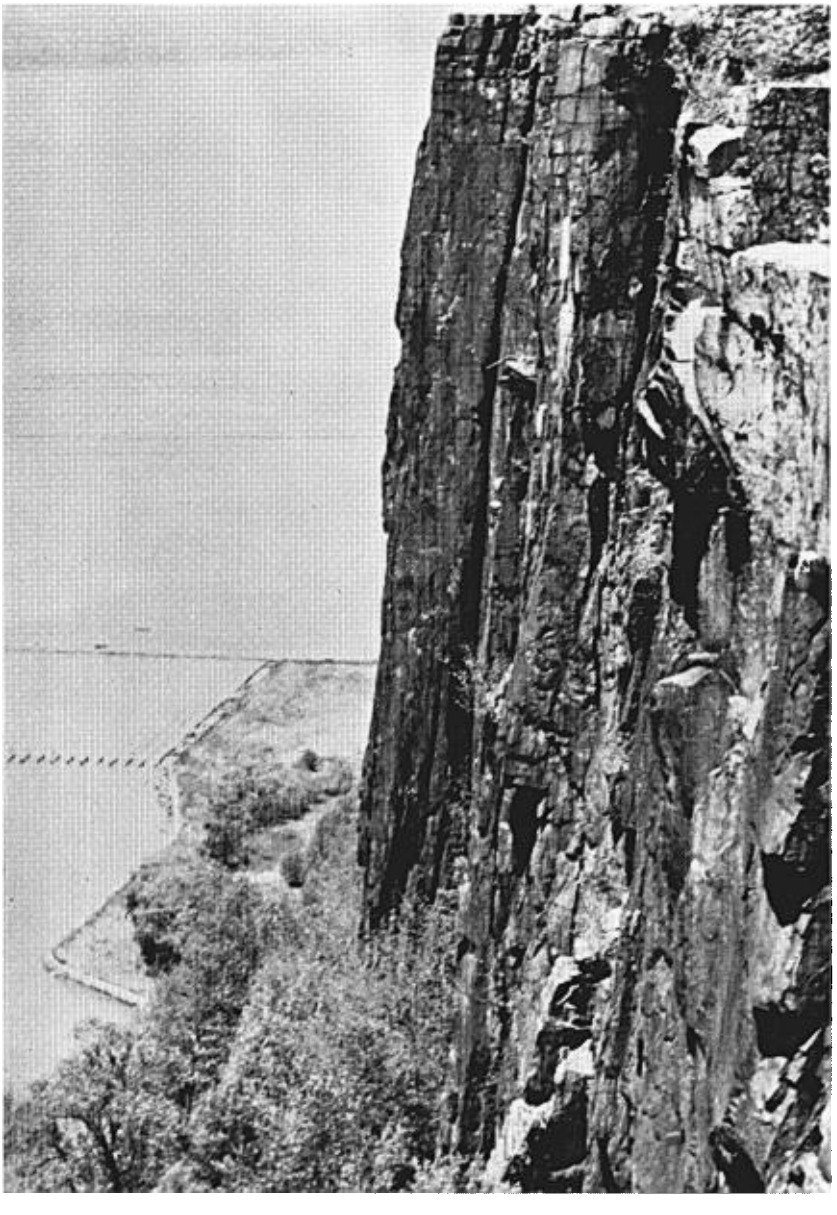


Figure 2. Nesting cliff of Peregrine Falcons overlooking the Hudson River. This is one of two alternate cliffs used by the pair at eyrie no. 3. Photograph by Richard A. Herbert.

scrapers in midtown and downtown Manhattan, on three of New York's bridges, and on a gas tank and a high school in The Bronx, a northern borough of New York City. The apparent impact of human interference was particularly noticeable in the New York City wintering population, which gradually increased during World War II, when the war effort removed many pigeon fanciers, falconers, and others normally responsible for curtailing this population. By 1946 the number of wintering Peregrines in Manhattan and The Bronx had risen to 16, but by 1952 the number had dropped to 7. Females dominated the New York skyscrapers and appeared to have territorial attachments for certain buildings.

In addition to the unattached, wintering Peregrines, New York City had one year-round resident pair of Peregrines from 1943 to 1953. This pair, which regularly roosted on the Grand Central Building in winter, hatched four clutches of eggs on two different skyscrapers about 1.35 miles apart in midtown Manhattan. Over a ten-year period they attempted nesting on several skyscrapers within a one-mile radius, giving rise to a newspaper legend that there were several pairs of Peregrines nesting in midtown Manhattan. In the winter and spring of 1943 two other pairs of Peregrines occupied Riverside Church and a gas tank in The Bronx, but these pairs did not remain.

Ratcliffe (1962) states that, in Great Britain, only where big cliffs are available is the Peregrine found nesting close to human dwellings, while Cade (1960:238) says that in Alaska very high cliffs seem to be avoided by this species. In our experience the important factors appear to be the isolation and dominance of the air which the eyrie affords; in New York City the successful nestings occurred on the 16th and 23rd floors of the two respective skyscrapers. On the Hudson several of the eyries had recreational areas and bathing beaches below the talus slope; such activity below the cliff did not disturb the birds, but any approach from above was immediately alarming.

In the city, as on the cliffs, the Peregrine heralds its presence by splashes of "whitewash" (excrement stains) on the pinnacles of Riverside Church, on the statues of the Roman athletes atop the Whitehall Building in lower Manhattan, and on outcroppings of many older skyscrapers. Pigeons also nest and roost on these buildings, but the excrement of such grain-eating birds makes a solid, dense mass. The Peregrine's mark is a splash, its perches loftier and more exposed.

The Peregrine has adapted well to the city habitat. Attracted, doubtless, by the abundant supply of pigeons and Starlings (*Sturnus vulgaris*), the falcons might have had considerably greater nesting success in the city had it not been for the opposition of pigeon fanciers (whose flocks of exercising pigeons were raided by the falcons), the American Society for

the Prevention of Cruelty to Animals, and the New York press, which printed accounts of the "murders" of pigeons by the falcons and even of their supposed attacks on humans (New York Times, 25 June 1945; 17 August 1959).

FIELD IDENTIFICATION

The Hudson and New York City population of Peregrines consists of birds of the eastern North American subspecies, *Falco peregrinus anatum*. These birds are larger, richer, and darker in color than the sand-colored falcons seen in fall coastal migrations in this region and believed by the authors to represent an arctic population. None of the numerous Peregrines banded as young nestlings in the northeastern states have to our knowledge been recovered south of Georgia and Arkansas. This suggests that Peregrines banded as coastal migrants in the fall and recovered in South America are from a different population.

The Peregrine's plumage is fresh and at its best in late fall after a molt of three to four months. It appears somewhat faded in the spring, and the females are apt to appear tan-colored on breast and belly. Over the years several adult birds on the Hudson were identified by peculiarities in markings or by variations in individual behavior. Three of these were occupants of their respective eyries for many years. The male at the no. 1 eyrie, which appeared in 1938 when already in adult plumage and which was present through 1955, had a tuft of white feathers about an inch in diameter on his head. His redoubtable female (Figure 1), a very dark bird present 1942–57 (fourth to occupy the eyrie after two previous females had been seized by a falconer and one had been shot) was conspicuous by her aggressive defense of the eyrie, and was further identified by the fact that she laid her eggs a month earlier than the other females on the Hudson. The male at the no. 3 eyrie was a trim, beautifully proportioned falcon, identified by his distinctive coloring. He was a very pale bird with creamy white breast but with exceptionally dark markings. As noted by Beebe (1960:150), contrasting markings are characteristic of *F. p. anatum* but this bird was the most strikingly marked of this species that we have seen. His crown and malar stripe were slate black, his back bluish, and his belly heavily barred like that of a female—a surprising distinction in view of his advanced age, for the plumage of the Peregrine tends to become paler with age. This bird appeared at the eyrie in adult plumage in 1940, and at the time of his disappearance in April, 1956, his age must have been at least 18 years, since the Peregrine does not normally breed until two years old.

In addition, such behavioral characteristics as the extreme "nervousness" of the female at the exposed no. 6 eyrie and certain distinctive

courtship habits of the female at the no. 7 eyrie suggested that the same female was in residence for a number of years, but these birds could not be positively identified.

From 1938 through 1944, 22 young were banded in the Hudson eyries (18 were banded by the senior author either alone or in association with others, and 4 by W. R. Spofford); yet none of the eyries appeared to be occupied by a banded bird throughout the period of our study. However, the birds at the no. 8 eyrie were too distant for us to distinguish bands.

GENERAL BEHAVIOR

Although we have sought to generalize in noting the habits of the Hudson Peregrines, perhaps the most notable fact about them was that they varied greatly as individuals. No two individuals nor pairs were the same in behavior. No two pairs, it would seem, had the same problems. Each eyrie was a world of its own, distinct in pattern.

