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Re-Establishment of Atlantic Puffins (*Fratercula arctica*) at a Former Breeding Site in the Gulf of Maine (Re-Establecimiento del Frailecillo del Atlantico (*Fratercula arctica*) en el Golfo de Maine)

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RE-ESTABLISHMENT OF ATLANTIC PUFFINS (*FRATERCULA ARCTICA*) AT A FORMER BREEDING SITE IN THE GULF OF MAINE

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Abstract.—Of 774 Atlantic Puffin (*Fratercula arctica*) nestlings transplanted from Great Island, Newfoundland to Eastern Egg Rock in Muscongus Bay, Maine, 147 are known to have returned to the Gulf of Maine, of these, 36 nested at Eastern Egg Rock, 17 at Matinicus Rock, and one at Machias Seal Island. Inter-island movements between these colonies decreased with age: 44% of 2-yr olds observed moved between islands, the proportion was 25% for 3-yr olds and 14% for 4-yr olds. At Eastern Egg Rock, the average age at first breeding increased from 4.2 yr in 1981 to 5.8 yr in 1985. Pairs that nested earlier in the season were more successful in producing a fledgling than those that nested later.

This study demonstrated that young puffins learn the location of their natal island sometime after they are 2 wk old, and they will return and nest at a transplant site or nearby existing puffin colony. This study also demonstrated that young transplanted puffins develop a breeding schedule associated with conditions at their release site, rather than conditions where they were hatched, i.e., a genetically determined timetable for breeding.

RE-ESTABLECIMIENTO DEL FRAILECILLO DEL ATLANTICO (*FRATERCULA ARCTICA*) EN EL GOLFO DE MAINE

Resumen.—De 774 pichones de *Fratercula arctica* transplantados de Great Island, Newfoundland a Eastern Rock en la bahía de Muscongus, Maine, se conoce que 147 han regresado al golfo de Maine, de los cuales 36 anidaron en Eastern Egg Rock, 17 en Matinicus Rock, y uno en la isla de Machias Seal. Movimientos entre islas de las distintas colonias disminuyeron con la edad: 44% de los individuos observados de 2 años de edad se movieron entre islas, así como 25% de 3 años y 14% de 4 años de edad. En Eastern Egg Rock, la edad promedio al alcanzar madurez sexual aumentó de 4.2 años en 1981 a 5.8 años en el 1985. Parejas que anidaron temprano en la temporada fueron más exitosas produciendo pichones que aquellas que anidaron más tarde.

Este estudio demuestra que las aves juveniles aprenden la localización de su isla natal en algún momento despues que cumplen 2 semanas de edad, y que ellos regresarán y anidarán en el lugar del transplante o colonia activa más cercana. Este estudio también demuestra que los juveniles transplantados ajustan sus patrones de reproducción a las condiciones prevalecientes en el lugar que son liberados en vez de las condiciones de donde fueron traídos, e.j., patrones reproductivos determinados genéticamente.

There have been few long-term studies examining the effects of seabird chick relocation on natal site fidelity. The only major exception to this is the work of Fisher (1971), who relocated 3124 fledgling Laysan Albatross (*Diomedea immutabilis*) from Midway Atoll to other Laysan Albatross colonies up to 400 km away, only to have most return to Midway Island.

Serventy (1967) experienced similar results with 50 fledgling Short-tailed Shearwaters (*Puffinus tenuirostris*) that were transplanted to another island. None of these transplanted birds returned to the release site. However, both Serventy and Fisher found that if birds were relocated well before they reached fledging age, some of the transplanted birds would return to the release site.

From 1973 to 1981, 774 Atlantic Puffin (*Fratercula arctica*) nestlings were transplanted from their natal burrows on Great Island, Newfoundland, to test and develop techniques for re-establishing puffins near the southern limit of their former North American breeding range. This study documents the first successful use of the transplant technique for re-establishing seabirds to historic nesting habitat, a technique that could have broad application to management of endangered seabirds. This paper reviews return rates, inter-colony movement, and breeding of the transplanted puffins through 1985.