THE PAIRING BOND

Permanency.—Although Hagar (*in* Bent, 1938: 44) casts some doubt on whether or not the Peregrines of the Massachusetts cliffs (where the birds did not winter) mated for life, and whether or not "the female of the previous season returns directly to the cliff, if still alive (as has been generally assumed)," the birds resident on the Hudson did appear to mate for life, unless one was removed from the cliff by some catastrophe. (One pair at the no. 1 eyrie remained intact for 14 years.) This was true, not only of the Hudson birds, but also of the pair resident in New York City and of the pair on the Sun Life Building in Montreal (Hall, 1955: 19, 22).

Replacement of mates.—In rare cases the catastrophe that removes one of the pair may take the form of a battle with another Peregrine for the eyrie, but this is exceptional. Although Beebe (1960: 163) was impressed by the lack of intraspecific aggressiveness among mated pairs of *F. p. pealei* on Langara Island in British Columbia, in our experience individuals of *F. p. anatum* tend to respect territorial boundaries, and territorial behavior in Alaskan Peregrines has been well described by Cade (1960: 197–198). Peterson (1948: 139) relates an incident in which two falconers trapped a breeding male at an eyrie and released him a month later at the same eyrie, *after* another male had taken possession of the cliff. Thus both birds were invested with territorial rights, and a battle royal ensued until the Peregrine that had replaced the trapped bird was driven from the cliff.

On 12 February 1943, two males battled for possession of the no. 3 eyrie, one of the finest cliffs on the Hudson (Figure 2). The defending male, the pale bird present since 1940, was the victor. On 1 April 1945,

an adult female and an immature female battled for possession of the no. 3 eyrie, the resident male taking no part in the fight. The immature female, thought to be the defending bird, drove the adult from the eyrie. The immature female proved to be a nonbreeding bird. Similar battles took place at the Montreal eyrie, where one female nested continuously on the Sun Life tower from 1936 through 1952 (Hall, 1955: 22). In 1944 her first mate was engaged in a battle of several days' duration which ended in his death. In 1950 her second mate disappeared and was immediately replaced (Hall, 1955: 13, 15, 18).

The primary attachment of the male, and of occasional females, appears to be to the territory, and mating may be incidental to this attachment. If the female of a pair is killed, the male usually continues possession of the cliff and tries to attract a female to it; but if the male of a pair is killed, and no replacement appears before the breeding season, the female is likely to desert. Both of these incidents occurred in the winter of 1951–52 on the Hudson; on 7 January 1952, the male at the no. 2 eyrie was found shot and his female deserted the cliff in March; the female at the no. 5 eyrie was found shot in November, 1951, but the male remained on the cliff and attracted a new female the following spring. Hickey's report (1942) of two females fighting for the same clutch of eggs also suggests that unsuccessful females lack the site tenacity of males.

Invasion of an occupied territory by a wandering Peregrine does not necessarily mean that the intruder is challenging the resident's possession of the cliff. Although the invader is frequently met by a challenge from the resident male—a series of aerial maneuvers and threatening stoops—most wandering Peregrines pass on their way unmolested.

On the Hudson most of the wandering Peregrines were females. Usually they were driven away from the cliff by the resident pair or by the female alone, but late in the breeding season of 1950 we saw an unusual incident in which a strange female appeared to be welcomed or at least tolerated by a resident pair (which had no young).

Visiting the no. 7 eyrie on 28 June, we watched the pair perch on the cliff after unsuccessfully pursuing a white pigeon. At this time the intruder, a dark, molting female, flew slowly into the eyrie territory, too high above the cliff for us to distinguish her markings. She circled the cliff, evidently watching its residents. They seemed to watch her, too, following her flight with rotating heads, but surprisingly they made no move to intercept her, nor did the resident female rise with her ringing battle cry. Instead, with much conversational *ee-chupp*ing (see under "Calls," below) they seemed to be calling in the stranger. While the resident female was perched on the cliff "talking" to the strange female flying above, the resident male executed what seemed to be a courtship

flight directed at the strange female, as if to entice her in to the cliff. He zoomed over the river, stooping and plummeting with folded wings almost to the surface of the water, then soaring into the blue. After his flight he perched on the nest ledge, while the strange female presently disappeared over the treetops above the cliff. For some minutes the male wailed, presumably calling to the resident female, who at length flew to the ledge where he was concealed. Both then disappeared from view. We heard their conversational notes for some time, this normally indicating copulation. Both birds then left the cliff on brief flights. Half an hour later they returned with the strange female flying high above them. The date of this observation and the fact that yearling Peregrines often molt a month or two earlier than adults suggest that the strange female was a yearling.

Although in our opinion the courtship flight is somewhat similar to the challenge that the male issues in defense of his territory, we were convinced that the behavior of this resident pair toward the strange female was "friendly," as evidenced by their *ee-chup* calls to her and by their return to the cliff accompanied—although at some distance above—by the stranger.

Similar incidents occurred at the no. 1 eyrie and the no. 8 eyrie when a wandering female invaded each territory. The explanation of these occasional incidents may be that the resident birds recognized the intruders either as mated neighbors or as passage birds, and knew that they were not contenders for, nor threats to, the eyries. On the Hudson, however, most wandering females apparently were unmated birds. Mated females from the eyries occasionally wandered, whereas males seldom left the cliff except on hunting expeditions.

WINTERING HABITS

On the Hudson the various pairs wintered along the cliffs at or near their eyries, in contrast to the absence of the Peregrines from the New England eyries in winter (Hagar, *in* Bent, 1938: 65). This may be due to the bountiful food supply of the Hudson area.

In the past, local ornithologists believed that the Hudson birds wintered in New York City, and various spring "arrival" dates on the cliffs were recorded in the 1930's in the minutes of meetings of the Linnaean Society of New York. Further confusion was created by the Hudson Peregrines' occasional hunting of Starlings and pigeons in the towns adjacent to, or across the river from, their cliffs, leading to the belief that they were wintering birds there. In the late 1930's when Great Horned Owls (*Bubo virginianus*) were nesting and wintering in the immediate vicinity of the no. 1 eyrie, the pair of Peregrines frequently flew across the river

in the late afternoon to roost on the Hunt's Point gas tank in The Bronx, about 5.5 miles distant.

However, winter records for the Hudson eyries from the early days of the century are in fact extant. In 1907 G. E. Hix recorded the first winter record of a Peregrine in Palisades Park 12 February; on 12 February 1913 Ludlow Griscom noted the second winter record for the Palisades when he saw the pair at the no. 1 eyrie (Ludlow Griscom, *in litt.*; also *Abstr. Proc. Linn. Soc. New York*, 24–25: 38). J. T. Nichols (*in litt.*) recorded the pair at the no. 1 eyrie 16 November 1915. In their unpublished manuscript, "Birds of the Englewood region" (prepared in 1918), these two observers stated that the "Duck Hawk" was a regular permanent resident in small numbers. Our own numerous winter records will be presented in another paper.

Though an occasional pair has wintered in New York, most of the New York City birds were unattached, wintering females. There is little proof of their origin, but we believe that most of these birds came from New England and northeastern eyries rather than from the Hudson. Of the banding records extant in 1962, only three winter recoveries were from New York City. The dates of these recoveries—one in November and two in December—suggest that the birds were wintering, yet surprisingly two of the three were males. One was a first-year male, banded as a nestling on the Delaware River and killed 3 December in Brooklyn; the second was a first-year male banded as a nestling on the Sun Life Building in Montreal and killed 25 December in Brooklyn; while the third was a female, banded as a nestling at a Massachusetts eyrie and killed in New York City in November, 1952, 13½ years later. This last bird was reported (Edward Brown, pers. comm.) to have occupied and bred in the same territory for many years. Our records indicate that she was a wintering bird.

There are also three winter recoveries from two nearby counties, of Peregrines banded at two Vermont eyries and one Pennsylvania eyrie. The reported sex ratio of all Peregrine recoveries in the 1950's was almost six to one in favor of females, suggesting to us that females wander more than males. However, there is also an old, unproven hypothesis that females outnumber males.

Of six recoveries from nestlings banded on the Hudson, three are winter records (one male and two females) of birds dying in Jersey City, New Jersey; two were shot and one was found dead with a partially eaten and presumably poisoned pigeon in January, 1944. Three other Hudson recoveries (two females and one bird of unknown sex) are of wintering birds taken in nearby towns of New Jersey. There is also one summer recovery from New York City, of a male banded as a nestling and picked up four

years later in downtown New York. According to the agent of the American Society for the Prevention of Cruelty to Animals, this bird was dying of "a growth in its throat." The date was 20 August 1946 and the description of its condition suggests trichomoniasis.