STUDY AREAS

Transplanted puffin chicks were reared and released each year at Eastern Egg Rock (43°52'N, 69°23'W), a small island located in the mouth of Muscongus Bay, about 10 km east of New Harbor, Maine. In addition, observations were made on the two other Gulf of Maine puffin nesting islands: Matinicus Rock (43°47'N, 68°51'W), 32 km east of Eastern Egg Rock in outer Penobscot Bay about 30 km offshore from Rockland, Maine and Machias Seal Island (44°30'N, 67°06'W), approximately 217 km east of Eastern Egg Rock and 16 km offshore east of Cutler, Maine (Fig. 1).

Eastern Egg Rock is a treeless 2.9 ha island with a central meadow dominated by mixed grasses (*Phleum pratensis* and *Agropyron repens*) and thickets of red raspberry (*Rubus idaeus*) and common elderberry (*Sambucus canadensis*) that overlie shallow peat soil of about 0.5 m depth. The southern and western shores of the island consist of large jumbles of angular granitic boulders. Puffins had not nested at Eastern Egg Rock since 1887 when the species was extirpated by overhunting (Nettleship and Evans 1985, Norton 1923).

Matinicus Rock is a 7 ha island with a 3 ha central meadow overlying a shallow peat soil with outcropping granitic ridges. A lighthouse, established on the island in 1846, was occupied until December 1983 by the U.S. Coast Guard. In 1984 the light station was automated and leased to the National Audubon Society which now places summer warden-biologists on the island. Prior to the re-establishment of breeding puffins at Eastern Egg Rock, Matinicus Rock was the only Atlantic Puffin colony in the United States. In 1985, about 100 pairs of puffins bred under boulders and in deep rock crevices around the periphery of the island, with most birds at the eastern and northern ends of the island; there are no known instances of puffins nesting in grassy-turf habitat there.

Machias Seal Island is a 6 ha treeless island with a grassy meadow with a band of large granitic boulders around the periphery. Within the

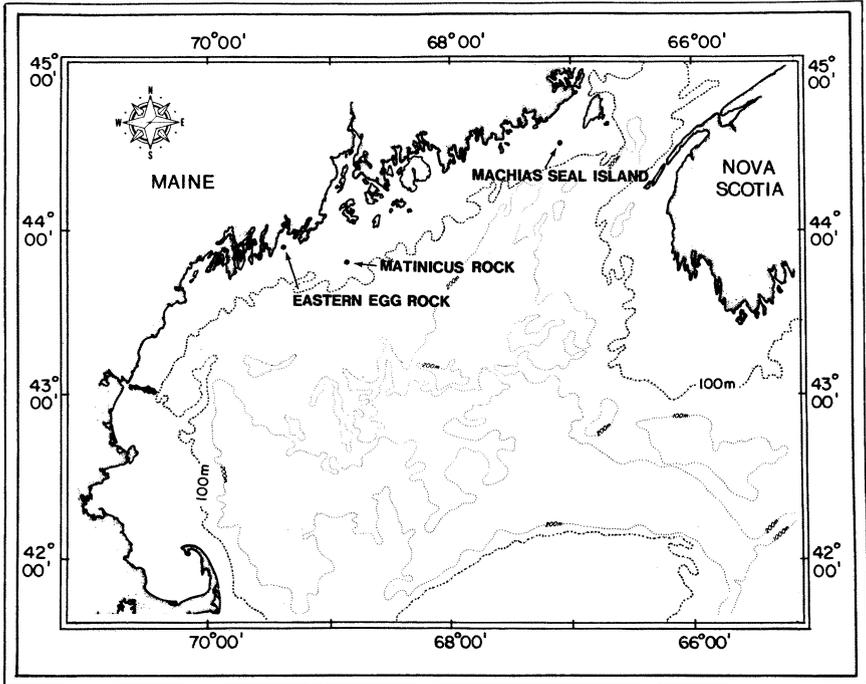


FIGURE 1. Atlantic Puffin colonies in the Gulf of Maine.

meadow area is a manned lighthouse and outbuildings operated year-round by Transport Canada. The island supports the largest colony of Atlantic Puffins in the Gulf of Maine, with virtually all 800–1000 pairs (1984 estimate) breeding in rock crevices among the boulders (Nettleship and Evans 1985).