THE DAILY CYCLE

The hunting exploits of the Peregrine have so captivated the human imagination that one sometimes gets a picture of this swift "engine of death" clashing and brawling about the skies with unabated fury, striking into oblivion every hapless bird of passage. On the Hudson the Peregrine had no concern about making a living. He was a bird of leisure, and at almost any hour of the day one could find him, regal and dignified, perched on his twist of cedar or rock column, surveying his domain (see Figure 1). His bright eyes missed no movement on the cliff. With a barely perceptible movement of his head, he scrutinized the observers on a distant rock or a swallow skimming the river far below.

In the spring, processions of migrants of many species passed the Peregrine's eyrie, but except for an occasional reconnaissance flight after a brazen Crow (*Corvus branchyrhynchos*) or a threatening stoop at a hawk intruding near the nest ledge, the Peregrines permitted most of these migrants to pass without arrest. The Peregrine is not a hasty fighter. He does kill, but, like most predators, he kills only to eat.

The hunt.—When the Peregrine does hunt in dead earnest, his manner is often deceptively casual. With no apparent intent, he will watch a pair of homing pigeons cross the river half a mile north of his eyrie. When they are almost, it would appear, to the safety of the farther shore (but actually not more than halfway across the stream) and almost a mile distant from his perch, he takes off from the cliff on some seemingly irrelevant impulse, flying on a northward course as casually as a Peregrine *can* fly with his vigorous, always somewhat hurried flight.

There is a moment—just a moment—when pursued and pursuer, pigeon and Peregrine, seem to be flying at equal speeds. The pigeon will surely make the farther shore. Flying at better than 45 miles an hour, a champion racer, the homing pigeon is confident in his wings; he does not take cover. Yet the hawk is still gaining speed, quickening and shallowing his wingbeats until it appears that all of the motion is in the primaries. The race will be neck and neck, it seems. But suddenly, it appears that the pigeon is flying backwards, so great becomes the Peregrine's head-on speed. In a flash, the gap is closed; the Peregrine has overtaken the pigeon in a shallow stoop. Yet still the pigeon flies unharmed; the Peregrine has not seized it. But—and this is the mark of a great avian athlete who is seldom overextended—the Peregrine has overtaken merely to roll

over and seize the pigeon from underneath. Whether taken from above or below, the pigeon hangs limp in the talons of the Peregrine. Almost from the moment of the strike, it is dead.

It should be noted, however, that the Peregrine's hunt is not always either spectacular or successful. Hickey (1942) describes an occasion when he and the senior author saw a Peregrine make seven unsuccessful attempts to take seven different racing pigeons. Much depends on the maneuverability of the prey and its tendency to take cover. Almost alone among the birds that pass the Peregrine's eyrie, the racing pigeon does not immediately take cover. Most of the migrants—Blue Jays, flickers, swallows—and even the Bald Eagle (*Haliaeetus leucocephalus*) and the Red-tailed Hawk (*Buteo jamaicensis*) have been seen by us to take cover when the Peregrine sallies forth from his pinnacle.

In the spring, when young Peregrines are in the nest, the frequency of hunting increases. Blue Jays are moving up the river in numbers, straggling single file above the treetops at the top of the cliff. The male Peregrine watches the jays intently, his eyes moving as they move, his half-open wings quivering as he waits the moment of pursuit when the jays reach the center of the mile-wide river and are most remote from cover. At this moment he launches himself into the air. Again his flight appears deliberate, almost slow, as he gains altitude. When still far behind the quarry, he levels off, too distant and too far below to threaten the jays, it seems. But with quickening wingbeats he gains great speed; yet surprisingly, he is losing altitude rapidly while the jays are still above him. This seems a curious maneuver, but is a correct one, for at sight of the falcon, the jays, with folded wings, dive for the water, plummeting past the falcon to within a few feet of the river, as he tries unsuccessfully to intercept them. Then he singles out one jay, pursuing it relentlessly just above the water and seizing it in a quick, shallow stoop.

In this fashion, one May day at the no. 1 eyrie, the male brought in two jays from his afternoon's hunt, giving them whole to the two young on the nest ledge. A third jay was knocked into the water, where it was pounced on by several gulls, while a fourth which he pursued escaped to the farther shore.

Some weeks later, when the young were several days on the wing, we watched the female at this eyrie bring in a jay. She pursued no such pattern of artistry as the male in the hunt. When the Blue Jay was only a short distance out from the cliff, she took off in straightforward pursuit, and after three or four stoops she struck the jay a glancing blow, knocking it down momentarily to the water. As the jay then flew weakly above the water, she easily picked up the bird and passed it to one of her young on the wing. This points up the susceptibility of small corvids to capture

over water by Peregrines. Cade (1960) relates a similar account of the capture of a Gray Jay (*Perisoreus canadensis*) in the Yukon.

Feeding and night ledges.—The Peregrine usually carries his kill to an established feeding perch, such as a ledge or a dead tree on the cliff. Feeding ledges are distinct from nest ledges and night perches and in our experience the adult birds never feed themselves on a currently used nest ledge. On the Hudson each eyrie contained one or more main feeding ledges, and when young were present, two or three additional ledges might be set up near the nest ledge.

Although the site of a feeding ledge may vary from year to year, at some eyries the same feeding ledges were used for many years. At the no. 1 eyrie the main feeding site was a fallen dead cedar (*Juniperus virginiana*) bridging a chasm of rock which is within a hundred yards of the two most favored nest ledges. This same dead cedar served as the main feeding ledge at the no. 1 eyrie for more than 30 years and was a landmark to observers of the early 1930's.

All of the pairs on the Hudson had one or more night perches, well-marked with whitewash, used primarily for shelter at night or during a rainstorm. Usually the night perch was a small, shallow ledge with an overhang. Frequently it was so narrow that the bird faced sidewise or inward toward the cliff.

Food.—The most common prey of the Hudson Peregrines was the homing pigeon (these being routinely banded), except during spring and fall migrations when Blue Jay and flicker feathers regularly floated down the cliff. Occasionally a Starling's head or a bandless pigeon lay on the feeding ledge. In one year (1940) we thought that the male at the no. 1 eyrie hunted Starlings, while the female hunted pigeons, but in later years this did not prove true. However, the male does seem to have more success in catching small birds. Young birds often catch butterflies and dragonflies.

In the early 1930's Cleon Garland, a pigeon fancier and game warden, picked up more than 100 pigeon bands from feeding ledges at the no. 1 and no. 3 eyries. One band, recovered in February, 1932, dated back to 1897. As the feeding ledges are often difficult of access, Mr. Garland developed an ingenious method of checking them without climbing down the cliff. By means of a hook and heavily weighted fishing line he drew up a collection that included remains of shorebirds, Green Herons (*Butorides virescens*), Red-headed Woodpeckers (*Melanerpes erythrocephalus*), Mourning Doves (*Zenaidura macroura*), Rufous-sided Towhees (*Pipilo erythrophthalmus*), Common Grackles (*Quiscalus quiscula*), and, of course, flickers and Blue Jays (Cleon Garland, pers. comm.). Even a

duck (species unknown) was taken by a female at the no. 1 eyrie (Robert Menegus, *in litt.*, 7 March 1953).

The contention of many pigeon fanciers that the Peregrine prefers white pigeons may have some factual basis. Certainly a white pigeon offers a more conspicuous target to stoop at; we often saw the falcons with white or light-colored pigeons.

Although the extent of the Peregrine's hunting varies somewhat with the season, one homing pigeon (the average weight is about one pound) will more than sustain a pair for a day. However, on one occasion (24 June 1953), we watched the female of a pair at the no. 7 eyrie slowly consume an entire pigeon while the male wailed on a nearby ledge "asking" for a share of the prey and occasionally flying to her. Engrossed in her repast, she completely ignored him, feeding for an hour. When only the wings of the pigeon remained, she carried them off to another ledge. The male flew in to this ledge several times, with much conversational *ee-chupp*ing, seeking a share, but each time he was routed. On his seventh try, he emerged with one pigeon wing—a scant dinner—while the female flew about the cliff with the other wing.

This is unusual behavior. Normally the birds of a pair share a kill, often transferring the prey from one to another. Sometimes a portion of the kill is left on the ledge to be consumed later; on one occasion we saw the male return to a kill 24 hours later. When young are in the nest, remains of partially consumed birds are apt to be scattered about on nearby ledges, but these are usually fed to the young in due course and the entire carcass consumed. Normally the female does as much hunting as the male, but in the courtship and early breeding season (until the young are about three weeks old) the male does most of the hunting and feeds the female.

As on the Hudson, the chief prey of the city-dwelling Peregrine was the racing pigeon, except for such Peregrines as the Riverside Church bird. Located near an enormous winter Starling roost that covers three city blocks with excrement, the Riverside bird regularly fed on Starlings.

Whether the city pigeons (feral Rock Doves) that nested on the same skyscraper as a wintering or nesting falcon—usually several floors below—and the occasional Sparrow Hawks (*Falco sparverius*) that nested there can be termed "commensal associates" is a moot question. By preference the Peregrines struck into the flocks of racing pigeons exercising over the rooftops. These pigeons offered a more accessible, vulnerable target, while the city pigeons fed on the ground, where the falcons could not readily strike, and took cover close to buildings. On occasion, however, when there was sufficient space, the Peregrines did stoop at city pigeons. In the spring of 1948 a New York City pair frequented Central Park after

deserting the eyrie on the St. Regis Hotel; in the park they were often seen stooping at city pigeons.

Calls.—The vocalizations of Peregrines throw considerable light on their activities. A querulous wail, drawn out and rising in pitch at the end, is a call used in various circumstances. It is the territorial call of the male which, in early spring, does much flying about and wailing on the cliff. Wailing is the usual note of a Peregrine flushed off the cliff *when there are neither eggs nor young.* The birds also summon each other by wailing, as when the male wails to the female to entice her into a nest ledge, or when the female wails to the male for food, or when the male, carrying food back to the cliff, wails to the female to come and take the food in an aerial transfer.

A note used in more intimate contexts is the *ee-chup* note, described by Hagar (*in* Bent, 1938: 42) as a *wichew* note. Whenever the birds are close together on the cliff, and particularly during copulation and incubation, this is the note one usually hears. The *ee-chup* note is never heard *unless there are two birds on the cliff.* There are several variations of this call. A call also frequently heard during nesting is a soft *chirp* with which the birds greet each other on the ledge.

The alarm note or battle cry of the Peregrine is a drawn out *kaa-aa-ack, kaa-aa-ack, kack, kack, kack, kack, kack,* rising in pitch on the long-drawn opening notes and increasing in tempo on the last syllables. When the bird is merely scolding (a response of lower intensity), this is shortened to a rapid *kack-kack-kack-kack-kack-kack-kack-kack.* Witherby *et al.* (1939: 10–11) describe the latter as a shrill, chattering *kek-kek-kek-kek*; and the battle cry as "a hoarse, almost quacking 'kwaahk-kwaahk, kwaahk' of more intense excitement."

A bird (male or female) flushed off a nest ledge where there are eggs or young or even a scrape will utter this scolding cry or the battle cry as it circles the cliff, but if there are neither eggs nor young nor a scrape on the ledge, its wailing note will show that it has little interest in the ledge.

A seldom heard note is a clucking, like the cluck of a hen (*Gallus gallus*) or Barn Owl (*Tyto alba*), which the female uses in feeding very young birds, causing them to open their bills. By the age of two weeks or more the young give a low whine as the adult approaches with food. Hall (1955: 13) says that he heard chirping from the young while the eggs were still intact, a few hours before the first egg hatched.

NESTING

Courtship.—The breathtaking courtship flights of the Peregrine have been well described by Hagar (*in* Bent, 1938: 44–46). On the Hudson, copulation and courtship have been observed from 12 February to late

June (in an unsuccessful nesting season). Normally they took place in February and March. Once incubation begins there is little courtship or copulation; but if the nest is broken up, the cycle may build up again. Thus there is considerable variation in dates of courtship.

In the early stages of nesting the male seems to be the dominant member of the pair and he is often seen trying to entice the female into the recesses of a nest ledge. Another almost invariable act in the courtship and incubation pattern is his proffer of some portion of his kill to the female.

Nest ledges.—Among casual observers of the Peregrine at these cliffs, one sometimes heard the remark that "there are hundreds of ledges where they might be nesting." In this, evidently, the Peregrine and human point of view are sharply divergent, for there were usually only two or three ledges on each cliff that the Peregrines used for nesting, and many of these appeared to be traditional choices. Along the Hudson the same nest ledges of the nos. 2, 3, and 4 eyries were used half a century ago (the late Beecher S. Bowdish, pers. comm.).

Because of these traditional preferences, it is difficult to be categorical in defining the requirements of a nest ledge, for some unused ledges appeared to us to be superior to the chosen nest site. By preference the nest ledge was, like all other perches, high up on the cliff, commanding an extensive view. On the Hudson a physical requirement appeared to be that it should have sufficient soil or gravel to make a scrape (the hollow or depression in which the eggs are laid) and to provide drainage. In addition, many preferred nest ledges had a little grass and a stunted deciduous tree—there are few live cedars left on the cliffs—growing to a height of three to eight feet, an asset in sheltering the young (see Figure 1). One preferred nest ledge on the north cliff of the no. 3 eyrie had two 25-foot deciduous trees above it, large enough to shade the incubating bird and to afford a shaded perch to its mate, but this was exceptional; in selecting nest sites the Hudson Peregrines avoided cliffs with large trees, although in summer they frequently sought shade in large trees on nearby cliffs. Most of the ledges faced east, as do the cliffs, for the birds avoided the afternoon sun; but one or two ledges faced north. Nest ledges varied greatly in size and adequacy, some being as capacious as four feet wide and some so cramped that it would seem the young must fall off.

Most of the Hudson cliffs had two or three known nest ledges. At the no. 1 eyrie three nest ledges were regularly used, but six are known to have been used over a 30-year period. However, two of these were used only once, and one has not been used since the early 1930's. The two most favored ledges were within 100 feet of each other and within 100

yards of the main feeding perch, the fallen cedar. Two other ledges, a quarter of a mile to the north, were used for second and third nesting attempts. After a nesting failure, the birds moved to another, usually inferior, ledge.

One of the Hudson eyries, located in an abandoned quarry high up on the river bank, had only one nest ledge. Thus the birds at this cliff were forced to re-nest on the same ledge if their first clutch failed to hatch. In one year this pair successfully nested on top of the cliff, probably in a second nesting. This is the only known instance on the Hudson of Peregrines nesting in this fashion.

Hickey (1942) stated that an absolute requirement of the Peregrine appeared to be "that the eggs must be laid in a hollow which is scraped out of dirt, gravel or similar material," while Cade (1960) stated that the substrate of a scrape is not important or that no scrape at all may be needed "if a containing structure for the eggs is present or can be found." Equally divergent positions have been taken abroad by Ferguson-Lees (1951) and by Ratcliffe (1962).

The correctness of both views is well illustrated in the history of city-nesting falcons that have successfully nested and reared young in New York City without a scrape, but whose chances of success were greatly increased by a scrape or nest box with suitable scrape material such as gravel, earth, or debris. The function of a scrape appears to be twofold: to prevent the eggs from rolling off the ledge and to provide drainage for the young.

The first known nesting in New York City occurred in 1943 when a pair of falcons successfully hatched three young on a coping of the St. Regis Hotel (Figure 3). In 1946 the falcons nested on this ornamental coping on the 16th floor and hatched three young. The ornament, in the shape of a shield, had a depression above it in which the eggs were laid and the young hatched. When removed from the nest at about three weeks of age, the young were soiled and fetid with excrement because the declivity in which they were reared had no drainage. In 1947 three young were again hatched in this declivity. In 1945 the same pair of falcons hatched three young on the roof of an abandoned building at West End Avenue and 72nd Street, about one and one-half miles distant from the St. Regis. The nest was located 23 stories up between a partition of the roof and the building, in a space of about 30 × 4 inches. It had no scrape. The three young were just ready to fly when the nest site was raided by pigeon fanciers and police (New York Times, 25 June 1945).

Thus it appears that, although a scrape or nest box with scrape material is not an absolute essential, it is an important factor in nest success and is eagerly sought by the falcons. On the Hudson the pair at the no. 2

Figure 3. Nesting site of Peregrine Falcons in New York City. The St. Regis Hotel showing the corner shield ornament between the fifteenth and sixteenth floors (arrow), where the falcons three times successfully hatched young. Photograph by Richard A. Herbert.

eyrie was never successful on one ledge that lacked drainage. The Sun Life Building falcons of Montreal laid eggs on various outcroppings of the building in 1938 and 1939 (Hall, 1955), but it was only after two nest boxes were put out for them that they nested successfully. Groskin (1952) has described how a heap of debris deposited by the wind enabled Peregrines to nest in Philadelphia in 1946.