METHODS

At the time of collection on Great Island, Newfoundland (47°11'N, 52°49'W), puffin chicks varied in age from 2 to 40 d with a mean age of 17 d. The age of each chick collected was determined after measuring the flattened left wing chord to the end of the fleshy wing tip (in downy chicks) or longest primary, and estimating age from a growth curve of known-aged puffin chicks from Great Island (Nettleship 1972, unpublished). The time interval between the removal of a chick from its natal burrow on Great Island to placement in an artificial burrow on Eastern Egg Rock was, on average, less than 17 h.

The captive chicks were reared in sod burrows, constructed with L-shaped interiors. They were fed two 50 g meals of Atlantic smelt (*Osmerus mordax*) or common silversides (*Menidia menidia*) daily, the first at 0800 h and the second about 1600 h (EDT). This diet was supplemented weekly with 100 mg of vitamin B₁, 100 I.U. of vitamin

E, and 100 mg of a multiple-maintenance vitamin, administered by placing the tablets or capsules inside the fish. This vitamin supplement was based on that used by the New York Zoological Park for their colony of Tufted Puffins (*Fratercula cirrhata*).

The puffin chicks were confined to their burrows during the first 7 d by placing a wire-mesh screen over the burrow entrances; after that time the screens were removed to allow the chicks to exercise outside the burrow entrance and depart for sea when ready. Prior to fledging, each chick was banded with a numbered monel or stainless steel USFWS band and a colored plastic leg band. In 1973–1977, the color bands identified only the year class of each chick; in 1978–1981, the color bands were individually numbered, allowing easier identification of individual birds. Where possible, birds banded prior to 1978 were identified by reading the numbers on the metal bands with a spotting scope from an observation blind.

Owing to the limitations of identifying birds banded in 1973–1977, only those chicks transplanted in 1978–1981 were used to analyze inter-island movements. Further details on burrow construction and maintenance techniques of the young in captivity were given by Kress (1978).

To enhance the likelihood of having fledglings reared on Eastern Egg Rock return to the island in subsequent years, 20 wooden puffin decoys were positioned at conspicuous locations around the island in 1977. The number of decoys was reduced to four in 1982 and has remained constant through 1985.

To further improve the probability that transplanted puffins would colonize Eastern Egg Rock, the USFWS poisoned Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*) there during the summers of 1974 and 1975 and gull nests were destroyed in subsequent years (Kress 1983).

At Eastern Egg Rock, the location of nest sites and numbers of breeding birds were determined by noting where puffins delivered fish. Fledging success and overall productivity was estimated by assuming that a chick fledged successfully where food had been delivered for at least 21 consecutive days, based on the fact that most chick mortality occurs soon after hatching (Harris 1984, Nettleship 1972). Chick survival could not be determined directly because of the inaccessibility of the young in the boulder habitat and the need to keep disturbance to a minimum.

RESULTS

Rearing and fledging success.—Only two chicks out of 774 died while in transit between Great Island and Eastern Egg Rock, and 730 (95%) of the 772 transplanted puffin chicks successfully fledged. The average departure age for 578 fledglings in 1976–1981 was 49 d (± 2.9 [SE], Table 1). Although most puffin chicks were transplanted when 7 d old, seven were transferred when only 2–3 d old. The survival of these two 3-d-old chicks supported the recent findings of Barrett (1984) that Atlantic Puffins can thermoregulate when only 3 d old.

Returns.—One hundred and forty-six (20%) of the 730 chicks that

TABLE 1. Age at fledging of transplanted puffins at Eastern Egg Rock, 1976–1981.

Year	Age at fledging (d)			
	<i>n</i>	\bar{x}	SE	Range
1976	96	48	0.36	43–55
1977	99	47	0.25	43–53
1978	89	53	0.25	47–59
1979	92	49	0.24	44–55
1980	100	48	0.27	45–52
1981	99	48	0.29	44–55
Totals	578	49	0.28	43–59

fledged between 1973 and 1981 were resighted at either Eastern Egg Rock, Matinicus Rock or Machias Seal Island in subsequent years (Table 2). The number of puffins from each year class seen at least once after their fledging year varied dramatically, ranging from 0 to 56.

Of those birds recorded, one was first seen when 1 yr old, 58 when 2 yr old, 23 when 3 yr old, and eight when 4 yr old. Although some birds may have visited one of the study areas prior to the time they were first observed, it seems likely that most puffins were identified soon after they returned, owing to the intensity of observation and the small size of the colonies at Eastern Egg Rock and Matinicus Rock.