Throughout the years of our study we could not authenticate frequent reports of city- or bridge-nesting falcons. Pigeon fanciers several times advised us that falcons were nesting on the Williamsburg Bridge in midtown Manhattan. Peregrines were reported to have nested successfully on Bear Mountain Bridge (John Orth, pers. comm.), which spans the upper Hudson some three miles north of the no. 7 eyrie herein reported. The caretaker and engineer of the Riverside Church in the upper part of Manhattan Island told us that Peregrines were nesting there. So far as we were able to determine, all of these sites were usually occupied only by an unattached female, the only pairs which we saw being the St. Regis pair and an occasional pair roosting on the George Washington Bridge, about three miles from the no. 1 eyrie. However, unattached males were occasionally present in the city, and it is possible that nesting was attempted at the sites reported but that the eggs rolled off the ledges.

For several years a pair of Peregrines was reported nesting on The Travellers' Insurance Building in Hartford, Connecticut. Aided and abetted by a Hartford newspaper columnist, a playful rivalry sprang up between The Sun Life Assurance Company in Montreal and The Travellers' Insurance Company regarding their respective falcons, and the activities of the falcons became a feature of their house organs. When we visited The Travellers' Insurance Company in late July, 1949, the senior author was allowed to venture onto a ledge off the 27th floor where the falcons were said to have nested. The adults were present, but he saw no evidence of young nor eggs nor prey. The date, of course, was very late.

Egg laying.—In a normal season on the Hudson, the birds began to lay during the first week of April, the eggs being laid at intervals of approximately two days. Although the number of eggs varies, four are usual in a first clutch in this region, while three or less are usual in later clutches. (On many of the ledges it is impossible to see all of the eggs.) If unsuccessful in their initial attempt, the birds often lay a second or third clutch.

The female at the no. 1 eyrie from 1942 to 1957 regularly laid a month early, beginning the first week of March. This is the most extreme variation from normal that we have known on the Hudson, although one other female in 1939 and 1940 also had an early nesting cycle. Similar individual variations occur in other areas. The Sun Life Company falcon in Montreal laid approximately a month earlier than the birds in the surrounding area (Hall, 1955). The cause of this variation is not known, but we think it probable that the time of egg laying is genetically controlled. Annual variation in egg-laying dates is known to be correlated with such factors as spring temperatures and age of the female (Nice, 1937: 97–107), but the probability that some females are consistently early has received little attention from ornithologists, possibly because of the failure of individual songbirds to reach an advanced age and thus provide adequate evidence of the phenomenon.

Incubation.—The confusion surrounding reported incubation periods of birds of prey (Nice, 1953) still seems to involve the Peregrine. Hagar (*in* Bent, 1938: 50) gave the period as from 33 to 35 days among the birds he observed in Massachusetts. Jourdain (*in* Witherby *et al.*, 1939: 12) regarded this as probably too long and listed the period as 28–29 days for each egg. Hall's (1955) average of 39 days for nine clutches of the Sun Life falcon involved a period from the laying of the first egg to the hatching of the last one. His measurement falls outside the tight definition of incubation period recommended by Nice (1954) and others, but if one deducts the seven days usually necessary for the laying of a complete clutch of four eggs (in one year there was a clutch of five) Hall's

measured incubation period is not very disparate from that cited in Witherby *et al.*

We did not succeed in obtaining an incubation period on a per egg basis as we were anxious to avoid disturbing the birds during the egg-laying part of their nesting cycle. On the Hudson, incubation did not usually begin until the laying of the second or third egg, depending on air temperatures. It began most frequently on the fifth day with the laying of the third egg and averaged 32–33 days from this time of commencement until the hatching of the last egg. This period thus represents the incubating time of the adult birds and not the period required to hatch a single egg, which would be slightly less. Prior to incubation it would appear that the eggs can stand a greater degree of temperature variation. However, on one occasion, 20 April 1953, when the temperature had dropped to 34°F with a northwest wind, we found the male incubating one egg. If the bird, male or female, is flushed from the ledge at this one-egg stage, desertion is a frequent result.

The male's role in incubation has not been sufficiently documented. The tendency to incubate is strong in the male as in the female. His interest in the eggs and young appears to be as great as the female's; we have seen him spread his wings to shield the eggs from a hot sun. The male takes a regular part in incubation, often taking short turns while the female is feeding. As the larger and heavier bird, dominant on the nest ledge, the female incubates whenever she chooses, whereas the male must often "beg" for his turn, standing on the ledge and "talking" to the female. As might be expected, the female does most of the incubating, invariably taking over the eggs for the night. On the Hudson, falconers sometimes took advantage of this fact to seize the adult female on the nest ledge.

At the no. 1 eyrie, where the female did perhaps three-quarters of the incubating, a typical day was recorded by the senior author on 4 May 1941 as follows (the times are based on the 24-hour clock).

0900. Female incubating eggs. Male perched on cliff nearby.
0935. Female turns eggs, and resumes incubating in quarter-turn counter clockwise.
1005. Male circled cliff and disappeared.
1030. Female turns clockwise in quarter turn—think she turned eggs also.
1120. Male returns without food. He wails and chirps, greeting female. Female chirps back and turns eggs, making two complete circles. She now faces out to river.
1145. Much wailing and talk by male. Female chirps back occasionally.
1150. Several crows fly into eyrie territory, fussing around cliff. Twice the male seems about to pursue them, but does not. I think he wants to incubate.

1200. Male lands on nest ledge. Female seems to greet him by bowing her head. Much *ee-chupp*ing. Female does not get off eggs; male presently leaves ledge and stoops at crows.
1203. Female turns eggs, making complete circle.
1205. Male flies up river rapidly.
1225. Female turns eggs. She now faces in toward cliff.
1240. Male returns and perches.
1250. Female turns eggs, still facing inward.
1300. Male flies up river, landing on his regular perch of last year.
1420. Male returns carrying rust-colored pigeon; flies twice past nest ledge wailing to female. Female answers with an *ee-chup*, but does not fly out to take pigeon from him. Male deposits pigeon on cedar feeding perch, and perches on snag near nest ledge.
1426. Male flies in to nest ledge and walks halfway in, but female only turns eggs and continues incubating.
1450. Female turns eggs. Male still waiting for her to leave.
1521. Female gets off eggs, and male takes over. He turns eggs and settles down. Female flies up river and returns in five minutes, flying about.
1530. Female puts in to feeding perch, where she begins feeding on pigeon.
1700. Female returns to nest ledge and takes over the eggs. Her approach is very different from the male's deferential approach to her. She lumbers in as if she owned the ledge. Male gets up hastily as she seems about to step on him.

Young.—If the birds were successful in their first clutch, normal hatching dates on the Hudson were approximately from 15 to 20 May. These were also the hatching dates of the New York City pair. At the no. 1 eyrie the normal hatching date of the female present from 1942 to 1957 was almost a month earlier.

Although Witherby *et al.* (1939: 12) mention a fledging period of five to six weeks, 30 to 35 days was the more usual period on the Hudson. Hagar (*in* Bent, 1938: 50) notes a fledging period of 33 to 35 days. The young seem able to fly after a fashion at four weeks, but they appear reluctant to leave the nest ledge until they are able to fly well, this at about five weeks. Some young remain on the nest ledge longer than five weeks. Males regularly fly before females and if banding is done when the young are about four weeks old young males often flush off the ledge. Young have occasionally fallen from the nest ledge, but this is exceptional because almost from the moment of hatching they possess a marked ability to avoid the edge of the ledge, however narrow it may be.

The plumages of the young have been well described by Bent (1938: 52–53). They change from the creamy white down of newly hatched birds to a coarse gray down that begins to appear in about 10 days. Before the birds leave the ledge, they are in the streaked buff and brown juvenal plumage of their first year.

Both male and female feed the young, but in the early stages the fe-

male does most of the feeding, tearing the prey and allowing the young to pluck bits from her beak. Within a week they can be seen tugging at the remains of prey on the nest ledge, and before they leave the ledge they are well initiated in tearing and plucking the prey for themselves. For about a month after they leave the nest ledge, the young are fed by both adults; on one occasion we saw the male feed a young bird that had been fledged five weeks to the day.

DISCUSSION

NESTING BEHAVIOR 1950–56

Detailed field observations and the history and productivity of the eyries are covered in another paper now in preparation. Here it is sufficient to note that the production of young on the Hudson and in New York City increased markedly during the war years, 1941–45, because of the rationing of gasoline, the restricted movements of falconers and gunners, and the total absence of road building. In these years production averaged two young per eyrie per year; thereafter productivity decreased; in 1951 the last young hatched in the Hudson eyries; and by 1961 the population was extirpated.

During the years of the population decline, from 1949 to 1955, the birds engaged in much unusual nesting behavior, herein reported. In these years the birds were subject to molestation in various forms—road building, seizure of young by falconers, and shooting. Weather was also a deterrent in the breeding failures of 1950–53.

Our most remarkable observation in these years was the late date at which the birds attempted renesting. In 1950 the early-nesting pair that normally incubated during March, a month earlier than the other pairs, incubated a clutch of eggs until 15 June; and in 1952 this same pair appeared to have incubated until mid-July. In 1953 they were incubating on 10 June. In both 1951 and 1952 this pair incubated four clutches, which we think is a record for this species. In 1952 their fourth nesting attempt was made in early July, after they had incubated their third set of eggs for more than two weeks. No other such extremes in the renesting of Peregrines are known to us.

Hickey (1942: 187) after reviewing egg collectors' records of *F. p. anatum* reported that "if the eggs are lost at a rather advanced stage of incubation, no further attempts at nesting are known to have been made." On the basis of his own field work on *F. p. pealei*, Green (1916: 475) concluded that "if incubation is advanced it will be more like three weeks before the new set is laid." Yet our unusual female, having incubated a first clutch for three weeks to four weeks in March, 1951, laid eggs on

another ledge and commenced incubation in the incredibly short space of 12 days. It appeared that only two eggs were laid in the second clutch, and thus only three days were consumed in laying, but as incubation does not begin until half the clutch is laid, this remarkable female went through the pre-egg stage of the nest cycle in one week, despite the fact that her previous nesting had been well advanced. (On an earlier occasion, too, the senior author had known this female to renest following a three- to four-week incubation of the first clutch.)

This second clutch, discovered on 12 April 1951, was found abandoned on 17 April. On 21 April we found the female incubating a third clutch of three eggs on another ledge. On 2 May, 12 days later, we found this third nest broken up; three eggs, one broken, remained on the ledge. Within two weeks, on 14 May, we found the female incubating on a fourth nest ledge; on 16 May we again saw her incubating here, but on 30 May we found the nest ledge abandoned.

At three eyries on the Hudson in the years 1950–53, copulation and courtship were seen until the late date of 26 June. At one eyrie an egg was laid on 5 June and a bird was seen incubating on 10 June. The lack of success in these persistent efforts suggests that late, repeated renesting attempts have small chance of success, even under otherwise favorable conditions. Not only were initial attempts more successful than later efforts, but early-nesting pairs, such as the one at the no. 1 eyrie, had a higher percentage of success than late-nesting pairs. This observation may not apply in remote areas where the birds are not subject to human disturbance, and where weather is often presumed to be the determining factor in early nesting. However, Broley (1947: 11) notes that in Florida, where inclement weather was not a factor, there was a greater degree of nesting success among early-nesting Bald Eagles (that lay in early November) than among late-nesting eagles (that lay in December and have many addled eggs).

The late dates at which the birds attempted breeding in the years 1950–53 led us to speculate on how late they could successfully breed on these cliffs, and recalled an unverified story of a young Peregrine falling off a nest ledge of the no. 7 eyrie in late September (S. Grierson, pers. comm.). It seems probable that young hatched along the Hudson River in July might not survive on the open ledges exposed to the midsummer sun; the heat of the rock, which shrivels inch worms when placed there, might be a lethal factor to young birds. However, the no. 7 eyrie where the young were reported in September has some shaded ledges. It might be of interest to compare the hatching dates of the Hudson birds with those of cave-nesting Peregrines mentioned by Bent (1938: 49).

NATURAL PREDATORS

Although predators, especially the raccoon (*Procyon lotor*), are popularly blamed for the disappearance of eggs, even from Peregrine eyries, their role, along the Hudson at least, was so minor as to be negligible. In the Hudson eyries, the Peregrine was well able to cope with its natural enemies except, on rare occasions, for the formidable Great Horned Owl. Numerous encounters between passing Red-tailed Hawks, Ospreys (*Pandion haliaetus*), and Bald Eagles have produced no more than threatening gestures on each side, the Peregrine being content to stoop at but not strike these able peers.

Ordinarily the Great Horned Owl is a bird too powerful to warrant attack unless the Peregrine has eggs or young. Enderson (1964: 340) mentions flushing one of these owls which was immediately struck by a pair of nesting Prairie Falcons (*Falco mexicanus*) and soon killed. Broley (1947: 17) reports that Great Horned Owls cause much disturbance among nesting Bald Eagles and frequently take over their nests. When eagles are displaced by horned owls that preempt their nests, the eagles usually rebuild that same season but do not lay.

A number of Great Horned Owls nested along the Hudson cliffs during the 1930's and 1940's, usually at some distance from the Peregrines, but in 1935 the owls had a nest with three young less than 100 yards from the no. 1 eyrie where the Peregrines were incubating. Once during this dual occupancy of the cliff the senior author visited the cliff with two falconers. They flushed the owls, believing that, as on previous occasions, the Peregrines would merely stoop at them when the owls were in the open. When flushed, one owl took cover, flying close to the cliff; the other owl flew out over the river and was struck a stunning blow by one of the falcons, loud enough to be heard by the senior author who was some distance away on the cliff above. The owl fell, spinning slowly round and round, with wings set at a high angle. As it fell, the second Peregrine struck it, whereupon it dropped to the road below. Two hikers ran to capture the harassed creature, but the owl eluded them, taking refuge in a small tree beside the road. Minutes later, the owl flew slowly out of the tree. In a lightning stoop, the Peregrine struck again, and the owl fell, heavily inert, hitting the talus slope and bouncing out of sight. In this second encounter, the owl was thought to have been killed. But an hour or two later the senior author saw a Great Horned Owl, thought to be the injured bird, fly into the cliff from the road below, pursuing a discreet path beneath the level of the treetops.

The owls successfully reared young that year (1935), but the Peregrines abandoned their eggs, roosting nightly on the Hunt's Point gas

tank in The Bronx (New York City), about 5.5 miles distant from their eyrie, where the senior author frequently saw them. This is the only occasion when the Peregrines are thought to have abandoned their eggs because of the owls, but from 1935 to 1941 the pair at the no. 1 eyrie, which had several resident owls on its long series of cliffs, often roosted on the gas tank during the fall and winter months, probably because of the proximity of the owls on the cliffs. Other observers (Cleon Garland, *in litt.*) also noted that the Peregrines departed from their cliff in the late afternoon, flying toward New York City. By 1953 the population of Great Horned Owls had decreased markedly (there were none south of the no. 3 eyrie), and owls were not a factor in the nesting failures of the years 1950–56.

Black snakes (black snake, *Coluber constrictor*, or pilot black snake, *Elaphe obsoleta*) are other predators which, on rare occasions, may molest Peregrine eyries. On 6 June 1943, the senior author was watching a nest ledge on the south cliff of the no. 3 eyrie—a first-class cliff with a rock wall so sheer that it appeared impossible to reach the ledge without wings or rope. On the ledge was a young bird 10 days old. The female was feeding the young bird, and the male was perched nearby. Their activity at this time was entirely normal. Suddenly both adults darted into excited action, flying back and forth in front of the ledge, issuing the *kack-kack-kack* alarm call, diving at the ledge from a height of 20 feet, and perching momentarily at its edge. Then the female flew slowly off the ledge dragging a huge black snake in one foot. Unable to carry the snake, she lost altitude rapidly. Some 30 feet out from the cliff, she dropped the snake, which fell 60 feet to the talus slope. The snake, probably *Elaphe*, was about six feet long and weighed probably three to three and one-half pounds, or more than the falcon. This episode speaks volumes for the strength and agility of the snake in reaching the ledge, and for the courage of the falcon in defending its young. Whether the snake would have attacked the young in the nest is not known. Williams (1951) relates an episode of a rat snake (*Elaphe*) overpowering and strangling an adult Red-shouldered Hawk (*Buteo lineatus*), a species that normally preys on snakes. Thus the black snakes may account for the disappearance of eggs at some of the Hudson eyries.

The raccoon was conspicuous by its absence from the eyries of the Hudson. Although raccoons and gray foxes (*Urocyon cinereoargenteus*) were of occasional occurrence on the talus slope, we never saw one on top of the cliff. Apart from the fact that birds' eggs are more easily obtained in trees and thickets than on sheer cliffs, some of the eyries appeared to be utterly inaccessible to a raccoon. Further, it is difficult to imagine that a raccoon would interfere with an incubating Peregrine on its nest ledge

as long as other eggs were more readily available. One pair of Peregrines is known to have attacked a Bobcat (*Lynx rufus*) on top of a cliff outside of our area (Richard Thorsell, pers. comm.). As a matter of fact, in our experience on the Hudson the Peregrines' abandoned eggs were usually left to bleach and whiten on the ledge, untouched by predators.

AGE AND NESTING SUCCESS

The age and possible senility of the Hudson Peregrines have also been considered as factors possibly affecting nesting success. Hickey (1942) suggested that the age of the females at two of the Hudson eyries in 1939 and 1940 may have been the cause of sterility, citing their failure to lay and the fact that courtship lasted a month past the normal period.