Recoveries.—Seven (1%) of the 730 chicks that fledged were reported dead. Six were found 35 to 200 km southwest of Eastern Egg Rock along the shore within 20 d after fledging; one 2-yr-old bird was found dead near the mouth of the Moisie River, Quebec, in the Gulf of St. Lawrence, 1450 km north of Muscongus Bay.

Inter-colony movements.—Of the 147 fledglings known to have survived to at least 1 yr of age, 118 were sighted at Matinicus Rock, 87 at Eastern Egg Rock, and 27 at Machias Seal Island (Table 3). Examination of the 1978–1981 year classes (individually color-marked cohorts—see Methods) showed that 53% ($n = 38$) of the 73 puffins observed visited both Eastern Egg Rock and Matinicus Rock with the remainder (47%) restricted to a single site: 37% ($n = 27$) at Matinicus Rock, 7% ($n = 5$) at Eastern Egg Rock, and 3% ($n = 2$) at Machias Seal Island.

Movements between islands in the same season were age-related. Forty-four percent of the puffins fledged from the 1978–1981 cohorts made at least one inter-colony movement when they were 2 yr old ($n = 39$), a proportion that declined to 25% and 14% at 3 ($n = 68$) and 4 yr ($n = 50$) of age, respectively. Only two breeding puffins are known to have visited an island other than their breeding colony and both of these sightings are late in the season after their chicks had fledged.

Most birds that made inter-colony movements between Eastern Egg Rock and Matinicus Rock changed locations several times within a season. For subadult puffins (1–4 yr old), time spent at each colony during a

TABLE 2. Returns of transplanted puffins that fledged from Eastern Egg Rock.

Year class	Total number of fledglings	Individuals identified in subsequent years ^a	
		<i>n</i>	%
1973	5	0	0
1974	54	0	0
1975	91	8	9
1976	98	9	10
1977	99	56	56
1978	91	23	26
1979	92	26	28
1980	100	16	14
1981	100	9	6
Totals	730	147	20%

^a Individual birds sighted at least once after fledging year.

single visit varied from 1 to 27 consecutive d and averaged 2.3 d (± 2.7 [SD], $n = 399$).

With increasing age subadult puffins made increasingly frequent visits to islands. This is illustrated by changes in patterns of attendance by the 1978 transplant cohort in their visits to Matinicus Rock and Eastern Egg Rock. There were 71 visits from this cohort (1 d long or more) when they were 2 yr old, 123 visits when they were 3 yr old and 205 visits when they were 4 yr old.

Lengths of individual visits also increased. Island visits averaged 1.5 consecutive d (± 1.0 [SD], $n = 71$) for 2-yr-old birds, 2.6 d (± 3.48 [SD], $n = 123$) for 3-yr-old birds, and 2.8 d (± 3.5 [SD], $n = 205$) for 4-yr-old birds, differences that were significant between 2- and 3-yr-old birds ($t = 2.43$, $df = 156$, $P < 0.01$), but not between 3- and 4-yr olds ($t = 0.72$, $df = 258$, NS).

Native puffins produced at Matinicus Rock and Machias Seal Island also moved between colonies. Eleven chicks of 239 banded at Machias Seal Island were recorded at Matinicus Rock as 2-yr olds. In 1982, 9% (5 of 58) of chicks banded at Machias Seal Island in 1980 visited Matinicus Rock. Similarly, 9% (6 of 70) of Machias Seal Island chicks banded in 1983 visited Matinicus Rock in 1985. In contrast, there have been no Matinicus Rock sightings of 41 and 70 Machias Seal Island chicks banded in 1981 and 1982 respectively. In addition, one Machias Seal Island puffin (age unknown) was sighted at Eastern Egg Rock and one 2-yr-old Matinicus Rock bird was observed at Machias Seal Island.

Breeding attempts and performance.—A total of 54 transplanted puffins are known to have bred at three islands in the Gulf of Maine (as of 1985): 36 at Eastern Egg Rock, 17 at Matinicus Rock, and one at Machias Seal Island (Table 4). The first record of a transplanted puffin breeding occurred at Matinicus Rock in 1980 involving a bird from the 1975 year class which mated with an unbanded Matinicus puffin.