Our observations do not bear out this hypothesis, nor does the history of the Sun Life Company falcon, a bird easily identified by a deep indentation on her chest. From 1940 through 1952 when she disappeared, she hatched 26 young, and at the age of 18 years or more was still producing young (Hall, 1955). Further, in a healthy population one may suppose that truly senile birds would not long succeed in retaining a mate or a nest ledge.

On the Hudson the male at the no. 1 eyrie from 1938 through 1955 (distinguished by a tuft of white feathers on his head) must have been 20 years or more of age at the time of his disappearance, as Peregrines do not usually breed until 2 years of age. When first observed in 1938, he was in adult plumage. A highly productive female present at this eyrie from 1942 to 1957 must have been 17 years of age or older at the time of her disappearance. A distinctive male at the no. 3 eyrie appeared in 1940 and at the time of his disappearance in 1956 was at least 18 years of age. Ratcliffe (1962) says that 7 years is the longest known occupation of an eyrie by a single Peregrine in Great Britain, and that this occurred only once. Demandt (1953) accepts Horst's (1937) conclusion that a German eyrie was occupied by the same female for 18 years.

In our opinion the age of the Hudson Peregrines was not a factor in their nesting failure. Broley (1952: 126) says that eagles have lived for 40 years in zoos and may have lived longer in the wild. She mentions a Bald Eagle that laid an egg after 30 years in captivity. Flower (1938) states that the average age for the 100 oldest Passeriformes (excluding domestic canaries) in captivity was 20 years and two months. Parrots, he states, have a potential of about 50 years; an Eagle Owl (*Bubo bubo*) lived for 68 years in captivity, and a Bateleur Eagle (*Terathopius ecaudatus*) for 55 years. Prestwich (1955: 8) notes that a Golden Eagle (*Aquila chrysaetos*) began to lay eggs after 15 years in captivity and was continuing to lay them at the age of 30. A female Peregrine that crashed

into the American Telephone and Telegraph Building in New York City carrying a racing pigeon was 13½ years old; she was banded on 4 June 1939 as a nestling in Massachusetts and died on 13 November 1952. This is the greatest recorded age of a wild banded North American Peregrine that has come to our attention.

The known longevity records attained by three of the Hudson Peregrines and the Sun Life Company falcon were probably due to favored eyrie sites and the fact that the Hudson birds were nonmigratory, and further to World War II and its gasoline rationing, which temporarily removed many of their human persecutors. The Sun Life falcons were also benefitted by the fact that the owner of the building, The Sun Life Assurance Company, protected the nesting falcons and publicized a favorable "image" of the predators. Had the Peregrines in New York City had an equally sympathetic public, their nesting success might have been greatly enhanced.

In view of the advanced age attained by some of the Hudson Peregrines, the first-year mortality of the young may be quite high. This conclusion parallels that of Beebe (1960: 173), who was impressed by the very high reproductive success of Peregrines along the British Columbian coast. His estimate of 2.7 young fledged per occupied eyrie is slightly higher than our Hudson River estimate of 2 young per eyrie fledged during the war years.

Although senility has not been a factor in nesting failure on the Hudson, yearling females may be a factor in nesting failure. There have been no cases of yearling males occupying Hudson eyries, but in the 1940's there were two instances of an immature-plumaged female occupying an eyrie. In neither case were eggs laid.

DISAPPEARANCE OF EGGS

Eggs disappeared from several of the Hudson eyries, particularly in the years 1950–53 when the six southernmost eyries were subject to extreme disturbance. The eyrie at which this occurred most frequently was the exposed no. 6, where eggs disappeared as early as 1940. This is the eyrie situated in a quarry with easy access from above. During the year 1950–53 the female was missing primaries early in the season and may have been shot at. We picked up a rifle shell within 100 yards of the eyrie in 1951, and the resident park policeman admitted that there had been target shooting below the cliff. The female at this eyrie was marked by nervous and shy behavior.

In 1940 three eggs were seen at the no. 6 eyrie on 12 April, while a fourth egg, broken, lay on the ledge 18 inches away, obviously rolled or kicked there by the falcons. (This ledge is flat and capacious so that eggs

do not roll off; it is accessible to a raccoon, but there was no evidence of raccoons.) To prevent their removal by egg collectors, these eggs were marked, but on 18 May 1940, when the ledge was again examined, they had disappeared.

On 5 June 1950, from the top of this same cliff, we saw one fresh, reddish-buff egg, probably laid that morning, on the ledge below, and certainly not more than one day old. There was almost no scrape as yet. Four days later this egg had disappeared. There was a better scrape than on our previous visit, suggesting that the egg had not disappeared on the day it was laid. On 12 April 1951 we saw one fresh, unincubated egg on this ledge. For fear of disturbing incubation we did not again visit the eyrie until 21 April, when we found this egg abandoned, though still on the ledge. On 19 April 1952 we again saw a freshly laid egg on this ledge, but two weeks later it had disappeared.

The eggs of the Sun Life Company falcon disappeared on several occasions (Hall, 1955: 12, 18). The Sun Life falcon laid her eggs in one of two nest boxes on a ledge surrounding the 26th floor of the Sun Life Building. There being neither raccoons nor skunks (*Mephitis mephitis*) on the Sun Life Building, Hall assumed that the falcon herself ate her eggs. In 1949 small pieces of shell were found in the nest box, and one observer (Cleghorn) later saw the female eating an egg (Hall, 1955: 18). Ratcliffe (1958) also found that Peregrines occasionally eat their own eggs. A captive Barred Owl (*Strix varia*) at the Trailside Museum, Bear Mountain, New York, likewise disposed of two eggs, apparently eating them whole without leaving any traces in the cardboard carton which she occupied. Likewise, a captive Barn Owl at the Trailside Museum was thought to have eaten one of her eggs (John Orth, pers. comm.). It seems possible that such birds eat their eggs or otherwise dispose of them when disturbed, in the same fashion as frightened mammals that occasionally eat their young. (A domestic rabbit may eat one litter because of "nervousness," but may successfully rear the next litter.)

Because of her proximity to frequent visitors and observers, nervousness may have been a factor in the disappearance of the Sun Life falcon's eggs. It may even have been responsible for the disappearance of one young on 12 May 1952, four days after hatching; there were no signs of the young bird's body in the box, although the other two young were present (Hall, pers. comm., 12 September 1952). Prestwich (1955: 13) narrates an incident of a female Kestrel (*Falco tinnunculus*) that hatched five eggs, in a cage about five by two by three feet high, on alternate days and ate each young bird when it was one day old; the fifth young was taken from her when it hatched. However, Lee S. Crandall (pers. comm., 1953) former Curator of Birds at the New York Zoological Park,

where falcons and birds of prey were kept in larger quarters, advised us that they had no record of these birds having eaten or otherwise disposed of eggs or young.

It might be assumed that a bird, having once disposed of or eaten eggs, does not thereafter hatch any young, but develops the habit of eating all her eggs. This was not true of the Sun Life falcon. In 1942, two eggs of her clutch of four disappeared, while two hatched; in 1948 her clutch was photographed by the senior author but later disappeared; in 1949, four eggs disappeared, one by one; in 1950 one disappeared while three hatched; in 1951, three eggs disappeared one by one during incubation, and the embryo in the fourth died only a few days before hatching; in 1952, one egg disappeared from the nesting ledge while three are reported to have hatched (Hall, 1955: 18, 19).

In the Hudson eyries we have no proof of eggs having been eaten, but an occasional egg or even, on one occasion, a clutch disappeared when such disappearance could not be attributed to egg collectors or predators. On the Hudson it was always a fairly fresh and never a long-incubated egg that disappeared. At the no. 3 eyrie on 20 April 1953 we found the male incubating one fresh egg. (The incubation of one egg is abnormal, but the temperature had dropped to 34° F with snow flurries.) Three days later this egg was gone, only a few bits of shell remaining on the ledge. At the no. 1 eyrie the female was incubating two fresh eggs on 16 May 1953, but a week later only one egg remained on the ledge. Again in 1955 at the no. 1 eyrie we found the male incubating one fresh egg on 23 April; four days later this egg was gone. These instances suggested egg eating.

Usually, however, it is a bleached or addled egg that disappears, giving rise to speculation as to whether the Peregrines may have some knowledge of the progress of the egg, or may notice its color and eject it from the nest.

ABANDONMENT OF EGGS

Even more puzzling than the disappearance of eggs was the abandonment of partially incubated eggs, left to whiten on the ledge while the birds were making second and third nesting attempts on nearby ledges, a phenomenon frequently noted in the disastrous years of 1950–53. We hope to describe this in detail in another paper. Hickey (1942: 188) says that "incomplete clutches may be abandoned if exceptionally nervous birds are molested." Birds that have been interrupted in their nest cycle by such factors as blasting, shooting, road construction, visitors, or weather appear to build up some sort of cumulative nervousness, so that

even a very slight disturbance may subsequently cause abandonment of an incomplete or even a complete clutch.

In discussing the effects of a Florida hurricane on nesting Bald Eagles, Broley (1947: 18, 19) pointed out that it had far more than its immediate effect; it appeared to create a psychosis of some sort in the birds and was calamitous to nesting, even though it occurred four to six weeks before the nesting season, and *even though all of the nests were rebuilt in plenty of time for normal nesting.* In 24 of the 45 rebuilt nests, no eggs were laid; and in 21 nests where eggs were laid, they did not hatch, although the birds incubated for two months.

Broley (1947: 19) also noted that the hurricane interfered with the nesting schedule of Great Horned Owls, and that poultry in the area had lost their drive to incubate. In the same article he quoted F. B. Hutt (then Professor of Animal Genetics at Cornell University). Concerning the chain of physiological factors involved in the cycle of eagle courtship and nesting, Hutt considered that "the role of bird psychology in these processes must not be underestimated."

An analogy might be drawn with the Hudson Peregrines which, when disturbed by any of several causes—road construction, attempts to trap the adult birds, or even weather—abandon their eggs and attempt to renest on another ledge. Renesting attempts are increasingly unsuccessful as the birds lose "confidence" and become progressively more nervous, unwilling or unable for physiological reasons to incubate their eggs.

In the population decline of the Hudson Peregrines the role of DDT and other pesticides and poisoning via the food chain has not been determined. Ratcliffe (1963: 74) reported that the eating of their own eggs by falcons has characterized the spectacular population decline of the British Peregrine in recent years. Although aware that this behavior pattern took place at least occasionally in the pre-DDT years, he regards its recent frequency as the result of the birds ingesting chlorinated hydrocarbons. We carried out no chemical tests, such as the British did, either on the eggs of these birds or on the birds themselves.

Mebs (1960) has noted a drastic population decline of this species in Germany, which he attributes to fanatical persecution by carrier pigeon fanciers. He states that the successful production of young noted in the years immediately after World War II has now all but ceased in many areas. Despite all persecution the breeding pairs remain at their eyries until they, too, are eliminated.

The precise role that continual persecution of the Hudson birds played in clutch abandonment and in the failure of the females at two eyries to lay an observable clutch in the late 1950's remains to be elucidated.

SUMMARY

Until the mid-1940's 8 to 10 pairs of Peregrine Falcons occupied eyries in the lower Hudson River Valley, another pair hatched four clutches on two New York City skyscrapers, and up to 16 or more birds wintered in New York City (including its northernmost borough, The Bronx) in a single year. Wintering Peregrines were usually females, apparently from eyries in the northeastern United States or southeastern Canada. The Hudson Peregrines appeared to mate for life, but if one of the pair was killed, a replacement frequently took place; one pair remained intact for 14 years. Territorial defense appeared to be intrasexual, but was particularly strong among males. Prey of the Hudson Peregrines tended to be racing pigeons, Blue Jays, and flickers, while city birds preyed on racing pigeons and Starlings.

On the Hudson, nest ledges at each of the eyries were one to six in number, renesting usually being on a ledge of inferior quality. Although a scrape was not essential for the eggs, it tended to increase nesting success, and sites permitting a scrape were sought by the falcons. First clutches usually numbered four, while second and third clutches numbered two to three. Hatching was normally from 15 to 20 May, and fledging was about five weeks later. One female regularly laid a month early over a 16-year period.

A wailing note is usually given when a Peregrine with no eggs or young is flushed from the cliff, a conversational *ee-chup* note when two birds are together on the cliff, and a *kack-kack-kack-kack* alarm or scold note under conditions of intense excitement. On the nest ledge the adults sometimes greet each other with a soft chirp note.

Productivity of this population increased markedly during the war. In 1941 through 1945 production at three eyries averaged 2 young per year, but thereafter a downtrend occurred, and by 1961 the population was extirpated. In these years the birds were subject to extreme persecution by humans. When the birds were unduly molested, abandonment of clutches and persistent renesting occurred. In both 1951 and 1952, one female incubated four successive clutches. Egg disappearance was an occasional phenomenon of these years, and egg eating by the falcons was inferred. As three Peregrines in this study are known to have attained the ages of at least 17, 18, and 20 years, respectively, senility seems to be without importance in nesting success.

ACKNOWLEDGMENTS

The senior author made a study of the Hudson eyries and the New York City birds from about 1930 until his death in 1960. Most of these data have not been published, although some statistics on the Hudson eyries for the years 1939 and 1940

were included in the survey made by Hickey (1942). In 1949 the junior author joined in the study, and assumed the responsibility of gathering and eventually of publishing the data. Many data gathered prior to 1940 were supplied by Dr. Joseph J. Hickey, without whose help and encouragement this manuscript could not have been prepared. Thanks are due also to Dr. Dean Amadon for his critical reading of an earlier draft of the present manuscript.

NOTE

Publication of this paper has been made possible by a gift to the American Ornithologists' Union in memory of Richard A. Herbert (1907–1960), who throughout most of his life was an ardent and discerning student of the biology and conservation of the Peregrine Falcon.

LITERATURE CITED

BEEBE, F. L. 1960. The marine Peregrines of the northwest Pacific Coast. Condor, **62:** 145–189.

BENT, A. C. 1938. Life histories of North American birds (Part 2) Order Falconiformes and Strigiformes. U.S. Natl. Mus., Bull. 170.

BROLEY, C. L. 1947. Migration and nesting of Florida Bald Eagles. Wilson Bull., **59:** 3–20.

BROLEY, M. J. 1952. Eagle man. New York, Pelligrini and Cudahy.

CADE, T. J. 1960. Ecology of the Peregrine and Gyrfalcon populations in Alaska. Univ. California Publ. Zoöl., **63:** 151–290.

DEMANDT, C. 1953. Brutbiologie Probleme beim Wanderfalken (*Falco peregrinus*). J. f. Orn., **94:** 99–102.

ENDERSON, J. H. 1964. A study of the Prairie Falcon in the central Rocky Mountain region. Auk, **81:** 332–352.

FERGUSON-LEES, I. J. 1951. The Peregrine population of Britain. Bird Notes, **24:** 200–205; 309–315 (original not seen).

FLOWER, S. S. 1938. Further notes on the duration of life of animals.—IV. Birds. Proc. Zool. Soc., London, **108A:** 195–235.

GREEN, C. DE B. 1916. Note on the distribution and nesting habits of *Falco peregrinus pealei* Ridgway. Ibis, **(10)4:** 473–476.

GROSKIN, H. 1952. Observations of Duck Hawks nesting on man-made structures. Auk, **69:** 246–253.

HALL, G. H. 1955. Great moments in action The story of the Sun Life falcons. Montreal, privately printed.

HICKEY, J. J. 1942. Eastern population of the Duck Hawk. Auk, **59:** 176–204.

HORST, F. 1937. Wie gross ist das Jagdgebiet des Wanderfalken? Beitr. Fortpfl.-biol. Vögel, **13:** 98–99.

MEBS, TH. 1960. Probleme der Fortpflanzungsbiologie und Bestandserhaltung bei deutschen Wanderfalken (*Falco peregrinus germanicus*). Vogelwelte, **81:** 47–56.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow. Vol. 1. A population study of the Song Sparrow. Trans. Linn. Soc. New York, **4:** 1–247.

NICE, M. M. 1953. Incubation periods of birds of prey. A historical review. Vogelwarte, **16:** 154–157.

NICE, M. M. 1954. Problems of incubation periods in North American birds. Condor, **56:** 173–197.

PETERSON, R. T. 1948. Birds over America. New York, Dodd, Mead and Co.

PRESTWICH, A. A. 1955. Records of birds of prey bred in captivity. London, privately printed.

RATCLIFFE, D. A. 1958. Broken eggs in Peregrine eyries. Brit. Birds, **51:** 23–26.

RATCLIFFE, D. A. 1962. Breeding density in the Peregrine *Falco peregrinus* and raven *Corvus corax*. Ibis, **104:** 13–19.

RATCLIFFE, D. A. 1963. The status of the Peregrine in Great Britain. Bird Study, **10:** 56–90.

WILLIAMS, G. G. 1951. Rat snake overpowers Red-shouldered Hawk, *Buteo lineatus*. Auk, **68:** 372.

WITHERBY, H. F., C. R. JOURDAIN, N. F. TICEHURST, AND B. W. TUCKER. 1939. The handbook of British birds. Vol. 3. London, H. F. and G. Witherby.

Liston Front Range Lighthouse, R.D. 2, Middletown, Delaware.