TABLE 3. Returns and breeding attempts of transplanted puffins at three islands in the Gulf of Maine.

Year class	Number of fledglings	Eastern Egg Rock			Matinicus Rock			Machias Seal Island		
		Number sighted	Breeding ^a		Number sighted	Breeding ^a		Number sighted	Breeding ^a	
			<i>n</i>	%		<i>n</i>	%		<i>n</i>	%
1973	5	0	—	—	0	—	—	0	—	—
1974	54	0	—	—	0	—	—	0	—	—
1975	91	1	0	0	8	6	75	1	0	0
1976	98	2	2	100	9	1	11	1	0	0
1977	99	42	19	45	36	7	19	2	0	0
1978	91	17	7	41	18	2	11	9	1	11
1979	92	17	5	29	24	1	4	5	0	0
1980	100	7	3	43	16	0	0	6	0	0
1981	100	1	0	0	7	0	0	3	0	0
Totals	730	87	36	41	118	17	14	27	1 ^b	11 ^b

^a Based on observations of transplanted bird delivering food to a nest site at least once; birds that produced an egg that did not hatch would go undetected.

^b Only one transplanted bird was seen delivering food to a nest site; however, owing to the relatively large size of the puffin population at Machias Seal Island, some other transplants may have bred but gone unnoticed.

Transplanted puffins first bred at Eastern Egg Rock in 1981. Of the four pairs that bred, one pair consisted of one member each from the 1976 and 1977 year classes, two pairs consisted of both members from the 1977 year class and both members of the fourth pair were unbanded. After 1981, increased numbers of unbanded puffins began to breed at Eastern Egg Rock. By 1985, six unbanded puffins bred at Eastern Egg Rock, four were paired with transplanted birds and two were a pair suspected of having occupied the same nest site since 1981. At Matinicus Rock, 17 transplanted puffins have bred, 13 paired with unbanded birds (believed to be native Matinicus birds) and four bred with other transplanted puffins.

TABLE 4. Breeding performance of puffins at Eastern Egg Rock, 1981–1985.

Year	Number of chicks hatched	Chick survival to day 21 ^a	
		<i>n</i>	%
1981	4	4	100
1982	14	12	86
1983	10	6	60
1984	14	10	71
1985	20	16	80
Totals	62	49	78

^a Food delivered to nest site for at least 21 consecutive days (see text for details).

Of 62 breeding attempts known to have occurred at Eastern Egg Rock in 1981–1985, 49 (78%) produced chicks that survived to at least 21 d of age (Table 4). This performance figure was high because only pairs whose eggs survived to hatch were detected and recorded (see Methods). Thus, the total number of breeding attempts by transplanted birds probably exceeded 62. Fledging success was correlated with hatching date. During the years 1982–1985, 38 successful nests had a median hatching date of 18 Jun., whereas, 17 unsuccessful nests had a median hatching date of 11 Jul. ($t = 3.16$, $P < 0.005$). A similar trend was observed at Great Island by Nettleship (1972), who found that chicks hatched before 30 Jun. had a greater chance of reaching fledging age than chicks hatched later.

Although more transplanted puffins were seen at Matinicus Rock than Eastern Egg Rock (118 vs. 87), 41% of those visiting Eastern Egg Rock eventually nested there compared to only 14% which nested at Matinicus Rock (Table 3). The 1975 transplant cohort was an exception. Of the eight members known from the 1975 transplant, six bred at Matinicus Rock, and none at Eastern Egg Rock even though there were regular sightings of this cohort at the latter site between 1977 and 1979 when these birds were 2–4 yr old.

At Eastern Egg Rock, puffins nested at 24 different sites in 1981 through 1985. Most nests were on the southern end of the island in extensive boulder habitat, grouped in loose clusters each containing several pairs. Puffins also nested in rock crevices on the west and northwest shores of the island in small groups of two or three pairs.

Age at first breeding.—The average age for the six known-age puffins that colonized Eastern Egg Rock in 1981 was 4.2 yr, far below the average of 5 or 6 yr observed in most other colonies (Harris 1984, Petersen 1976). Of the 35 known-age breeding puffins at Eastern Egg Rock through 1985, 26% have bred when 4 yr old; 49% at 5 yr old; 20% at 6 yr and 6% at 7 yr. Since the colony was established, the average age at first breeding has increased from 4.2 yr (1981) to 5.8 yr (1985), a difference that is statistically significant ($t = 4.25$, $df = 6$, $P < 0.0025$, $n = 11$).

In contrast, of 17 transplanted puffins that bred at Matinicus Rock, 13% first bred when 4 yrs old, 33% at 5 yr, 27% at 6 yr, 13% at 8 yr, and 7% each when 9 and 10 yr old. This suggests that transplanted puffins breed for the first time at a younger age at Eastern Egg Rock ($\bar{x} = 5.1$ yr) than they do at Matinicus Rock ($\bar{x} = 6.1$ yr) ($t = 2.94$, $df = 17$, $P < 0.005$, $n = 51$).

Breeding chronology.—Puffins returned to Eastern Egg Rock as early as 4 Apr., and laid eggs as early as 23 Apr. The beginning of the hatch was very consistent between years. At Eastern Egg Rock the first fish delivery was observed on 8 Jun. in 1983, 10 Jun. in 1984 and 8 Jun. in 1985. In 1985 the median hatch occurred on 15 Jun. for pairs which had bred together at least once previously. The median hatch date for pairs breeding together for the first time was 6 d later. At Eastern Egg Rock, most adults departed the island by mid-August. The breeding chronology

described for puffins at Eastern Egg Rock was very similar to that at Matinicus Rock.

DISCUSSION

Inter-colony movements.—Most inter-colony movements occur in the years prior to first breeding and such movements decrease as puffins become established at a colony. In this study, only 14% of 4-yr olds (age at first breeding) were making inter-colony flights in comparison to 44% of 2-yr olds and 25% of 3-yr olds. By the time puffins reached 6 yr old, most were breeding; inter-colony flights were very rare from this age group and were unknown from older cohorts. This suggests that most inter-colony movements occur in the years prior to first breeding and such movements decrease as puffins become established at a colony.

Inter-colony movements of prebreeding puffins are also known from the British Isles, Norway, Iceland, and the Faeroe Islands (Harris 1984). Harris (1983) found a two-way movement between the Isle of May and Farne Islands which are about 100 km apart. In his study, 23% of the young produced on the Farnes may have eventually bred elsewhere, but breeding adults did not relocate to different islands. In this study only 18 transplanted puffins have nested at Matinicus Rock and Machias Seal Island, representing an emigration of 11% away from Eastern Egg Rock.

Age at first breeding.—In the Westmann Islands of Iceland and in Scotland, most puffins first breed when 5 or 6 yr old, and very few first breed when they are 4 yrs old (Harris 1984, Petersen 1976). The 4-yr-old average age for first breeding at Eastern Egg Rock may be due to the abundance of suitable nest sites there and the absence of competitive, established breeders.

The 1977 cohort (56 birds) has favored Eastern Egg Rock both in numbers visiting and breeding, which suggests that the small numbers in the 1975 and 1976 transplants found the presence of puffins at the established Matinicus Rock colony more attractive than the vacant nest sites at Eastern Egg Rock.

Breeding chronology.—Puffins on Great Island, Newfoundland, begin breeding 10–14 d later than puffins at Eastern Egg Rock and Matinicus Rock. The peak hatch at Great Island is 1 Jul. and most adults depart the colony in late August (Nettleship 1972).

The similarity between the Eastern Egg Rock and Matinicus Rock breeding chronologies suggests that transplanted puffins breed in response to proximate conditions (e.g., water temperature and food availability) in the Gulf of Maine, rather than maintaining a genetically determined nesting chronology adapted for southeast Newfoundland waters.

Management implications.—The re-establishment of puffins at Eastern Egg Rock offers management possibilities for some endangered seabirds threatened by factors such as introduced predators, eroding habitat, volcanic activity or other conditions that would make additional nesting colonies desirable. In species where young are independent at fledging,

the transplant technique may prove useful for establishing new colonies within historic ranges. However, such programs must extend at least several years as post-fledging survival of transplanted young varies greatly between years and young, newly established colonies are vulnerable to extreme changes in the marine environment.

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